SCOTTISH CARBONIFEROUS CONODONTS

by

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The Scottish Carboniferous conodonts described by Hinde and figured by Smith in 1900 are re-described and re-figured. Additional specimens from the John Smith collection are described. Collections from eight localities in the central and east of the Midland Valley have been made to extend the knowledge of the geographical spread and stratigraphic range of conodonts in Scotland. It has been found necessary to propose one new genus. Altogether seventeen genera: *Apatognathus*, *Euprioniodina*, *Hibbardella*, *Hindeodella*, *Ligonodina*, *Prioniodus*, *Trichinodella*, *Dalryella* gen. nov., *Metalonchodina*, *Ozarkodina*, *SPATHognathodus*, *Subbryantodus*, *Cavagnathus*, *Gnathodus*, *Idiognathodus*, *Polygnathodella*, *Streptognathodus*, and fifty-three species are described. Twenty-one new species are proposed. On the evidence of conodonts the Scottish Carboniferous Limestone is considered to be equivalent to the upper part of the Upper Mississippian. The well-known faunal and floral break near the base of the Scottish Millstone Grit is paralleled by a change in the conodont fauna, the change being equivalent to that occurring at the Mississippian/Pennsylvanian boundary in N. America.
I INTRODUCTION

The most cursory perusal of micro-palaeontological literature reveals a marked dearth of information concerning the occurrence and distribution of conodonts in this country compared with the spate of publications that has appeared in America in the last 25 years. Two important papers by Hinde provide the foundation for work on conodonts from the Lower Palaeozoic in America (1879), and from the Lower Carboniferous in Scotland (1900). In the second paper Hinde described (and Smith figured) several species from the Carboniferous Limestone of the West of Scotland. It was discovered in the course of recent work in this University that this paper was most inaccurate and that the John Smith Collection contained many undescribed forms. In view of subsequent reference to the paper (Holmes 1928) there was an obvious need for revision of the material and its extension by further collecting, particularly since conodonts from the upper part of the Lower Carboniferous are both rare and little known in America.

With this end in view, samples from over 100 stratigraphic levels ranging from the topmost beds of the Calciferous Sandstone to the middle of the Millstone Grit have/
have been collected from several localities in the Midland Valley of Scotland (see fig. 1) and over 250 disintegrations carried out, yielding over 700 specimens of conodonts. Most of the samples proved to be barren of conodonts although only three were completely barren of organic remains. A marked similarity has been found between the conodonts collected and those described from the Upper Mississippian of America, the latter being less common and less well-known than those from older and younger strata. The well-known faunal and floral break near the base of the Millstone Grit is paralleled by a marked change in the conodont assemblages and this change is equivalent to that occurring at the Mississippian/Pennsylvanian boundary in America. The number of specimens so far separated is considered to be too small to warrant a statistical treatment of assemblages for stratigraphic zoning.

This study is a contribution to the knowledge of the occurrence and distribution of conodonts in this country and will, it is hoped, prove useful to American workers in bridging the gap between the well-known conodont faunas of the Lower Mississippian and the Pennsylvanian. Thirty-nine named species of seventeen genera are described including one new genus/
genus and twenty-one new species.

The work was carried out in the Grant Institute of Geology, University of Edinburgh.
Fig. 1

SKETCH MAP OF THE MIDLAND VALLEY
SHOWING COLLECTING LOCALITIES

THE
ROYAL EDWARD
SPECIAL

FIRTH OF FORTH

Kirkcaldy
Kinghorn
Port Seton
Dunbar

EDINBURGH

B
Kilsyth

C
Bathgate

G
Toppa

F

Glasgow
Motherwell

H.B.F.

0
Miles
20

GLASGOW

Dalry
Stewarton

Kilwinning

Douglas
Muirkirk

Author's Colln.
John Smith Colln.
II DEFINITION

The original definition of conodonts (Pander 1856, p.5) commences:

"Small, lustrous, elongated fossils sharply pointed upwards or towards one end, gradually or rapidly expanded towards the lower surface, more or less curved, mostly provided with sharp edges (keels) one anteriorly and one posteriorly and strongly resembling fish teeth in external form."

Pander then goes on to describe the point and the base and variations in shape, quoting various species as examples; he concludes:

"There can be no doubt that the hollow base was occupied by a pulp and that a simple pulp formed a simple tooth and a compound pulp, a compound tooth."

In the light of later work it seems advisable to extend and amend slightly the first paragraph of this definition, defining conodonts as follows:— Minute, lustrous, tooth-like fossils composed of calcium phosphate and carbonate, ranging in shape from single curved cones, through series of cones supported on bar-like or blade-like extended bases to complex dental plates consisting of a broad-based platform nodose, denticulate or ribbed on the upper surface and frequently with a denticulate blade-like projection.

Dimensions/
6.

**Dimensions**

Although a few large specimens have been reported, most conodonts are less than 2 mm. long, their longest dimension being usually in the range of 0.75 - 1.25 mm.
III HISTORY OF PREVIOUS RESEARCH

(a) General

There are over 600 publications containing references to conodonts but of these the majority are notes of their occurrence and only about 150 can be classed as papers on conodonts.

The first mention of conodonts appears to be Eichwald's (1854) announcement of Pander's discovery. Except for a single fragmentary specimen (Ehrenberg 1856) the first figured descriptions of conodonts are those in Pander's monograph (1856). By 1879, the date of Hinde's important paper, they had been discovered in Sweden, England, U.S.A., Germany, Scotland and Canada, in that order; since then they have also been found in Czechoslovakia, Poland, Denmark, Belgium, Egypt and Australia.

In the early twenties of this century the study of conodonts gained momentum. Of the 600 or so references only a quarter are pre-1921, while the bulk of the remainder date from the last 15 or 20 years. Branson & Mehl have undoubtedly been the most prolific workers, their major contributions beginning in 1933. Among other workers C. L. Cooper entered the field in 1931, S. P. Ellison Jr. in 1937, while Walter Youngquist/
Youngquist has been the most prolific investigator of the last five years. These and other workers such as F. H. Gunnell, C. R. Stauffer, J. W. Huddle and R. R. Hibbard — like Branson & Mehl — are further exploring and refining the morphology and stratigraphical distribution of conodonts isolated from the matrix.

Natural assemblages of conodonts in matrix are, however, more suitable for the study of the zoological affinities of the group, and these have been investigated from this point of view by Scott (1934 & 1942), Du Bois (1943), Schmidt (1934) and Rhodes (1952).

These two approaches to the study of conodonts are complementary, the investigation of isolated specimens being a desirable preliminary prior to the identification of the units within assemblages since these units are inevitably partly obscured by being imbedded in matrix. The integration of the two methods will lead to a better understanding of conodonts and the conodont-bearing organism and a beginning has already been made on these lines by Rhodes (1952).

(b) **Zoological Affinities**

The precise zoological position of the conodont-bearing organism, the conodontifer, is still in doubt. Controversy/
Controversy regarding the zoological affinities of conodonts occurred even before the publication of the first work on them, a monograph by C. H. Pander (1856). Evidently Pander submitted specimens of conodonts to eminent palaeontologists of his time and of those Barrande and Carpenter expressed the opinion that conodonts were probably the ends of segments of some trilobite is given as a footnote (p. 323) in the first edition of Murchison's "Siluria" 1854.

Pander himself, after exhaustive comparisons of the microscopic structure of conodonts with that of the teeth of fossil and extant fishes, was unable to establish identity between conodonts and fish teeth. Nevertheless Pander did not doubt that they functioned as teeth and stated (p. 8):

"We can maintain, however, with reasonable certainty that they were, like the teeth of the cyclostomes and squalids, inserted into the mucous membrane of the mouth; but which of the teeth belonged to the jaws, which to the lips, which to the tongue and which perhaps to other parts of the palate is at present indeterminable."

Pander was aware of a further difficulty in the classification of conodonts. Diligent search then and since has failed to reveal the nature of the conodontifer, and the resulting dubiety is clearly shown by the fact that subsequent students have referred conodonts to the Vermes, the Arthropoda, the Mollusca, primitive Vertebrata and the Pisces.

Owen/
Owen (1858, p. 545) in the appendix to the later editions of Murchison's "Siluria" deprecated the formal publication of "these minute ambiguous bodies from the oldest fossiliferous rocks as evidence of fishes". While agreeing that they have marked similarity to the teeth of myxinoids and lampreys he concluded that they have most analogy with the "spines and hooklets or denticles of Naked Molluscs and Annelides".

In 1861 Harley suggested that conodonts were spines of "crustacea" (sic) similar to Limulus, while Newberry (1873a) tentatively suggested that they might be dermal ossicles of cartilaginous fishes but later stated (1875) that they were most probably annelid remains.

Hinde (1879) after extensive work on scolecodonts (annelid jaws) considered conodonts were not annelid remains. He also rejected any supposed relationship to gastropod and crustacean remains on the grounds that no other hard parts attributable to these groups had been found in close stratigraphic proximity to conodonts. That they may have belonged to naked molluscs he considered unlikely and he concluded, as did Pander, that conodonts were the teeth of primitive fish comparable with the myxinoids.

James (1884) formally advanced the theory that conodonts/
conodonts were "the jaws and lingual teeth of molluscs". In 1886 Rohon and Zittel rejected all hypotheses concerning the affinities of conodonts except the annelid hypothesis and after stating that conodonts have structurally nothing in common either with the dentine of selachians and other fishes, the horny teeth of cyclostomes, the radular teeth of molluscs, the hooklets of crustaceans; they concluded that:

"both in form and structure, they agree remarkably with the masticatory apparatus of the Annelida and Gephyrea."

This conclusion was reversed by Bryant (1921, p.12) who, after comparing the structure of scolecodonts and conodonts, remarked:

"On the whole the longer I have studied these organisms, the more have I become convinced that the true conodonts have hardly anything really diagnostic in common with annelid jaws."

He considered them to be the remains of "some primitive type of fish".

Ulrich in 1878 noted the resemblance of conodonts to annelid jaws and somewhat diffidently concluded that conodonts were "the hooklets of species of annelids". Later, however, in conjunction with Bassler (Ulrich & Bassler 1926), a classification of conodonts was proposed in which, after comparative study of the myxines, they considered that conodonts were the teeth of primitive fishes.
All these authors with the exception of Hinde, who found one doubtful "assemblage", worked on separate, detached conodonts and so had no evidence indicating the possible arrangement of the units in the animal.

Eichenberg (1930) obtained assemblages from the Culm of the Harz and considered conodonts to be gill-rakers, but did not say to which group of the Pisces they belonged. He commented, however, that he was very familiar with similar structures in some recent Dipnoi, in Chimaera and in various teleosts.

Scott (1934) found groups or assemblages of conodonts preserved on slab surfaces, in what was presumed to be the approximate orientation of the living conodontifer. Schmidt (1934) made similar finds, but whereas Schmidt considered the assemblage indicated that the conodontifer was a fish, Scott stated: (p.455)

"All observations and all evidence available to the writer, point to the annelids as the natural possessors of conodonts."

In 1942 (p.298) Scott writes of the conodont assemblage:

"Such an apparatus would not only form an excellent screen to prevent undesirable objects from entering, but would also present a formidable barrier for the escape of desirable food once it had passed beyond the battery of teeth. The manipulation of the assemblage would not be a difficult matter. In so far as/
"as manoeuvrability is concerned it could operate with equal ease either as the jaw apparatus of an annelid or as gill rakers of a fish."

Pander must have had a similar idea as in support of his argument he quotes from Owen's "Odontography" the statement that in *Perca fluviialis*:

"although none of all (sic) the teeth are sufficiently developed to kill by piercing or laceration they all combine to hold, to crush and to aid in the deglutition of a living prey."

Of the above mentioned workers who favoured an annelid origin none dealt with the great disparity in chemical composition between conodonts and scolecodonts, although Hinde (1879) had noted the difference. Scolecodonts are silico-chitinous in composition, whereas conodonts have been conclusively proved to be phosphatic by Ellison (1944) and Lindberg (1946). Ellison after physical, chemical, optical, spectrographic and x-ray studies referred the mineral matter of conodonts to the apatite group; Lindberg refined that conclusion to the dahllite-froncolite isomorphous series of the apatite group. Ellison's subsidiary conclusions were that conodonts could be classed as the remains of fish or other lower vertebrates on the basis of their size, shape, assemblage associations, internal structure, associated bony material and jaw parts and stratigraphic occurrence. In addition he challenged their assignment to other zoological groups/
groups because creatures in other groups do not have hard parts of similar size and shape composed of calcium phosphate.

This precise statement concerning the phosphatic composition of conodonts was in some measure anticipated by Du Bois (1943). Work similar to Scott's on assemblages led Du Bois to the conclusion that annelids were the most likely possessors of conodonts. Concerning the disparity in chemical composition he quotes F. W. Clarke (1924) as stating that:

"some annelids are rich in phosphorous and the tubes formed by the genera Leodice, Hyalinoecia and Onuphis are in this respect most remarkable."

Since these tubes are ectodermal secretions it is not impossible that in the buccal cavity, which originates as an embryonic invagination of ectoderm, the secretion of calcium phosphate could occur. As a support for the contention that phosphatic teeth in annelids are not impossible he draws attention to the fact that the change from chitin to phosphate secretion was not too great to be made by the inarticulate brachiopods. He suggest further that the possible relationship of the Brachiopoda to the Annelida is not without significance in this connection.

Loomis in 1936 re-advanced the gastropod hypothesis but/
but ignored the difficulty of divergent chemical composition, while Denham in 1944, stating that conodonts do not appear to be internal organs, suggested they might be chitinous copulatory claspers of extinct worms similar to present day nematodes.

All the above mentioned workers except Harley and Denham have considered conodonts to be teeth or tooth-like ingestive aids. This assumption, however, was seriously challenged by Hass (1941). Examination of thin sections confirmed the lamellar structure of conodonts noted by Pander, but Hass preferred to consider this to be layering by accretion, i.e. from without, and not by internal growth from the pulp. He adduces evidence of repaired broken cusps in support of the theory of deposition from a surrounding medium and concludes (p. 81) that:

"conodonts functioned as internal supports for tissues within or on the body of some marine organism at places subject to stresses."

The regeneration of broken parts Hass considers to be incompatible with conodonts having been fully erupted teeth. He also stresses the lack of any signs of wear on the cusps and considers this lack of wear to indicate that conodonts were never used for biting or chewing.

Similar work on thin sections was reported by Beckmann.
Beckmann in 1949, who was apparently unaware of Hass's 1941 paper. Beckmann obtained more detail of the fine microstructure of conodonts and reached rather different conclusions. In addition to the layered cone-in-cone structure seen by Pander and by Hass, Beckmann observed fine capillary canals more or less at right angles to the lamellae. These canals radiate from the pulp cavity and in many cases penetrate to the outer surface of the conodont. They are interpreted by Beckmann as channels along which phosphatic material secreted by the pulp was transported to the outer surface of the conodont and there deposited. Repetition of this results in a clearly visible layered structure. He found strong similarity in structure between conodonts and selachian dermal plates and had no doubt whatever that conodonts were to be referred to the Pisces. Indeed he referred various types to the mandibles and to the hyoid and branchial arches.

Weight might be lent to this hypothesis by the occurrence, supposedly in situ, of a prioniodid conodont in contact with a branchial arch of *Coelacanthus lepturus* Agassiz (Demanet, 1939). But after examination of the specimen the present author considers it unlikely that this conodont was one of the gill rakers of this fish.

Almost/
Almost every author has commented on the marked absence of signs of wear on the cusps and denticles of conodonts. In the case of single cusps and compound bar-like forms this is not remarkable, as it can be inferred from their structure and configuration that such units were clearly unsuitable for mastication and were in all probability not so used. However, in the plate-like and leaf-like platform types the configuration is such that they would be effective as jaw armour and it is significant that wear, presumably resulting from trituration has been observed on such forms by Branson & Mehl (1933, p.5), Ellison (1941, p.135) and the writer (p. 125).

In addition conodonts have been found adhering basally to material:

"that appears bony but does not have the structure of ordinary bone. The materials to which the conodonts are attached could not be from annelide or from anything but vertebrates". (Branson & Mehl 1933, p.5). Kirk (1929) has recorded conodonts attached to material identical in composition with fish plates occurring together with them in the Harding Sandstone of Colorado. The plates are referred to the Ostracoderms but no conclusion as to the exact relationship between conodonts and ostracoderms is drawn.

The weight of evidence appears to be in favour of Pander's/
Pander's original decision to refer conodonts to the Pisces.

The chemical composition strongly suggests that conodonts belong to the vertebrates or to their more primitive precursors. The structure and form of individual conodonts suggest that they may have functioned as teeth, spines or dermal armour, but the variety of forms within assemblages, such as those reported by Scott (1934 and 1942) and their mutual relations, invalidate the last two and support the hypothesis that they were teeth. Hass's evidence of repair of broken conodonts is inconclusive and does not fully support his inferences. That some conodonts were broken and later repaired is indubitable but the method of repair is not wholly consistent with conodonts having been internal muscle supports.

Breakages do occur in vertebrate muscle supports and repairs are made by bone material, deposited in the fracture, uniting the broken edges. Hass's figures show that the broken part disappeared. This could be due to loss or resorption; and loss of the part is practically impossible in tissue, but could occur easily in the mouth or gills. Loss is, however, more likely than resorption as the time required for resorption would increase considerably the period of repair, and support would be lacking until repair was/
effected. Repair is by secretion of phosphatic material in approximately the same pattern and orientation as one would expect the missing part to have had. This is, in effect, regeneration rather than repair and is in harmony with Beckmann’s conception of the method of growth of conodonts by deposition, on the outer surface, of secretions originating in the pulp and passed outwards via radiating canals.

The evidence of wear on some of the forms considered to have been tritiorial plates, the attachment of some conodonts to bone-like material further supports the hypothesis that conodonts were oral armature, and their composition suggests that they belonged to chordates or primitive vertebrates.

Concerning the supposed form and size of the conodontifer the two authors who attempt reconstructions, Schmidt (1934) and Du Bois (1943), though differing in their conception of the form agree as to the size. Schmidt considers that the conodontifer was probably allied to unarmoured placoderms and similar to Chimaera and was about 45 mm. long and 12 mm. wide in the pectoral region and about 6 mm. wide at the nose. Du Bois suggests a worm about 50 mm. long and at least 3 mm. wide.

(c) Palaeontology
Little is known of the palaeocology of conodonts and there has been much conjecture concerning the probable environment of the conodontifer. Of the pioneer workers on conodonts Smith (1907) alone advanced a hypothesis concerning their ecological relations. Smith had found conodonts in the Carboniferous Limestone of the Midland Valley and in strata of Arenig-Llandeilo age in the Southern Uplands; in the former preserved in limestone and in the latter in red and green shales, considered to be abyssal deposits. He reconciled the occurrence in these two very different sedimentary environments by suggesting that the conodontifer was pelagic.

In 1921 Bryant concluded that the conodont-bearing Genesee sediments had accumulated in shallow water near shore and that the high concentration of conodonts in some lenses indicated a detrital origin.

Moore (1929), writing on Pennsylvanian ecology in North America, noted that conodonts were most frequently found in black fissile shales, the blackness being due to disseminated pyrite and organic matter, part of which he considered to be derived from land plants. Deposition of these shales is stated to have occurred in warm, shallow, toxic/
toxic waters (depth < 100 fms.). He concludes that the conodontifer was either specially adapted for life in such waters and hence dwarfed, or was restricted to the more or less aerated surface waters and died on entering the lower toxic zone. In 1936 he stated that conodonts occur in the marine parts of sedimentary cycles in dark fissile shale deposited in near-shore shallow water or possibly in lagoons.

The occurrence of conodonts in carbonaceous shale sandstone, conglomerate and limestone was noted by Gunnell (1931) who concluded that the conodontifer was a free-swimming organism.

Ruedemann (1934), conscious of the widespread occurrence of conodonts, considered that they belonged to nektonic organisms living in the waters of the deeper littoral zones or in conditions similar to those of the present Sargasso sea.

Branson & Mehl (1934b) stated that conodonts occur mostly in marine shales deposited in shallow water near shore and also that some conodontifers may have lived in brackish or in fresh water. Later they stated (1938) that the habitat of conodontifers appears to have been waters in which detritus was sufficiently abundant to prevent the formation of limestone. In 1940 they included clear-water conditions in/
in the habitat.

Marine and stagnant brackish water environments were postulated by Bailey (1935) from the frequent occurrence of conodonts in black carbonaceous shales. Smith and Whitlatch (1940) considered that the conodontifer inhabited cool, shallow, stagnant, possibly lagoonal waters, while Scott (1942) considered that the bottom waters, at least, must have been exceptionally calm and undisturbed otherwise the "assemblages" would have been disrupted.

Association of conodonts with marine fossils was noted specifically by Du Bois (1943) and casually by numerous other authors. The writer has found conodonts in association with articulate and inarticulate brachiopods, small gastropods, crinoids, fish scales and teeth, echinoid plates, scolecodonts, ostracods and carbonaceous material. The samples in which conodonts were most abundant contained crinoids, small gastropods and a few brachiopods. One sample contained *Productus sp*.

The widespread occurrence of conodonts in limestones, red, grey, green, black carbonaceous and sandy shales, siltstones, sandstones and conglomerates militates against the conodontifer having been benthic. To have survived as part of the benthos it must have been adapted to the bottom conditions/
conditions and it is unreasonable to suppose that adaptation to such widely different conditions occurred. In addition since many of the black shales are pyritous and probably accumulated in toxic bottom waters the conodontifer, as part of the benthos, would have had to tolerate foul sulphurous waters and yet be capable of living in the clear waters of limestone deposition.

While it is improbable that the varying lithology of conodont-bearing strata is an expression of wide adaptation, the contemporaneous existence of some species of conodontifers adapted to clean bottom condition with others adapted to foul conditions is not impossible. However, conodont faunas have been traced unchanged through diachronous lithological boundaries, indicating a constancy of species regardless of bottom conditions. "They do not show facies variation and recurrence as do all other organisms of the sequence" of Ordovician Silurian and Devonian rocks in central Kentucky. (C. C. Branson 1942). Widespread occurrence and this independence of facies indicate that the conodontifer was most probably nectonic. The physical dimensions of conodonts are such that it is unlikely that they belonged to plankton.

The/  

1 e.g. Sylamore and Grassy Creek of Missouri. Branson & Mehl 1933.
The association with marine fauna indicates a marine environment, but does not exclude the possibility that the conodontifer may have tolerated and lived in brackish or even fresh water.

"A great many marine animals can withstand salinity dilution, but very few fresh water animals can withstand increase in salinity". (Gunter 1944)

The author has found conodonts to be most abundant in marine shales close to limestones, though the limestones themselves are poor in conodonts. Ellison (1941), in stratigraphic tables of conodont occurrences in the Pennsylvanian, shows only one in a total of thirty occurrences that is not closely associated with a limestone. It seems most likely that the conodontifer preferred conditions approaching or waning from the conditions of limestone deposition, but, being nektonic, had a wide distribution with the result that conodonts are found in many types of sediment.

The abundant occurrence of conodonts in certain thin layers in black fissile shale and their relative absence above and below these layers is probably best accounted for by postulating abnormally large accumulations resulting from special conditions. Huddle (1934) has suggested either catastrophic/
catastrophic destruction of the conodontifer population or
the non-deposition of sediment as possible special condi-
tions, while Moore (1929) suggests accumulation of large
numbers of conodonts as a result of death of the conodonto-
ifer on entering toxic bottom waters.

At any rate such occurrences, although fairly
numerous, are the exception rather than the rule and by far
the greater amount of recent work has been on strata in
which conodonts are disseminated throughout an appreciable
thickness of sediment.
IV  PRESERVATION AND OCCURRENCE

Of the specimens collected for the present investigation none shows any sign of chemical disintegration but the majority are broken, few being sufficiently complete for figuring. Branson & Mehl (1941c) comment that European conodonts are in general less well preserved than those found in America, cross shattering being very frequent. In the case of the Carboniferous this may be the result of the greater deformation of strata in Europe compared with the almost flat-lying beds of the mid-continent strata of the U.S.A. Although this fracturing makes the identification of some specimens difficult and frequently doubtful it does not detract from the validity of identifications of platform types, since in almost every case the platform proper, the most diagnostic feature, is entire.

Conodonts have been found in samples from several horizons in the Carboniferous Limestone and the lower part of the Millstone Grit, but most of the samples investigated proved barren of conodonts. A list of localities and horizons is given in the appendix (p. 140). The most productive beds are:

(1) the shales overlying the Bilston Burn Bone Bed Limestone. (Grid. Ref. Sheet 32 269649)

(2)/
(2) the shales above the Skateraw Middle Limestone.  
(Grid Ref. Sheet 33 716733)

(3) the shales within and overlying the Castlecary Limestone

(4) the shaley parts of marine ironstone bands in the Millstone Grit at Joppa.  (Grid Refs. Sheet 32 316735 and 320736).

Samples of these yielded 30 or slightly more specimens per pound of material.

The shales below the Top Hosie Limestone, Kilsyth,  
(Grid Ref. Sheet 31 682781) and Skipsey’s Marine Band yielded in the range of 15-20 specimens per pound. All other productive samples had appreciably poorer yields ranging down to five per pound. An exhaustive investigation of the Top Hosie shales at the above locality by G. Y. Craig (Ph.D. Thesis, Edinburgh 1951) indicates that conodonts account for only one per cent of the micro-fauna and 0.6% of the total fauna.

A sample of the late Mississippian Pella Beds obtained from Youngquist yielded slightly more than 30 specimens per pound.

The stratigraphic positions of productive samples is shown in generalised vertical sections (figs.2a & 2b) and the conodonts obtained, together with those in the John Smith Collection (132 specimens), are tabulated in the faunal list (p. 28).
Table 1. Faunal list, correlating species with stratigraphic horizons.
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<td>*</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>Millstone Grit (shales in lower third)</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Castlecary LST &amp; Shales</td>
<td></td>
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<tr>
<td>Arden Limestone &amp;</td>
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<tr>
<td>Angle</td>
<td></td>
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<tr>
<td>Linn Spout</td>
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<tr>
<td>Glencary</td>
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<tr>
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<td>Stacklawhill</td>
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<tr>
<td>Top Hosie LST &amp; Shales</td>
<td></td>
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<tr>
<td>North Greens</td>
<td></td>
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<tr>
<td>Petershill</td>
<td></td>
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<tr>
<td>Skaterman Mid</td>
<td></td>
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<tr>
<td>2nd Adven</td>
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<td>Hurlet</td>
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<td>Bilston Burn Bone Bed</td>
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<td>Limestone &amp; Shales</td>
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<td></td>
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<td>Law</td>
<td></td>
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<td>*</td>
</tr>
<tr>
<td>Ponniel Water</td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>Upper Limestone Group</td>
<td></td>
<td>*</td>
<td>*</td>
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<tr>
<td>Lower Limestone Group</td>
<td></td>
<td>*</td>
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</tbody>
</table>

* Frequent
** Very frequent

Legend:
- *: Present
- #: Frequent

Table 1: Faunal List
Fig. 2a. CONODONT OCCURRENCES
EAST SCOTLAND

Generalised vertical sections showing distribution and occurrence of conodonts in the Midland Valley of Scotland.
CONODONT OCCURRENCES
CENTRAL & W. SCOTLAND

Fig. 2b.

BATHGATE

KILSYTH

DALRY DISTRICT

- sandstone dominant
- shales dominant
- limestone
- lavas

* conodonts present

Petershill 1st.
Wirkinston 1st.
Blackhall 1st.
Newtongrange 1st.
Dockra 1st.
Broadstone 1st.
Hosey 1st.
Kirkton 1st.
Petershill 1st.
Highfield 1st.
Third post 1st.
Lower LST Group
Upper LST Group

500 FEET
400
300
200
100
0
The stratigraphic distribution of conodonts in the Upper Palaeozoic rocks of the U.S.A. is well known, especially in the mid-continent States, but is almost unknown elsewhere.

The possible value of conodonts as stratigraphic fossils lies firstly in their wide geographical distribution, a distribution which may prove to be as wide as or even wider than that of the graptolites; secondly, in their independence of facies and thirdly, in their resistance to decay. While some forms were extremely long-lived and changed but little, most of the platform types have short stratigraphic ranges, none of those present in the lowest Carboniferous strata persisting throughout the system. According to Ellison (1946), of ten genera of platform types present in the Mississippian only two are found in the Pennsylvanian. Opposed to these points, however, it must be admitted that conodonts are relatively rare and strata in which they are sufficiently abundant to be easily found by inspection extremely few.

The known geographical spread of conodont occurrences, embracing four continents, suggests that they may be of value in inter-continental stratigraphic correlations, but until faunas are as well known elsewhere and in as much detail as elsewhere.
in the U.S.A. such correlations can be, at best, only tentative. Branson & Mehl (1941a) report a generic and possibly specific similarity between European and American conodont faunas and the author has found a marked resemblance between some Upper Mississippian conodonts and those from the Scottish Limestone. The resemblance of Gnathodus smithi sp. nov. to G. liratus Youngquist & Miller and to G. pustulosus Branson & Mehl is most striking. G. smithi occurs at the top of the Upper Limestone Group and the two American species occur in the highest beds of the Mississippian. Spathognathodus commutatus Branson & Mehl occurs in equivalent or slightly lower strata (Pitkin Limestone, Oklahoma) and has been found by the author in the Skateraw Middle Limestone. Other similarities are less close but the absence of Polymathodus, and of Idiognathodus and Streptognathodus, the first ranging up into the middle Mississippian and the other two first appearing in basal Pennsylvanian strata, strengthens the correlation of the Scottish Carboniferous Limestone with the Upper Mississippian. Concerning the latter Youngquist & Miller (1949, p.617) state:

"Conodonts of middle and upper Mississippian age are scarce and comparatively few specimens have been noted or described in the literature."

The occurrence of Polymathodella in Skipsey's Marine Band adds to this parallelism of conodont occurrences
in Scotland and the U.S.A. The genus has a short known range, occurring in strata which Moore et al. (1944) equate with the upper part of Westphalian A and Westphalian B. According to Currie (1937) and Weir & Leitch (1936) Skipsey’s Marine Band is in the *similis-pulchra* zone which ranges from high in Westphalian B to the base of Westphalian C (Trueman 1946) and so is at the upper limit of the range of *Polygnathodella*.

The abrupt change in the conodont fauna which occurs near the base of the Roslin Sandstone (Millstone Grit) marks a horizon that corresponds with the boundary in Scotland between the Upper and Lower Carboniferous and indicates that this boundary is equivalent to that between the Mississippian and Pennsylvanian, the first occurrence of *Idiognathodus* and *Streptognathodus* being indicative of basal Pennsylvanian. This parallels in some measure the occurrence of goniatitites. Bisat (1924), on the basis of a specimen from 30 ft. above the Castlecary Limestone in the Bilton Burn, puts the base of the Scottish Millstone Grit high in Zone E (*Eumorphoceras*) or low in Zone H. *Eumorphoceras* occurs in the Caney Shale (Weller et al., 1948) the bulk of which is Upper Mississippian but the highest beds of which are considered to be basal Pennsylvanian by Moore et al. (1944), who take the H/R boundary/
boundary as being equivalent to the base of that system. Bisat considers the Upper Limestone Group to be in Zone E which corresponds with the occurrence in the Caney Shale, Pitkin Limestone and Pella Beds, of specimens of Gnathodus and Spathognathodus closely similar to those occurring in the Upper Limestone Group.

Conodonts, therefore, add to the evidence for correlating the upper part of the Lower Carboniferous with the Upper Mississippian and indicate the equivalence of the boundary between the Lower and Upper Carboniferous in Scotland to that between the Mississippian and Pennsylvanian. Also they add to the evidence of a faunal break in the basal third of the Millstone Grit.

The fine discrimination of strata within groups does not appear to be possible on the basis of the conodonts collected by the author. *Gnathodus smithi* is confined to the Upper Limestone Group, occurring in the West in the Upper Linn Limestone, while in the Midlothian basin it is found only in the Castlecary Limestone and closely adjacent shales. In the latter area this species is absent from the Arden Limestone and underlying shales, which suggests that the Upper Linn Limestone considered to be equivalent to the Arden may be slightly younger. From the evidence at present available *G. smithi* appears to be diagnostic of the upper part of the/
the Upper Limestone Group.

One discrepancy in range has been noted. The genus *Apatognathus* is stated by Ellison (1946) to be confined to the upper Devonian and Cooper (in Weller et al. 1948) suggests that it may range into the Lower Mississippian, but in Scotland it occurs in the Carboniferous Limestone. Smith obtained specimens from the Upper Limestone Group and the author has collected them from shales near the Castlecary Limestone and the Skateraw Middle Limestone. The specimens are less broken than the type specimens figured by Branson & Mehl (1934) and those in the John Smith Collection are almost complete. There is no sign of abrasion on any of the specimens, such as might be expected had they been derived fossils. Moreover, since the John Smith specimens were obtained from limestone their introduction as detritus is, from their size, unlikely. Also there is no known marine Devonian strata near enough to have supplied *Apatognathus*. The range of *Apatognathus* must, therefore, be extended at least up to the top of the Upper Limestone Group.
VI PREPARATION TECHNIQUE

The initial problem in any study of micro-fossils is to obtain unbroken matrix-free specimens. This can be overcome with some measure of success by reproducing in the laboratory a process comparable in its effects to natural weathering, but greatly speeded up. Both mechanical and chemical means may be employed separately or consecutively. Mechanical crushing of the rock sample in a vice or crusher may be used but many specimens are crushed along with the matrix and such crushing is best limited to a first stage operation for reducing field samples to fragments of about half a cubic inch in volume.

When bedding planes or pore spaces are well developed in the sample a process of disintegration similar to frost weathering is effective. This is achieved by alternately boiling and cooling the sample chips in a saturated solution of sodium sulphate the volume of the solution being approximately equal to the volume of the sample. During heating the liquid penetrates along bedding planes and into voids and on cooling crystals of hydrated sodium sulphate form, with a larger volume than the liquid, and so provide an internal disrupting force. Frequent repetition eventually reduces/
reduces the sample to a mud-like paste and any contained fossils are released. The number of treatments necessary was found to vary from six to thirty according to the permeability and compactness of the sample.

When the rock sample contains a relatively small proportion of finely disseminated pyrite soaking in hydrogen peroxide is effective in inducing disintegration. The oxidation of the pyrite to iron sulphate greatly reduces the strength of the rock and the increase in volume together with the pressure of oxygen released during the oxidation provide a strong disruptive force. 100 vol. solution of peroxide was used, diluted on occasion to 50 vol. when the reaction became too vigorous. Since rise in temperature destroys the reagent the process was carried out in a water cooling bath. This method is inapplicable where pyrite is present either in abundance or in discrete aggregates. In the former case the reaction becomes extremely violent, the temperature rises rapidly in spite of immersion in a cooling bath, and all the available oxygen is evolved at or near the fragment surfaces before penetration and disruption are possible. In the latter case the reaction is too localised to disrupt the main body of each fragment.

Porous, pyrite-poor or pyrite-free rocks of clay grade may also be disintegrated by means of hydrogen peroxide.
The dried fragments are soaked in a 20 vol. solution to allow penetration of the solution into the fragments. The mixture is then boiled and the release of oxygen concomitant with the rise in temperature disrupts the fragments.

In cases where either peroxide or sodium sulphate is by itself comparatively ineffectual, disintegration of the sample may result from treatment by the two alternately; i.e. by using peroxide to produce voids and sodium sulphate to penetrate into these and burst open the fragments. In practice it has been found that sodium sulphate is most effective in the disintegration of fissile shales and porous mudstones. Hard, black, poorly fissile shales yield best to peroxide, as do some impure black limestones.

Limestones were dissolved in acetic acid, since that acid does not attack phosphatic material. 60% acid was used and was renewed every three days after washing the sample to prevent too great an accumulation of calcium acetate which, being strongly ionised, would inhibit the dissociation of the acetic acid into its ions and so reduce its acidic properties. In the dissolution of impure, slightly ferruginous limestones it was found that an accumulation of ferruginous mud around the fragments tended to inhibit the reaction. This mud was removed by boiling in water and decanting but on occasion it was/
was found necessary to supplement this treatment by boiling in 30% citric acid before returning the fragments to an acetic acid bath for further disintegration. Acetic acid gave most rapid results on porous calcareous shales; in one case disintegration became complete in six hours. In general at least one week was required to obtain a 50% disintegration. It would seem that the reaction is most rapid on "calcite mud", as evidenced in the rapid break-down of calcareous shale, and slower on crystalline calcite since crinoid ossicles frequently survive almost unscathed. This, however, may be due in part to dolomitisation of the ossicles.

The above methods, singly or in combination, were applied with moderate success.

After disintegration the finely divided residue was graded by sieving through a nest of three sieves; 30, 100 and 200 mesh. It was found that no conodonts were retained on 30 mesh, almost all were retained on 100 mesh and only a few, very small, fragmentary specimens passed through on to the 200 mesh. The scolecodonts found were retained on 200 mesh.

To increase the speed and efficiency of the search for conodonts, which constitute an extremely small part of the total material, use was made of the fact that all conodonts sink.
sink in slightly diluted bromoform and all 100 mesh sievings were separated into heavy and light fractions, using bromoform diluted to a specific gravity of 2.72.

A binocular microscope (field 6.5 mm.) was used for searching, the disintegrated material being scattered on a 4\(\frac{1}{4}\) x 3\(\frac{1}{4}\) inch, green backed, glass plate, and scanned between 5 mm. rulings. Conodonts were picked out and manipulated with a very fine camel-hair brush moistened in water, assembled in recessed perspex trays, and mounted on recessed slides, tragacanth with formaldehyde as a mould inhibitor being used as a fixative.

The photography of specimens for figuring presents two minor difficulties. The splendent resinous lustre produces troublesome high lights which can be obviated by coating with ammonium chloride and the high relief of some forms necessitates the insertion of a stop in the microscope objective to give sufficient depth of focus. A 1.3 mm. aperture in the focal plane of a X8 objective proves effective.
VII COMPOSITION AND STRUCTURE

In 1936 (Loomis) and even as late as 1944 (Denham), conodonts were considered to be chitinous in spite of Pander's statement (1856) that they were composed of calcium carbonate and the discovery of many subsequent workers that calcium phosphate is present as well as carbonate.

The smallness of conodonts and their relative scarcity make a complete qualitative analysis difficult to achieve, but one small fragment suffices for qualitative micro-chemical tests such as will indicate at least the presence of the principal components. On dissolution in hydrochloric acid (5N., cold) conodonts can be seen to effervesce slightly and the resulting solution gives positive reactions for calcium and phosphate. No analytical tests of the evolved gas have been made in the present investigation, but it was assumed to be carbon dioxide. The composition of the specimens examined is taken to be a mixture of calcium phosphate with a little calcium carbonate.

The presence of phosphate in conodonts and their easy solubility in fairly dilute hydrochloric acid shows that they are not composed of chitin or of horny material as these are attacked only by hot concentrated acid and contain no/
### Table 2

**CHEMICAL ANALYSES**

and Miscellaneous Properties

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<tr>
<th></th>
<th>DAHLLITE</th>
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<td>50.97</td>
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<td>P₂O₅</td>
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<td>CO₂</td>
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<td>F₂</td>
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<td>2.1</td>
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<td>H₂O</td>
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<td>3.96</td>
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<td>Others</td>
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<td>Insol.</td>
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<th>Shades of Brown</th>
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<td>3-5</td>
<td>3-5</td>
<td>3-5</td>
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<td>S. G.</td>
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<td>2.6-2.9</td>
<td>2.6-2.9</td>
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<td>Fusibility</td>
<td>Difficult on edges</td>
<td>Difficult on edges</td>
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<td>R. I.</td>
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<td>1.57-1.62</td>
<td>1.57-1.62</td>
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<tr>
<td>1.623-25</td>
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<td>State</td>
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<td>Crypto-crystalline</td>
<td>Amorphous or Crypto-crystalline</td>
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<th>HNO₃</th>
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Data from:  
no phosphate. The strengthening of chitinous structures with calcium phosphate is, however, not unusual but in the case of conodonts it has been clearly shown that they are not phosphatised chitin. Stauffer & Plummer (1932) reported a preliminary analysis by Ellsted of the University of Minnesota giving 30%-50% as the probable phosphate content of conodonts and no organic matter. Ellison (1944) found no organic matter and gives the phosphate content at 35% P₂O₅. (See Table no. 2)

It is evident that apart from a slight superficial colour resemblance conodonts have nothing in common with chitinous structures. They do, however, have a marked similarity to dahllite, collophane and fossil bone in physical properties and chemical composition, as the data compiled in Table 2 clearly demonstrates.

**Structure**

The micro-structure of conodonts was described in considerable detail by Pander (1856, p. 7, Tab. 3, figs. 1-5). That of the lamellar forms, the Conodontiformes, has since been investigated by Hass (1941) and Beckmann (1949), who agree substantially with Pander regarding the structure but differ in their conceptions of the method of growth. Pander considered/
considered that growth was by the formation at the surface of the pulp of layer within layer and that the youngest lamella was that in contact with the pulp. While this might be possible in the case of simple cones, and the bulk of Pander's material comprised simple cones, it becomes unrealistic when applied to more complex forms and especially to the platform types. Beckmann and Hass both consider growth to be by addition of layer upon layer outwards but disagree as to the method of deposition of the layers.

All conodonts do not show the lamellar structure to the same degree and in most it is obscure except along the cone axis. Where the lamellae are close-packed and the interlamellar spaces small the material appears to be homogeneous except in thin section at high magnification. However, in those places where the interlamellar spaces are wide, usually along the cone axis or towards the anterior of a blade, the lamellae are clearly visible and in some few cases almost all of the growth pattern is visible. (Plate XIV fig. 4).

That growth was by addition of material at the outer surface and not at the surface of the pulp is clearly shown by the regeneration of broken parts. Plate XIV fig. 1 shows the cusp of a prioniodid conodont which was broken and subsequently/
Fig. 3 Diagrams to illustrate the method of repair of a broken cusp. See also Plate XIV, figs. 1, 2, 6, 7, and 8.
subsequently regenerated during the life of the conodontifer. Examination of this specimen under high power shows that new material was added at the outer surface and the following sequence of events appears to have occurred: Immediately after the break the broken end was scaled off by a single layer forming a more or less plane surface at right angles to the cone axis, fig. 3 (c). The next layer formed a low dome over this plane surface leaving a large interlamellar space above the sealed break and extended down the sides of the cone, fig. 3 (d). The next few succeeding layers were widely separated in the direction of the cone axis, but increasingly more closely appressed laterally, fig. 3 (e), and changed in shape from a low dome to an acute cone. Once the acutely conical shape had been re-established, growth proceeded normally and the interlamellar spaces became less marked.

Where regeneration is incomplete there is a noticeable change in the slope of the sides of the denticle. Plate XIV fig. 8 shows a denticle with a partly regenerated point and Plate XIV fig. 6 shows the early stages of regeneration of a comparatively large denticle of the posterior end of a specimen of Lonchodus sp. A series of small cones marking/
marking the axis of the denticle is clearly visible and those in the regenerated part are off-set anteriorly from the line of those of the original denticle.

In some conodonts the laminar structure is not present throughout the specimen and is replaced by a cellular arrangement of phosphatic material. This is most frequently observed at the bases of denticles in bar-like forms such as *Hindecodella* and has led some authors, in particular Stauffer and Plummer (1932) and Huddle (1934), to consider the denticles to be inserted into the oral bar, much as are teeth into the jaw ramus of higher vertebrates. They quote the falling out of denticles on dissolution of a specimen in hydrochloric acid as evidence in support of this theory. Observation confirms that such peg-like, apparently inserted denticles (e.g. Plate XIV figs. 3 & 7) do tend to fall out when the specimen is treated with hydrochloric acid. However in some specimens the series of cones marking the growth axis and representing the relatively large inter-areas at the apices of the lamellar cones can be traced from the oral bar up into the cellular tissue (Plate XIV fig. 7), indicating that the denticles are outgrowths from the bar and not insertions into it. The phenomenon of loosening of the denticles on dissolution is considered to be the result of differential/
differential solubility of cellular and lamellar calcium phosphate. The peg-like appearance of denticles with cellular structure is a purely optical effect resulting from the strong reflection of light by the cellular tissue. In reflected light it appears white and opaque but in transmitted light it is dark, and every gradation can be observed from transparent and translucent amber-coloured denticles to those rendered quite opaque by cellular structure. Occasionally the whole gamut is present in one denticle.

It is considered, therefore, that the denticles of conodonts are an integral part of the oral units and are outgrowths therefrom. The individual denticles are not inserted as are teeth in a jaw.
VIII ORIENTATION AND TERMINOLOGY

The orientation of conodonts for the purpose of description is arbitrary, since the nature of the conodontifer and the precise arrangement of conodonts in that organism is unknown. Workers on assemblages are in doubt as to the anterior and posterior parts of the assemblages (Scott 1942 and Schmidt 1934) and express doubt even regarding the anterior and posterior of individual units within the assemblages. (Schmidt 1934).

For the purposes of description the units are considered to belong exclusively to the lower jaw with the full realisation that a form described as right lower could equally well be left upper and further that there need not necessarily have been any true "jaw" structure. The units are oriented with the denticles upwards, i.e. directed orally and their inclination directed posteriorly. In platform types the platform is posterior and the blade anterior. This is in most cases a reversal of the orientation adopted by Ulrich & Bassler (1926), Huddle (1934) and some others, but is in agreement with the usage adopted by more recent workers such as Branson & Mehl, Stauffer, Ellison, Youngquist and Rhodes.
Fig. 4  Diagrams illustrating the morphological features of three types of conodonts.
The terminology of the various parts of units, embracing such words as oral, cusp, denticle, etc., is based on the assumption that conodonts are teeth. A brief glossary of terms is included in Huddle's paper (1934) and in "Invertebrate Fossils" by Moore, Lalicker and Fischer (1952). For convenience and clarity a glossary of those terms used in this thesis is appended below.

**Glossary of Terms**

*Aboral*  Lower surface, surface of attachment.

*Anterior*  
(1) In bars and blades: the end away from which the denticles are inclined.
(2) In platforms: the direction of the blade.
(3) In *Hibbardella* and similar three-barred forms the two parallel bars are anterior.

*Antero-inferior*  That part of the bar in front of the cusp process bent inwards and backwards.

*Anticusp*  A downward projection below and continuous with the cusp.

*Appressed*  Of denticles, closely crowded.

*Arched*  Convex upwards: along the length.

*Bar*  Elongated structure about as thick as high bearing denticles.

*Blade*  Elongated structure markedly higher than thick, bearing denticles.

*Bowed*  Curved in the horizontal plane: convex outwards.

*Carina*  A nodose or denticulated ridge extending across the oral surface of platforms.

*Compressed*
<table>
<thead>
<tr>
<th>Term</th>
<th>Description</th>
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</thead>
<tbody>
<tr>
<td>Compressed</td>
<td>Flattened laterally.</td>
</tr>
<tr>
<td>Cusp</td>
<td>Large main denticle situated above the escutcheon.</td>
</tr>
<tr>
<td>Denticles</td>
<td>Small spine-like teeth growing upwards from a bar or blade.</td>
</tr>
<tr>
<td>Escutcheon</td>
<td>Aboral concavity, pit or navel: the attachment scar.</td>
</tr>
<tr>
<td>Flange</td>
<td>A lateral ridge usually parallel to the oral and aboral surfaces.</td>
</tr>
<tr>
<td>Flexed</td>
<td>Bent sharply inwards.</td>
</tr>
<tr>
<td>Fused</td>
<td>Of denticles, laterally confluent.</td>
</tr>
<tr>
<td>Germ denticles</td>
<td>Minute teeth the points of which do not erupt on the oral surface; visible in transmitted light.</td>
</tr>
<tr>
<td>Inner side</td>
<td>The concave side.</td>
</tr>
<tr>
<td>Limb</td>
<td>Part of a bar on one side of the cusp.</td>
</tr>
<tr>
<td>Lip</td>
<td>Thin membrane-like edge of the escutcheon.</td>
</tr>
<tr>
<td>Oral</td>
<td>The denticulate, nodose or tuberculate side, directed upwards.</td>
</tr>
<tr>
<td>Parapet</td>
<td>One side of the oral surface of a platform.</td>
</tr>
<tr>
<td>Platform</td>
<td>The oral surface of the laterally expanded end of some conodonts.</td>
</tr>
</tbody>
</table>
The classification of conodonts presented difficulties to Pander and these difficulties are now increased rather than resolved. They arise partly from the nature and mode of occurrence of conodonts, and partly from weaknesses in the Linnean system of nomenclature.

Trueman (1924) after stating (p.355) that:

"A fossil usually represents a part - often a small part - of the living animal or plant"

suggest (p.356) that:

"A palaeontological classification must be of such a character that a name or symbol is available to designate every recognisable form which characterises a distinct horizon".

At present the only accepted system of names is the Linnean, in which there is an inherent zoological relationship between categories. The application of this system to fossils which represent the major part of organisms probably introduces only slight zoological inaccuracies, but in the case of fossils which are only a very small part of the organisms the zoological error can be great. This is especially true of conodonts.

Manifestly, from the evidence of Scott (1934 and 1942) and others the conodontifer possessed various types of conodonts and these zoologically are, in each "assemblage" individually/
individually one. These types are, however, morphologically different and have been assigned to different families. This offence against biological veracity can be justified on the grounds that conodonts usually occur as separate, discrete units, physically unrelated to each other and to the animals of which they were parts and these units often characterise distinct horizons. "Assemblages" are rare and have not yet provided incontrovertible evidence of the precise mutual relations of the various types of conodonts included in them. The fact that the occurrence and distribution of most of the morphological groupings are stratigraphically significant especially in the upper Palaeozoic sediments of N. America prompts the writer to accept, in the spirit that half a loaf is better than no bread, the view of several American workers that the zoological inaccuracy of a morphological classification is outweighed by its utilitarian value.

In this classification conodonts are given the status of an order, the Conodontophorida Eichenberg 1930, and divided into two sub-orders. Those conodonts with a fibrous structure comprise the sub-order Neurodontiformes Branson & Mehl 1942 and are confined to Lower Palaeozoic strata. The Conodontiformes Branson & Mehl 1944 consist of laminar calcium phosphate and range from the Ordovician to the Trias/
Families within this sub-order are based on morphological features. In the Distacodidae Ulrich & Bassler 1926 the shape of the cusp and its cross section, the number and character of the denticles and the absence, or presence and size of a pulp cavity are diagnostic. The Prioniodidae and Prioniodinidae Ulrich & Baseler 1926 are similar in being bar-like forms, but differ in the position of the cusp, in the size and spacing of the denticles and in the degree of arching. In the Prioniodidae the cusp is anterior or terminal and the bar frequently bowed or laterally flexed, while in the Prioniodinidae the cusp may be absent but is usually in the median third and the bar is more arched than bowed. Some of the Prioniodinidae tend to be more blade-like than bar-like.

In the Polygnathidae Ulrich & Bassler 1926 and the Gnathodontidae Branson & Mehl 1944 the shape and size of the platform is of diagnostic value as is the presence, length and height of the carina and the size of the blade. Genera of these two families differ markedly in the size of the escutcheon. In the former it is small, whereas in the latter it is large and frequently occupies the whole aboral surface of the platform.

Altogether/
Altogether there are three families in the Neurodontiformes and five in the Conodontiformes with a total of about one hundred genera.
SYSTEMATIC PALAEOONTOLOGY
CLASS CYCLOSTOMATA

Order CONODONTOPHORIDIA Eichenberg 1930

Order comprising minute teeth, variable in shape, and ranging from simple cones through series of cones supported on an oral bar to complex dental plates, composed principally of calcium phosphate and occasionally attached to fragments of similar material assumed to have been jaws.

Sub-order CONODONTIFORMES Branson & Mehl 1944

Conodontiphoridae with laminated teeth of calcium phosphate.

Family PRIONIODIDAE Ulrich & Bassler 1926

More or less bar-like dental units with a major denticle or cusp, erect or posteriorly inclined, situated at or near the anterior end and in most forms an elongate denticulate posterior extension.

Genus APATOGNATHUS Branson & Mehl 1934

Units consisting of a sharply arched base, the limbs of which are denticulate, bar-like, parallel or slightly/
slightly divergent and joined at the apex by a thin lamella. The cusp is apical, large and curved towards one limb of the arch and the denticles are small and discrete. The symmetry of the arch is always broken by the inclination of the cusp and often by inequalities of limb denticulation and by skewing.

_Apatognathus geminus_ (Hinde)  

**Plate I  figs. 1, 2.**

1900 _Prioniodus geminus_ Hinde  


1928 _Prioniodina gemina_ Holmes  


**Diagnosis**  
_Apatognathus_ with asymmetrical denticulation and marked skewing. One or more prominent denticles beside the cusp; apical lamella very small. The inner limb is laterally tumid.

**Description**  
The denticulate bar is sharply flexed near the mid point and skewed; with the inner limb horizontal the outer limb slopes posteriorly downwards. The denticles are small, sharply edged and pointed and closely appressed at their bases. Those of the inner limb are smaller and more closely spaced than those of the outer limb and are twice as numerous. Towards the apex the denticles are larger and the apex is occupied by a large, laterally carinate and slightly curved/
curved cusp which lies in the same plane as the outer limb of the bar. The latter is moderately thin and deep with a narrow aboral trench flanked by thin lips running the length of the bar. The inner limb is laterally tumid, as thick as or thicker than deep and also has a narrow aboral trench. Beneath the cusp the aboral trench is expanded into a small escutcheon with a pronounced lip, the apical lamella, closing the apex of the arch.

Occurrence
Upper Limestone, Glencart, Dalry.
Upper Limestone, Linn Spout, Dalry.
Skateraw Middle Limestone, Dunbar.


Apatognathus porcatus (Hinde) Plate I figs. 3, 4.


Diagnosis: Similar to Apatognathus geminus but denticles uniform in height up to the cusp and bilateral tumidity of inner limb more marked.

Remarks: The specimen illustrated in figure is Hinde's holotype of Prioniodus porcatus. It is the inner limb and cusp of an Apatognathus similar to geminus but differing from it in that the denticles do not grade in height towards the cusp.
cusp. The specimen shows clearly the very marked bilateral swelling of the bar, the swelling becoming more marked towards the cusp and making the bar thickness about one and a half times its height.

**Occurrences**
Upper Limestone, Monkcastle, Kilwinning.
Skateraw Middle Limestone, Dunbar.

**Holotype**

Genus **EUPRIONIODINA** Ulrich & Bassler 1926

Prioniodus-like units with a denticulate anticusps.

**Euprioniodina angulata** (Hinde)  
Plate I fig. 5

1900 **Prioniodus angulatus** Hinde  

1928 **Hibbardella angulata** Holmes  
Proc.U.S.Nat.Mus. vol.LXXII, p. 11, Pl. 4, fig. 33.

**Diagnosis**

Euprioniodina with a bowed posterior bar, compressed cusp and anticusps at 90° to the bar.

**Description**
The bar is fairly stout, deep and strongly bowed and bears a series of seven, compressed, posteriorly inclined denticles decreasing in size posteriorly. The cusp is tall, stout, moderately compressed and sharp edged and has a slight backward inclination. Below the cusp the bar is bent sharply downwards and slightly inwards to form an anticusp/
cusp bearing seven short discrete denticles directed upwards and inwards. The aboral surface is narrow, trenched throughout and has a small escutcheon below the cusp.

**Occurrence**  Upper Limestone, Glencart, Dalry.

**Holotype**  J. S. Colln. H.M.G.S., Edinburgh. S.885.

Genus **HIBBARDELLA**  Ulrich & Bassler 1926

Units consisting of an arched, denticulate, anterior bar with a very tall central cusp. The denticles are discrete and belong to one series. The base of the cusp is usually produced into a short posterior bar. Escutcheon small.

For the purposes of description hibbardellae are considered to have been set in the centre front of a jaw with the bar transverse and the basal extension of the cusp posterior.

**Hibbardella brevialata**  sp. nov.  Plate I  fig. 6

**Diagnosis**  Hibbardella with a very short blade-like anterior bar, a stout curved cusp and a short thick posterior bar.

**Description**  The anterior arch is short and stout but more blade-like/
blade-like than bar-like and is inclined anteriorly outwards and upwards. The limbs meet almost at $90^\circ$ at the base of the cusp and bear two denticles each; these are slender, sub-circular and not more than one third the height of the cusp. The cusp is stout, recurved and compressed towards the base but sub-rounded distally. At the base of the cusp a short, thick, posteriorly pointed bar extends backwards. The aboral surface of the anterior arch is sharp; that of the posterior bar broad and flat and tapering posteriorly. There is a small triangular escutcheon at the base of the cusp from which a median groove extends along the aboral surfaces of the posterior bar and each limb of the arch.

**Occurrence**  
Lower Limestone, Law, Dalry.

**Holotype**  
J. S. Colln. H.M.G.S., Edinburgh. R.S.10931

**Remarks**  
This species resembles species of *Trichonodella* in stoutness of cusp and shortness of arch limbs but it does not have the deeply excavate base typical of that genus.

**Hibbardella craigi** sp. nov.  

<table>
<thead>
<tr>
<th>Year</th>
<th>Species</th>
<th>Author</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1928</td>
<td><em>Hibbardella angulata</em></td>
<td>Holmes</td>
<td>Proc. U.S. Nat. Mus. vol.LXXII, p.11, Pl.4, fig. 32.</td>
</tr>
</tbody>
</table>

**Diagnosis**
**Diagnosis**  
Hibbardella with a very deep, thin, blade-like anterior bar and a very, slender tall cusp.

**Description**  
The dental unit comprises a thin deep oral blade flexed at about the mid-point into a low arch, slightly bowed anteriorly and surmounted by a cusp. Each limb of the arch is surmounted by six or seven compressed discrete denticles and is in depth greater than one fifth of the height of the cusp. The cusp, situated at the apex of the arch, is laterally compressed, tall, slender and has an anterior carina truncated below the mid height by a flat surface continuous with the front of the arch. The posterior carina of the cusp continues on to the upper surface of the posterior process which is thin and deep but broken off from the specimen figured. The aboral surface is sharp except below the cusp where it is occupied by a small T-shaped escutcheon, the leg of the T running into the posterior process.

**Occurrence**  
Lower Limestone, Birkhead, Dalry.

**Holotype**  
J. S. Colln. H.M.G.S., Edinburgh. S.884

**Remarks**  
Holmes identified this specimen with the genotype Hibbardella angulata (Hinde) Ulrich & Bassler 1926) (Prioniodus angulatus of Hinde) specimen A.4180, British Museum, but it differs from the holotype in that the sub-apical
apical angle is more obtuse and the limbs of the arch are much deeper. Most specimens of *Hibbardella angulata* have a more bar-like anterior arch than has the holotype and *Hibbardella craigi* is considered to be outside the range of variation in shape and depth of arch.

Genus **Hindeodella** Ulrich & Bassler 1926

Long almost straight to gently bowed and arched bars frequently with an anterior inflexion. Up to ten small denticles in front of the large strong cusp and a numerous series of small denticles often irregular and alternating in size behind it.

**Hindeodella complex** (Hinde)  

Plate II fig. 1

1900 *Prioniodus complex* Hinde  

1928 *Prioniodus complex* Holmes  
*Proc. U.S. Nat. Mus.* vol. LXXII, p. 20, Pl. 2, fig. 32.

**Diagnosis**  
*Hindeodella* of medium length; bar deep, fairly thin and anteriorly flexed inwards and downwards; cusp at point of flexure.

**Description**  
The bar is of moderate length, almost straight aborally posterior to the cusp but orally slightly bowed. It is/
is fairly thin and deep and anteriorly is curved inwards and downwards, the aboral edge making an angle less than $90^\circ$. There are twenty-five denticles directed orally, five of which are on the anterior process, the remainder posterior to the cusp. The cusp is almost vertical, long and subcircular in cross-section. The bar denticles are small, irregular and closely set but become larger and more inclined posteriorly. At the posterior end of the bar is a fairly large inclined denticate below which a series of small fused denticles form a thin deltoid keel. The aboral edge is sharp but bears a narrow median groove which is expanded on the outer edge below the cusp to form a small shallow escutcheon.

**Occurrence**  Upper Limestone, Glencart, Dalry.

**Holotype**  J. S. Colln. H.M.G.S., Edinburgh. S.890.

**Remarks**  This specimen is similar to *H. acuta* (Branson & Mohl), but differs from it in size, attitude and denticulation of the anterior process, in the stoutness of the bar and in the size of the posterior keel. *H. acuta* is thicker, has a shorter more upwardly directed anterior process and a much smaller keel.

*Hindeodella curta*
Hindeodella curta sp. nov.  

Plate II fig. 2

**Diagnosis**  Hindeodella with a very short, moderately thin bar, aborally straight and posteriorly very slightly bowed. Denticles alternately long and very short. **Description**  The bar is extremely short and has an almost straight aboral edge, but is very slightly bowed towards the posterior end. The bar depth increases rapidly in the anterior quarter length then tapers gradually posteriorly. The cusp is sub-rounded, posteriorly inclined and situated at the deepest point of the bar. Anterior to the cusp are two small compressed denticles the inclinations of which diverge, the more anterior being inclined forwards. Behind the cusp lie four large denticles, sub-rounded, inclined and decreasing in size posteriorly. A very small sharp pointed denticle lies between each of these or a germ denticle is visible within the bar. The aboral surface is separated from the lateral surfaces by a sinuous flange arising near the anterior margin and running to the posterior. This flange is arched below the cusp. The aboral surface tapers to an almost sharp edge which bears a very small elongate escutcheon below the cusp and a narrow median groove thence almost to the posterior end.

**Occurrence**  Shale 4 ft. above the Skateraw Middle Limestone, Dunbar.

**Holotype**/
Holotype  W. J. C. Colln.

Remarks  The extreme brevity of this species is unusual as most of the Carboniferous species tend to be long. Even fragments of other Hindeodellas, at most half the length of the complete specimens, are longer than this specimen.

_Hindeodella distorta_ sp. nov.  Plate II fig. 3

Diagnosis  _Hindeodella_ with a short, deep, compressed bar and a deep triangular posterior keel; bar bowed anteriorly.

Description  The bar is short, deep and compressed especially in the anterior third which is bowed inwards. This incurved portion is orally tilted backwards. There are twenty-five denticles on the oral edge, including the principal cusp situated about the middle of the anterior bowed part of the bar and a subsidiary posterior cusp. Four small denticles lie anterior to the cusp which is sub-rounded and directed slightly inwards and backwards. The bar denticles are unequal, compressed and closely appressed at their bases and their backward inclination increases towards the posterior subsidiary cusp. The subsidiary cusp is compressed, inclined at about $30^\circ$ to the horizontal and almost as large as the main cusp. A series of seven compressed germ denticles combine with an aboral extension of the/
the bar to form a posterior deltoid keel. The aboral edge is sharp save for a very small escutcheon below the main cusp.

**Occurrence** Upper Limestone, Linn Spout, Dalry.

**Holotype** J. S. Colln. H.M.G.S., Edinburgh. R.S.10932

**Hindeodella tenuis** sp. nov. Plate II figs. 4, 5.

**Non** Ctenognathus obliquus Pander 1856 Mon. der Foss. Fische p.33, Tab.2a, figs.11,12.


1928 Hindeodella obliqua Holmes Proc.U.S.Nat.Mus. vol.LXXII p.12, Pl.5, fig.5.

**Diagnosis** Hindeodella with a slender compressed bar slightly bowed; cusp broad based and compressed; anterior denticles erect; posterior denticles inclined.

**Description** The bar is thin, posteriorly straight and gently bowed in the anterior third. The anterior bowing is associated with an inward tilting of the oral surface and the anterior end is rounded. Six small, sub-vertical, compressed, sharp-edged denticles, unequal in height, are situated on the anterior part of the bar followed by a broad based, markedly compressed, cusp which is inclined backwards and slightly incurved. Posterior to the cusp are about twelve unequal compressed denticles inclined posteriorly. The posterior termination/
Termination of the bar is sharp and denticle-like. Germ
denticles are visible in the base of the cusp. The aboral
eedge is sharp but has a small deep escutcheon below the cusp
and a very narrow median trench running from just in front
of the escutcheon to the posterior end. This trench is
extremely narrow towards the posterior.

**Occurrence**  
Lower Limestone, Birkhead, Dalry.

**Holotype**  
S.894

**Figd. Specimen** (fig. 5) J.S. Colln., H.M.G.S., Edinburgh.
S.895.

**Remarks**  
The specimen shown in Fig. 5 (Hinde 1900, Pl.10,
fig. 29 and Holmes 1926, Pl. 5, fig. 3) is a fragmentary
specimen of *H. tenuis*, showing the cusp and the posterior
two-thirds of the bar. The incurving of the cusp is well
illustrated by this specimen which is from the same locality.

This species has a resemblance to *H. gladiola* E. R. Branson
in its posterior termination and the posterior part of the
bar. *H. gladiola* is, however, somewhat thicker and has a
sub-rounded cusp set near the anterior end of the bar.

**Indeterminable Hindeodellas**

The majority of hindeodellas are recovered as bar
fragments which from their configuration and denticulation
belong to several different species, but since they lack
anterior/
anterior and posterior termini cannot be specifically identified. The fragments are figured to give an indication of the variations in Carboniferous hindeodellas.

**Hindeodella sp.**


**Description** The specimen figured is a bar fragment showing typical hindeodellid dentition of small denticles intercalated between larger denticles, all slightly inclined posteriorly. The bar is thin, fairly deep, has slight lateral flanges and a median aboral groove. The denticles are tall, somewhat compressed and separate.

**Occurrences** Upper Limestone, Monkcastle, Kilwinning. Bone Bed Limestone, Lower Limestone Group, Bilston Burn, Midlothian. Shale above Skateraw Middle Limestone, Dunbar. Castlecary Limestone, Upper Limestone Group, Joppa.

**Figs. Specimen** J. S. Colln. H. M. G. S., Edinburgh. S. 878.

**Hindeodella sp./**
Hindeodella sp.  

Plate III fig. 1


Description  The specimens figured show the marked elongation common in carboniferous hindeodellas. The bars are long, rounded or laterally tumid and closely denticulate. The denticles are short, posteriorly inclined and occasionally fused at their bases. Between each pair of larger denticles are from two to four, usually three, smaller denticles. The bars are aborally grooved and have a gentle sigmoid curvature in oral aspect.

Occurrence  Upper Limestone, Monkcastle, Kilwinning.
Bone Bed Limestone & shales, Bilston Burn, Midlothian.
Posidonia-Band below Top Hosie Limestone, Kilsyth.
Skateraw Middle Limestone & shales, Dunbar.
Castlecairn Limestone & shales, Joppa.
Skipsey's Marine Band, Coal Measures, Motherwell.

S. 879 and S. 880.

Remarks  The specimen shown in fig. 1 is very similar to H. sp. Ellison 1941, Pl. 20, fig. 33, from which it differs, however, in having more slender denticles.

Hindeodella sp./
Hindeodella sp.  

Plate III fig. 3

1900 Ctenognathus obliquus Hinde  
Trans.N.H.Soc.Glas. vol.V p.344, pl.10, fig. 27.

1928 Hindeodella obliqua Holmes  
Proc.U.S.Nat.Mus. vol.LXXII p. 12, Pl. 5, fig. 4.

Description  
An indeterminable fragment of a very stout bar bearing a relatively short slender cusp and six posteriorly inclined denticles.

Occurrence  
Lower Limestone, Birkhead, Dalry.

Figg. Specimen  

Genus LIGONODINA  
Ulrich & Bassler 1926

Complex dental units consisting of a short to moderately long straight or down-curved bar set with discrete denticles and having a large erect or recurved cusp at or near the anterior end. The bar is sharply flexed near the cusp and is produced inwards and backwards as a short denticulate antero-inferior process which usually slopes posteriorly downwards.

Ligonodina complectens/
Ligonodina complectens sp. nov. Plate III fig. 4

1900 Prioniodus tulensis Hinde Trans. N. H. Soc. Glas. vol. V p. 343, Pl. 9, fig. 16.

Diagnosis: Ligonodina with a short stout bar bowed inwards; cusp towards posterior bar; bar antero-inferior process directed upwards.

Description: The bar is short, gently arched and bowed inwards and markedly swollen on the inner side at the base of the cusp which is situated near the posterior end. The cusp is moderately compressed, sharp edged and curved posteriorly. Two small, short, broad based denticles are present near the base of its posterior margin. In front of the cusp the bar proceeds forwards and slightly downwards bearing two widely separated rounded denticles the anterior one being fairly tall. At the position of this moderate sized denticle the bar is bent sharply backwards, inwards and upwards. This reflexed portion of the bar has at least two small discrete rounded denticles posteriorly inclined. The posterior end of the bar is pointed and curved outwards. The aboral surface is narrow and has a groove running the whole length. This groove encroaches on the inner lateral surface anterior to/
to the cusp and is slightly broader and deeper at the point of flexure.

**Occurrences**  
Upper Limestone, Glencart, Dalry.  
Lower Limestone, Law, Dalry.  
Shale above Skateraw Middle Limestone, Dunbar.

**Holotype**  

**Remarks**  
This species is unusual in having the anterior process directed upwards and the cusp is set further back on the bar than in other ligonodinids. The specimens from the Skateraw Middle Limestone although badly broken are easily recognisable because of these two unusual characteristics. The largest indicates a maximum size of this species at least twice that of the specimen figured.

**Ligonodina erecta** sp. nov.  
Plate III fig. 5


**Diagnosis**  
Ligonodina with a moderately thin, deep bar, erect compressed cusp anterior and a short sharp-pointed antero-inferior process.

**Description**  
The bar is deep, fairly thin, and short and has two very small denticles posterior. The depth of the bar increases/
increases rapidly anteriorwards and it is deepest below the cusp which is erect, tall, slender and compressed. Immediately in front of the cusp the bar is bent sharply inwards, backwards and downwards to form a short posteriorly sharp antero-inferior process. The process has three medium sized denticles one of which, adjacent to the cusp, is at the point of flexure of the bar and is anteriorly inclined. This denticle and the next are slender and rounded but the last of the three is broad based and compressed and has a lateral carina continuous with the sharp end and point of the bar. The aboral edge is narrow and has a median trench running throughout its length expanded below the cusp into a shallow elongate escutcheon.

**Occurrences**

Upper Limestone, Glencart, Dalry. Bone Bed Limestone, Bilston Burn, Midlothian.

**Holotype**


**Remarks**

The species has similarities to *L. recurvata* Branson & Mehl and *L. peracuta* Hinde. It differs from the latter in shape and attitude of the cusp and in the degree of reflexing of the antero-inferior process. In *L. peracuta* the reflexing is less acute and more downwardly directed. *L. recurvata* has a much stouter cusp which is both curved and inclined posteriorly. No entire specimens were found but
but the shape and thickness of the broken posterior end of the bar indicates that it was only very slightly longer than in the specimen figured.

**Ligonodina percuta** (Hinde)  
Plate III figs. 6, 7.

1900 Prioniodus percutus Hinde  

1928 Prioniodus percutus Holmes  

**Diagnosis**  
Ligonodina with a long, slightly arched denticulate bar, tall, slender, rounded cusp and a very short pointed antero-inferior process.

**Description**  
The bar, posterior to the cusp is long, gently arched and compressed and bears a series of long, slender, rounded denticles posteriorly inclined, with smaller denticles intercalated. All denticles are separated down to their bases. The bar curves downwards below the cusp which is tall, slender and rounded and stands almost vertically. In front of and below the cusp the bar is bent inwards and downwards to form a short stout antero-inferior process bearing two small denticles.

**Occurrences**  
Lower Limestone, Law, Dalry.  
Shales above Skateraw Middle Limestone, Dunbar.

**Holotype**  

**Remarks**
Remarks In reflected light the denticles of this specimen appear peg-like but in transmitted light (fig. 7) their continuity with the oral bar is apparent. The cusp and two of the denticles have regenerated points, in one case showing marked change of slope of the denticle sides at the position of breakage. The species resembles Upper Devonian forms in having a long posterior bar with comparatively large denticles.

Ligonodina tulensis (Pander) Plate III fig. 8

1856 Prioniodus tulensis Pander Mon. der Foss. Fische p. 30, Tab. 2a, fig. 19.
1900 Prioniodus tulensis Hinde Trans.N.H.Soc.Glas. vol.V p. 343, Pl. 9, fig. 15.

Diagnosis Ligonodina with a tall, stout, slightly compressed, curved and inclined cusp set on a short, thick, posteriorly rounded bar: antero-inferior process, compressed and sharp pointed, arising from the base of the cusp.

Description The bar is very short, thick and deep and tapers to a rounded posterior. A lateral flange is present about mid-height of the bar and slopes down to the aboral surface posteriorly. The posterior quarter bears three small denticles/
denticles. The cusp, the base of which occupies more than half the length of the bar is compressed and posteriorly curved near the base, straightening towards the point, where it becomes rounded. Its height is greater than three times the length of the bar. The antero-inferior process arises just in front of and below the cusp, is inclined orally inwards and so situated that its aboral edge lies in the same plane as the bar and cusp. Three of the four denticles on the process lie posterior to the cusp, the fourth springs from the base of the cusp. The last denticle is continuous with the posterior end of the process which meets the aboral surface in a point. The aboral surface has a leaf-shaped escutcheon below the cusp from which a groove extends to the posterior end of the bar and along the process.

**Occurrences**
- Upper Limestone, Glencart, Dalry.
- Bone Bed Limestone, Bilston Burn, Midlothian.
- *Posidonia* Band below Top Hosie Limestone, Kilsyth.
- Hawthorn Limestone, Muirkirk.


**Ligonodina ultima** sp. nov.

**Plate IV fig. 1**

**Diagnosis** Ligonodina with a short, thick, orally rounded and aborally flattened bar bearing a very stout compressed curved/
curved cusp. Antero-inferior process arising from about the mid line of the cusp.

Description. The bar is short and about as thick as high except posteriorly where it thins slightly. Its oral and aboral surfaces are sub-parallel, the former rounded and the latter almost flat. There are two widely separated denticles on the bar, the larger, near the posterior end, compressed and sharp edged. The smaller lies about the middle of the bar. The cusp is curved, stout, slightly compressed throughout its length and is twisted, the major axis of its elliptical cross section being parallel with the bar near the base, but at 45° to the bar near the point. Towards the point the cusp is sharp edged. Basally the anterior edge of the cusp curves to meet the base of the antero-inferior process which arises laterally from the bar at about the mid line of the cusp. The process is compressed, inclined inwards orally and has two compressed sharp edged denticles inclined posteriorly. The aboral surface of the process is narrow and bears a median groove which joins anteriorly the aboral median groove of the bar. At their union lies a small escutcheon elongated at right angles to the bar.

Occurrences/
Occurrences  Hawthorn Limestone, Muirkirk. Skateraw Middle Limestone, Dunbar.


Ligonodina sp.  Plate IV fig. 2

Remarks  The specimen figured is too fragmentary for specific determination. It differs from the other figured specimens in that the antero-inferior process continues aborally the line of the cusp and bears denticles directed inwards and upwards. This and the form of the cusp suggest close comparison with L. delicata Branson & Mehl (1934a, Pl. 14, fig. 23).

Occurrence  North Greene Limestone, Bilston Burn, Midlothian.

Figd. Specimen  W. J. C. Colln.

Genus PRIONIODUS  Pander 1856

Units with a denticulate bar or blade-like bar terminated anteriorly by a large cusp extended aborally as an anticusp to give the unit as a whole a pick-like appearance. The bar may be straight, arched or bowed and the cusp may be a single unit or compounded of several fused denticles. The anterior edge of the cusp is sometimes feebly/
feeble denticulate.

Branson & Mehl (1933b) consider that Prioniodus may have developed from early ozarkodinid forms by reduction and down-flexing of the anterior bar and its incorporation into the base of the cusp to form the anticusp.

Prioniodus brevis sp. nov. Plate IV fig. 3

Diagnosis Prioniodus with a short, broad based, compressed incurved cusp, a very short stout anticusp and gently arched, bowed posterior bar.

Description The cusp is short, compressed, broad based and curves inwards. The edges are sharp and the anterior edge is interrupted near the base by a small denticle. The posterior bar is thin, gently arched and bowed and bears seven sharp edged compressed denticles closely set. Its posterior termination is blunt and the denticles, like the cusp, are vertical. Denticles and bar together are about half the height of the cusp. Germ denticles are visible in the bar between the posterior denticles. The aboral edge is narrow and flat and has a median groove expanded into a lanceolate escutcheon below the cusp. The escutcheon is slightly more expanded on the inner side and is moderately deep.
deep. Height and length of specimen about equal.

**Occurrences** Lower Limestone, Law, Dalry.
Bone Bed Limestone, Bilston Burn, Midlothian.

**Holotype** J. S. Colln. H.M.G.S., Edinburgh. R.S.10934.

**Remarks** This species resembles the genotype *P. elegans*
Pander in general configuration and in showing the primitive prioniodid stage of denticulation anterior to the cusp.

The differences are:

1. *P. brevis* is more compressed than *P. elegans*.
2. It has larger denticles and a shorter broader cusp.
3. The bar of *P. elegans* is not arched.

Specimens of *Prioniodus spp.* do not appear to be common in the Scottish Carboniferous and most have the posterior bar broken making specific determinations doubtful. Assuming evolution from forms anteriorly denticulate and judging by their lack of pre-cuspal denticles they are of more advanced types than *P. brevis*.

**Prioniodus peracutus** Hinde


**Diagnosis**/
Diagnosis: *Prioniodus* having a tall, compressed cusp and large anticusp; posterior bar anteriorly arched, posteriorly declined; bar denticles posteriorly inclined.

Description: The bar is thin, slightly bowed and arched near the cusp. Posteriorly it slopes downwards and terminates in a sharp edge. The bar denticles, nine in number, are unequal, small and compressed. All have a slight posterior inclination and in the anterior part of the bar they are fused at their bases. The cusp is tall, compressed and laterally erect, but slightly curved inwards. The anterior edge of the cusp is carinate and the carina continues down below the bar as the slightly concave anterior edge of the anticusp, the depth of which is about one quarter the height of the cusp. The aboral surface of the bar is narrow but broadens at the base of the cusp whence it narrows towards the bottom of the anticusp. A median groove is present and is expanded into a fairly deep lachrymiform escutcheon at the junction of bar and anticusp.


Lectotype: J. S. Colln. H.M.G.S., Edinburgh. S.888. (Designated Type Specimen by Roundy 1926)

Remarks:
Remarks. The writer agrees with Houndy's designation of this specimen as the type specimen of *P. peracutus*. Hinde's syntypes (1900, Pl. 9, figs. 21 & 23), are generically different, fig. 23 is *Ligonodina peracuta* and fig. 21 appears to be another *Ligonodina*, but the specimen has been lost.

**Genus TRICHONODELLA Branson & Mehl 1933**

Bilaterally symmetrical units consisting of a stout posteriorly curved cusp and three denticulate bars, two lateral and one posterior. The aboral surface is deeply excavated.

*Trichonodella sp.*

**Plate IV figs. 5, 6.**

Description. The genus *Trichonodella* is not represented in the John Smith Collection and only one fragmentary specimen has been found by the author.

The cusp of this specimen is thick and almost square at the base becoming compressed and sharp-edged near the point. Each side of the cusp has near the base a shallow rounded groove parallel with the cone axis. At the base of these grooves the broken stumps of the anterior arch are visible. The base of the cusp is extended posteriorly as a broad orally convex, aborally concave bar bearing one very/
very small denticle. The aboral concavity of the posterior bar grades into the wide deep escutcheon.

**Occurrence**  Shales 4 ft. above Skateraw Middle Limestone, Dunbar.

**Figd. Specimen**  W. J. C. Colln.

**Remarks**  Trichonodella is similar to Hibbardella but differs in being generally much stouter and in having a very large deep escutcheon. The large size and the depth of the escutcheon are the most diagnostic features of *Trichonodella*.

**Family**  *PRIONIODINIDAE*  Ulrich & Bassler 1926

Arched, bar-like or blade-like dental units; most forms with an apical cusp, or large denticle in the middle third of the bar.

**Genus**  *DALRYELLA*  gen. nov.

Arched and bowed dental bars or blade-like bars bearing a graduated series of more or less compressed discrete denticles the largest denticle being in the posterior third length. The cusp (the denticle below which the escutcheon/
escutcheon is situated) is relatively small and is situated on the sharply inflexed anterior end of the bar. The escutcheon is small, situated anteriorly and extended posteriorly into a narrow aboral groove which runs the whole length of the bar.

**Range** From near the base of the Lower Limestone Group to the top of the Upper Limestone Group.

**Genotype** *Dalryvella dalryensis* sp. nov.

**Remarks** This genus differs from *Lonchodina* and *Prioniodina* in the position of the cusp and escutcheon. In these two genera the cusp is usually the largest denticle and is situated in the median third, at the apex of the arch. Also, in *Dalryvella* the bar denticles are more widely spaced and larger, and small intercalated secondary denticles are present in the anterior half of the bar. *Dalryvella* resembles *Metalonchodina* (Branson & Mehl) in general form but in the latter arching is usually less pronounced and the escutcheon is situated beneath the penultimate denticle towards which the other denticles are inclined.
Dalryella dalryensis gen. et sp. nov. Plate V figs. 1, 2.


Diagnosis Compressed oral bar arched and bowed bearing tall, broad based, compressed denticles widely spaced alternating with single small denticles in the anterior third length; cusp small, anterior; escutcheon small, circular.

Description The bar is moderately deep, compressed and asymmetrically arched, the arching being more pronounced anteriorly. The bowing, most marked at the third and fourth denticles, is convex inwards and the combination of arching and bowing produces an outward tilt of the oral surface in the posterior two-thirds of the bar. The small, sub-circular cusp is situated on the anterior inflexion of the bar and curves inwards and upwards. The five denticles posterior to the cusp are progressively larger and more compressed and curved inwards, those at the top of the arch being much compressed and sharp-edged. The sixth denticle is small. In the anterior half of the bar very small denticles alternate with the major denticles. The aboral edge is narrow and rounded and has a narrow median groove throughout.
throughout. The escutcheon is small, circular and deep and occupies the aboral surface of the anterior inflexion. A small flange runs along the outer lateral surface just below mid height of the bar.

**Occurrences**
- Upper Limestone, Dalry.
- Upper Limestone, Monkcastle Glen, Kilwinning.
- Linn Limestone, Glencart, Dalry.

**Holotype** (Fig. 1) J. S. Colln. H.M.G.S., Edinburgh. S.873

**Paratype** (Fig. 2) J. S. Colln. H.M.G.S., Edinburgh. R.S.10935.

**Remarks** The bar of the paratype (fig. 2) is complete but for the anterior inflexion. The holotype is broken posteriorly but since an entire unbroken specimen was lacking it was considered most representative of the species as it shows the anterior inflexion and the escutcheon.

*Dalryvella convexa* (Hinde)  

**Plate V** fig. 3


**Diagnosis** Compressed, arched and gently bowed bar with compressed, discrete sub-erect denticles; the largest denticle in the posterior quarter length. Aboral edge narrow and grooved.

**Description**
Description The bar is thin, moderately deep and is surmounted by a series of compressed sub-erect denticles, slender towards the anterior of the bar but broader based posteriorly. The denticles are discrete but more closely set than in dalryensis. Anteriorly single small denticles alternate with the major denticles. A small flange runs along both inner and outer sides of the bar at about mid height and curves down to the oral edge at both ends. The anterior inflexion is broken off, but the specimen figured is considered to be otherwise complete. The aboral surface is sharp save for an extremely narrow median groove.

Occurrences Upper Limestone, Monkcastle Glen, Kilwinning. Linn Limestone, Glencart, Dalry.


*Dalryella robusta* sp. nov. Plate V fig. 4

Diagnosis Bar stout, bowed and arched, surmounted by slightly compressed denticles increasing in size posteriorly and alternating with very small single denticles.

Description The bar is arched and slightly convex inwards, almost as thick as deep anteriorly but deeper posteriorly and is tilted orally outwards. The inwardly curved denticles are/
arc large, discrete, narrow based and very slightly compressed. Anteriorly they are almost perpendicular to the bar but posteriorly become more inclined. Very small single denticles are intercalated between the major denticles throughout the series. A pronounced lateral flange is present at about mid height on both sides of the bar and curves down to meet the aboral surface at both extremities. The aboral surface is flat to rounded anteriorly but becomes sharper posteriorly and has an almost imperceptible median groove throughout. The anterior inflexion is broken off but the beginning of the flexure is visible.

**Occurrence** Top of Upper Limestone, Auchenskeith, Dalry.
Lower Limestone, Law, Dalry.

**Holotype** J. S. Colln. H.M.G.S., Edinburgh. R.S.10936.

**Remarks** The bar in this species is stouter than in the genotype *D. dalryensis* and less bowed and arched. The bowing, however, is in the same sense (convex inwards). Anteriorly the denticles are almost round in cross-section, but towards the posterior of the bar become slightly compressed. The outward tilting of the oral edge of the bar and the curvature of the denticles is similar in both species but less marked in *D. robusta*.

*Dalryella sp.*
Dalryella sp.

Plate V fig. 5

Remarks Fig. 5 shows a single specimen from the Upper Limestone at Monkcastle Glen. The specimen is referable to Dalryella on the basis of arching and bowing of the bar and the size, attitude and spacing of the denticles. It differs from the other dalryellids figured in having no minor denticles and in being rounded to flat on the aboral surface which is conspicuously broad below the largest denticle.

Occurrence 7 to 10 ft. above the base of the Upper Limestone, Monkcastle Glen, Kilwinning.

Figd. specimen (the only specimen) J. S. Colln. H.M.G.S., Edinburgh. R.S.10937.

Dalryella sp.

Plate V fig. 6

Description The bar is short, compressed and arched, and bowing is almost absent. The anterior inflexion is extremely slight and appears like a small bump on the inner side of the anterior end of the bar. The cusp is slender, rounded and although broken appears to curve upwards. The other three denticles are compressed, curved and inclined posteriorly and larger than the cusp. Aborally the bar is thin and flat and a median groove is present terminating in a small circular escutcheon/
escutcheon below the cusp.

**Occurrence**  Shales above Skateraw Middle Limestone, Dunbar.

**Figd. Specimen**  W. J. C. Colln.

**Remarks**  The specimen resembles *D. convexa* in compression of the bar and denticles, but the denticles are more widely spaced, more inclined and fewer, and small intercalated denticles are lacking.

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**Genus** *METALONCHODINA*  Branson & Mehl 1941

Arched denticulate bars with one limb very short.

The short limb bears one large denticle followed occasionally by one or two small denticles; cusp apical.

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*Metalonchodina convexa* (Hinde)

Plate VI fig. 1


**Diagnosis**  *Metalonchodina* with anterior bar bearing one large denticle; escutcheon large, moderately deep and with a prominent inner lip; denticles incurved.

**Description**  The bar is sharply arched beneath the cusp, is/
is long and slender posteriorly but thick, short and pointed anteriorly. A large, broad-based, compressed denticle occupies the anterior part of the bar which tapers to a somewhat blunted point. The cusp is sub-rounded near the base, but compressed and sharp-edged towards the point and curves inwards. The five denticles posterior to the cusp are discrete, rounded, progressively smaller posteriorly, and curve upwards and inwards. From the anterior point to the apex the aboral surface broadens rapidly and is transversely flat. Thence to the first post-apical denticle it narrows very rapidly then tapers gradually to the posterior end and is more or less rounded. A median groove extends to both extremities from the large fairly deep escutcheon. The aboral broadening of the bar at the apex is more marked on the inner side.

Occurrence Upper Limestone, Monkcastle Glen, Kilwinning.


Metalonchodina sp.

Remarks Metalonchodinas are uncommon in the strata investigated. A few fragmentary specimens were found in the shales above the Skateraw Middle Limestone and in Skipsey's/
Skipsey's Band. The specimen figured is from the latter, but is too fragmentary for specific identification. It shows the foreshortened anterior bar with one large denticle, the cusp and two of the posterior denticles. The bar is much thickened apically, especially on the inner side. The escutcheon is oval, offset inwards from the mid-line and elongated almost at right angles to the bar.


Genus OZARKODINA Branson & Mehl 1933

Thin, arched and frequently bowed, blade-like units with laterally compressed denticles and an apical cusp. The aboral edge is thin and has a small escutcheon below the cusp.

Ozarkodina dubia (Hinde)


Diagnosis/
Diagnosis  Ozarkodina with a very deep, compressed blade, arched and strongly bowed.

Description  Anteriorly the bar is thickest at the oral edge, but posteriorly the greatest thickness is near the aboral edge. The anterior limb of the arch is deeper and shorter than the posterior. The cusp has a marked backward inclination and at the base is about three times as broad as the anterior denticles. Anterior denticles, four, are compressed, sharp-edged and fused from the mid-height downwards. Those of the posterior bar, eight, are compressed and fused for about two-thirds of their height. Germ denticles are visible in the bar just posterior to the cusp. The aboral edge is sharp except below and behind the cusp where it is slightly flared to form a small, elongate, lachrymiform escutcheon.

Occurrence  Lower Limestone, Birkhead, Dalry.


Remarks  The bar of this species is unusually deep for Ozarkodina. It has some resemblance to Spathognathodus abnormis Branson & Mehl 1934b but is distinguished from that species by its broad-based apical cusp and greater curvature of the bar.

Ozarkodina spp./
Ozarkodina spp.  

Plate VI figs. 4, 5.

Remarks  A few very small fragmentary specimens referable to either Ozarkodina or Bryantodus were found at several stratigraphical levels from the Lower Limestone Group up to Skipsey's Marine Band. On account of their very fragmentary nature none are described. Two somewhat larger fragments definitely referable to Ozarkodina are figured. Both specimens have both ends broken. They differ from \textit{O. dubia} in being less deep and in having a larger escutcheon. The specimen in fig. 4 has unequal denticles more closely spaced than those of \textit{O. dubia}. The other specimen (fig. 5) resembles \textit{O. delicatula} (Stauffer & Plummer) (Ellison 1941, Pl. 20, fig. 47) with which it may be conspecific.

Occurrence of Figd. Specimens  Skipsey's Marine Band, Motherwell.

Figd. Specimens  W. J. C. Colln.

Genus \textit{SPATHOGNATHODUS} Branson & Mehl 1933

\textbf{emend.} Branson & Mehl 1941

Compound blade-like units with almost straight aboral edge and straight or arched oral edge highest at or near the anterior end. Base laterally expanded near the mid-length/
mid-length to accommodate an escutcheon. The oral surface of the lateral expansion is usually smooth but occasionally denticulate. The anterior denticle is large and those posterior to it constitute a decreasing series.

**Spathornathodus commutatus** Branson & Mehl


**Remarks** The specimen figured agrees with the description of *S. commutatus* in everything except the number of denticles. This specimen has 13 denticles whereas Branson & Mehl's species is stated to have from 16 to 20. However, since increase in the length of the blade and number of blade denticles is a function of growth this specimen is considered to be an immature form of *S. commutatus*.

**Occurrence** Parting in Skateraw Middle Limestone, Dunbar.

**Spathornathodus currieae** sp. nov.


**Diagnosis** Thin, slightly bowed blade, tapering posteriorly bearing sub-erect closely spaced denticles fused almost to their tips. Largest denticle second in the series.

**Description** The blade is thin, gently bowed and very slightly arched and tapers posteriorly from a high rounded anterior/
anterior end. The denticles are sub-erect but towards the posterior end slightly inclined and form a graduated series decreasing in height posteriorly. The largest denticle is second in the series, about twice as broad as the others but only slightly taller than those immediately behind it. In front of this large denticle is a small denticle occupying the anterior end of the blade and the edge of this denticle is produced into a thin anterior lamina. The aboral surface is sharp in the anterior quarter of its length and has an extremely narrow median groove which broadens posteriorly and in the median third is flared to form a shallow lanceolate escutcheon. Posteriorly the aboral surface is narrow and grooved medianly.

Occurrence Skipsey's Marine Band, Motherwell.

Holotype W. J. C. Colln.

Remarks This species closely resembles S. spiculus (Youngquist & Miller 1949, p. 622, Pl. 101, fig. 4) from the late Mississippian of Iowa. S. spiculus is, however, more arched and has aborally a flared lip running from near the anterior end to the posterior, and its cusp is more prominent. This species is named in honour of Dr. Ethel D. Currie who has contributed much to the palaeontology of Skipsey's Marine Band.

SPATHOGRNATHODUS EXODENTATUS/
Spathomastodus exodontatus sp. nov.  

Plate VII figs. 4, 6.

Diagnosis Slender, bowed and slightly arched blade; large compressed cusp anteriorly penultimate; denticles in middle third irregularly set, one on the inner side, several on the outer side, all rounded; posterior denticles compressed and broad-based.

Description The blade is bowed and is slightly arched posteriorly with sub-vertical terminations. The anterior and posterior parts are thin, but the middle third is laterally thickened and bears on the inner side one small sub-rounded, erect denticle. On the outer side of the thickened part are four similar denticles. The cusp is large, compressed and posteriorly inclined and has in front of it one small compressed denticle. Posterior to the thickened part of the bar is a series of compressed sharp edged denticles all posteriorly inclined. A wide, fairly deep, lachrymiform escutcheon occupies the middle third of the aboral surface and extends anteriorly and posteriorly into a narrow groove.

Occurrence Shales 6" below Bone Bed, Bilston Burn, Midlothian.

Holotype W. J. C. Colln.

Remarks This species, in common with several Upper Devonian/
Devonian and Mississippian species of Spathognathodus, (e.g. \textit{S. costatus}, \textit{S. irregularis} and \textit{S. tridentatus}) has a marked thickening of the blade in the middle third with denticles offset from the midline. It differs, however, from these and allied species in having no transverse ridges linking the offset denticles to the crest of the blade.

\textit{Spathognathodus longifossatus} sp. nov.  
Plate VIIfig. 5

1900 \textit{Polygnathus scitulus} Hinde \textit{Trans. N.H. Soc. Glas.}, vol, V, p. 343, Pl. 9, fig. 10.

1928 \textit{Pandorodella scitula} Holmes \textit{Proc. U.S. Nat. Mus.}, vol. LXXII, p. 16, Pl. 6, fig. 27.

\textbf{Diagnosis} Tall, short, \textit{Spathognathodus} with an acutely conical cusp and straight aboral edge, more than half of which is occupied by an elongate lachrymiform escutcheon. Denticles posterior to cusp equal in thickness.

\textbf{Description} The blade is thin and slightly bowed but in lateral view is aborally straight. The cusp is tall, much compressed and sharp-edged anteriorly, and tapers gently except near the apex where the angle between its edges becomes much less acute. Behind the cusp stand eleven compressed denticles fused almost to their tips, all equal in breadth but decreasing gradually in height posteriorly.
The anteriormost of these is only slightly shorter than the cusp. The aboral surface is straight. Below the cusp and in the posterior quarter-length it is narrow and grooved medianly. This groove expands into an elongate lachrymiform escutcheon occupying the remainder of the base. The oral surfaces of the flared edges of the escutcheon are smooth.

**Occurrences**

Upper Limestone, Linn Spout, Dalry.
2" below Arden Limestone, Port Seton.
Upper Limestone, Stacklaw Hill, Stewarton.

**Holotype**


**Remarks**

This species closely resembles *S. cristula* Youngquist & Miller (1949, p. 621, Pl. 101, figs. 1-3) but differs from it in having a straight aboral edge, a shorter escutcheon and a much thinner and less prominent cusp.

Youngquist & Miller (1949) from examination of Smith's figure (1900, Pl. 9, fig. 10) considered that this species was probably closely related to *S. pellaensis*. Smith's figure, however, exaggerates the length of the specimen which is in fact much taller anteriorly than *S. pellaensis* and has a more central escutcheon. Both are straight aborally.

*Spathornathodus minutus* ? Ellison

Plate VIII fig. 1

1941 *Spathodus minutus* Ellison *J. P. 15*
p.120, Pl.20, figs.50-52.

Remarks/
Remarks  The specimen illustrated, although broken, closely resembles *S. minutus* (Ellison 1941, p. 120, Pl. 20, figs. 50-51). The greatest similarity is in the pre-cuspal denticles which are diagnostic of *S. minutus*. At least two denticles are present on the lower anterior edge of the cusp of the specimen figured while *S. minutus* has typically three such denticles.

The occurrence of this specimen in shales above the Skateraw Middle Limestone is somewhat lower than the range given for *S. minutus* (Pennsylvanian) but Ellison remarks (p. 120) that "Spathodids" [*spathognathodids*] are rare in the Pennsylvanian. "Therefore, little is known of their range".

Occurrence  Shales 4 ft. above Skateraw Middle Limestone, Dunbar.

Figd. Specimen  W. J. C. Colln.

*Spathognathodus pusillus* sp. nov.  Plate VIII figs. 2, 3.

Diagnosis  Deep bladed very slender *Spathognathodus* with no prominent cusp and denticles equal in height almost to the posterior end: escutcheon in the middle third of the length.

Description  The blade is deep, very slender, aborally almost
almost straight but tends to curve downwards posteriorly. It bears about 15 compressed denticles fused almost to their tips, almost erect in the anterior half but progressively more inclined posteriorly. The denticles are equal in height to the posterior quarter where the crest line descends rapidly to meet the short vertical posterior end of the blade. The anterior end of the blade is vertical. No denticle is markedly larger than the others but the second of the series tends to be a little broader. The aboral surface is narrow, almost sharp anteriorly and has a median groove which in the middle third of the length is expanded into a moderately deep elongate escutcheon. The flared lips of the escutcheon are orally smooth.

**Occurrence** Shale 2" above Skateraw Middle Limestone, Dunbar.

**Syntypes** W. J. C. Colln.

**Remarks** The depression about the middle of the crest line of the specimen in fig. 2 is not a diagnostic feature. Examination in transmitted light shows evidence of breakage and rejuvenation with suppression of one denticle. This species appears similar to *S. pellaonis Youngquist & Miller* but is deeper and more slender and the escutcheon is nearer the mid-length.

*Spathognathodus scitulus*
Sp pathognathodus scitulus (Hinde)  Plate VIII fig. 4,


Diagnosis  Spathognathodus with a stout, arched and bowed blade; prominent broad-based cusp; about nine denticles; escutcheon asymmetrical, forming a tongue-like projection on the outer side.

Description  The blade is fairly short, stout, strongly arched and gently bowed and bears eight or nine sub-erect to posteriorly inclined denticles, fairly stout and fused almost to their tips. In front of these stands a strong anteriorly compressed sharp-edged cusp the anterior edge of which makes an angle of about 45° with the aboral edge. The aboral edge is narrow and grooved below the cusp. Immediately behind the cusp it flakes out into a large asymmetrical escutcheon the inner border of which forms a long smooth curve. The outer side extends into a large tongue-like process, at right angles to the blade, occupying about two-thirds of the length of the inner side of the escutcheon. Posterior to this tongue the escutcheon tapers gradually and merges with the fairly narrow, slightly concave posterior aboral/
aboral surface. The oral surfaces of the escutcheon lips are smooth.

**Occurrences**
- Upper Limestone, Glencart, Dalry.
- Upper Limestone, Monkcastle Glen, Kilwinning.
- Shale 1" above Index Limestone, Port Seton.
- Shale 6" above Skateraw Middle Limestone, Dunbar.

**Syntype**
- J. S. Colln. H.L.G.S., Edinburgh. S.875

Genus **SUBBRYANTODUS** Branson & Mehl 1934

**Subbryantodus planidorsalis** sp. nov.

**Plate VIII fig. 5.**

**Diagnosis**
Long, moderately thick, closely denticulate bar arched and bowed and aborally excavate: cusp situated about the mid-length.

**Description**
The bar is long, slightly bowed, arched anteriorly but in profile is almost straight posteriorly where it is orally thickened. The posterior part is also slightly twisted so that the posterior denticles are inclined orally inwards. The anterior part of the bar is triangular in cross section, the apex of the triangle being directed orally. The cusp is compressed, sharp-edged and inclined posteriorly as are all the denticles. The denticles are sub-rounded, closely set and fused at their bases. Aborally a/
a long lanceolate escutcheon occupies the whole surface. Anteriorly, the bar is broken.

The specimen is presumed to be only slightly longer anteriorly than posteriorly as is normally the case in this genus and the allied Eryxantodus from which Subbryxantodus is differentiated mainly on the basis of the much larger escutcheon of the latter and the marked lateral thickening of the former.

**Occurrences**

Upper Limestone, Glencart, Dalry. Shales 3' below North Greens Limestone, Bilton Burn, Midlothian. Shales above Skateraw Middle Limestone, Dunbar.

**Holotype**


**Family** GNATHODONTIDAE Branson & Mehl 1944

Elongated platform or trough-like dental units with an anterior blade and broadly excavated aboral surface.

**Genus** CAVUSGNATHUS Harris & Hollingsworth 1933

Stout, elongated platform units with a median trench and anteriorly a very short high blade continuous with the outer parapet of the trench.

* Cavusgnathus inflexs*
Cavusgnathus inflexa sp. nov. Plate VIII figs. 6, 7.

Diagnosis  Cavusgnathus curved inwards anteriorly at the posterior edge of the blade; blade very short and attached to inner anterior side of the largest denticle.

Description  The platform is stout, broad and high and has a sub-central trench throughout, deep anteriorly and bifurcated at the posterior end. Both the outer and inner parapets are ornamented with transverse ridges which tend to become lines of nodes in the middle third-length of the inner parapet. Opposite the blade the inner parapet tends to become smooth. The trench is smooth and is broadest and deepest just behind the large posterior denticle of the blade. The blade is very short and high and forms an anterior extension of the outer parapet. It comprises five denticles the largest of which is posterior and in line with the outer parapet. The remaining four are compressed, fused and laterally inset so as to lie in line with the inner side of the posterior denticle. In profile the anterior end of the blade is rounded and protrudes only slightly beyond the inner parapet.

In lateral view the platform is gently arched orally but is almost straight aborally. The blade is of uniform/
uniform height except for the large broad-based posterior
denticle. The platform sides converge towards the aboral
surface in the anterior and posterior thirds of the specimen
to form anteriorly a sharp edge and posteriorly a narrow,
grooved edge. This groove expands in the middle third to
form a shallow sub-symmetrical lachrymiform escutcheon. The
escutcheon is slightly more expanded on the inner side.

**Occurrences** Lower Limestone, Law, Dalry.
*Posidonia* Band below Top Hogie Limestone, Kilsyth.

**Holotype** J. S. Colln. H.M.G.S., Edinburgh. R.S. 10939.

**Remarks** This species resembles *C. unicornis* Youngquist &
Miller but in *C. inflexa* the median trench is shallower, the
blade shorter and the large posterior denticle more prominent.
In *C. unicornis* the blade is not inset with respect to the
large denticle.

*Cavusgnathus navicula* (Hinde)  
Plate IX figs. 1, 3, & 5.

1900 *Polygnathus navicula* Hinde

1928 *Polygnathus navicula* Holmes

**Diagnosis** Slightly arched and bowed *Cavusgnathus*: median
trench very shallow posteriorly, deep anteriorly; blade
slightly/
slightly offset from outer parapet; blade denticles graduated.

Description

The platform is long, fairly slender and has a median trench which is very shallow in the posterior half-length but deep anteriorly. The ornamentation consists of transverse ridges on each parapet most of which extend almost to the median trench. Opposite the blade the inner parapet is nodose. The blade is stout, fairly short and consists of seven or eight broad-based compressed denticles fused for three-quarters of their height. The largest denticle is posterior and the others grade downwards anteriorly. The posterior end of the blade is offset outwards from the parapet and its anterior edge meets the aboral surface almost at 90°. The aboral surface is sharp anteriorly but the posterior two-thirds are expanded into a fairly shallow sub-symmetrical escutcheon anteriorly rounded and posteriorly pointed. The inner side of the escutcheon is the more expanded and extends laterally beyond the margin of the inner parapet.

Occurrences


Holotype


Remarks

Smith's (1900) badly drawn figure of this specimen.
specimen (Pl. 9, fig. 5) induced Youngquist & Miller (1949) to suggest that this specimen might be referable to Taphrognathus which occurs in older strata than does Cavusgnathus. This species is differentiated from C. inflexa by its shallower trench, longer offset blade and by the graduated blade denticles.

The offsetting of the blade is more marked in the holotype than in most specimens, but in all there is a noticeable outward bulge of the lateral surface at the base of the posterior blade dentine.

Genus GNATHODUS ¹ Pander 1856

Gnathodus carinatus sp. nov. Plate IX figs. 2, 4, & 6.

*Diagnosis* Compound units consisting of a long blade and a short narrow asymmetrical platform with a high denticulate carina.

*Description* The blade is long, slender, deep and slightly bowed and is surmounted by sub-equal, compressed denticles fused almost to their tips. It continues posteriorly across and beyond the platform as a prominent, denticulate carina.

*Note 1.* A commentary on this genus is appended below.

(PP. 118-123)
The platform is narrow and asymmetrical. Orally it has a greater lateral expansion on the inner side, which is parapet-like and bears about seven nodes tending to become in most specimens transverse ridges. Posteriorly it merges with the carina near the posterior end of the latter. The outer side of the platform is a low, narrow nodose ridge the outer wall of which is produced into a laterally directed, flared lip. In profile the platform is gently arched and the aboral edge of the blade slightly convex downwards. The aboral edge of the blade is narrow and has a median groove which below the platform expands into a broad moderately deep asymmetrical escutcheon.

**Occurrences**
- Lower Limestone, Birkhead, Dalry.
- Shales above Bone Bed Limestone, Bilston Burn, Midlothian.
- *Posidonia* Band below Top Hosie Limestone, Kilsyth.
- Shales above Skateraw Middle Limestone, Dunbar.

**Holotype** (figs. 2, 6) J. S. Colln. H.M.G.S. Edinburgh. R.S.10940.

**Field Specimen** (fig. 4) W. J. C. Colln.

**Remarks**
The most diagnostic features of this species are the very high carina, the very narrow platform and the marked inequality of the nodose oral surface on each side of the carina.

*Gnathodus clavatus*
Gnathodus clavatus sp. nov. Plate X figs. 1, 3, & 5.

Diagnosis Compound units with a long, slightly bowed blade, a fairly narrow sub-symmetrical platform and a fairly prominent carina.

Description The blade is long, fairly stout and bowed and increases in height anteriorly. It continues across the platform as a strong moderately high denticulate or nodose carina. The sides of the platform are sub-equal, crenulate or ribbed and merge with the carina at or near its posterior end. The inner wall of the platform is vertical while the outer is orally vertical but aborally flared. In profile the platform is arched and the blade straight aborally. The anterior end of the blade is vertical. The aboral edge of the blade is narrow and grooved and that of the platform occupied by a large asymmetrical escutcheon much expanded on the outer side.

Occurrences Lower Limestone, Law and Birkhead, Dalry. Upper Limestone, Stacklaw Hill, Stewarton.

(Author's colln.) A. 22, 23, 38-42, C. 3, Da. 1, Db. 1, 4-8, E.1, 2, 4-7, 9, F. 6, 7.


Remarks Although poorly represented in the John Smith Collection this species has been found by the author in almost every productive sample collected from the Carboniferous/
Carboniferous Limestone up to the Arden Limestone.

This species closely resembles *G. roundyi* Gunnell 1931 but has a shorter narrower platform and the blade is higher anteriorly. *G. roundyi* occurs in Middle Pennsylvanian strata.

**Gnathodus cruciformis** sp. nov. Plate X figs. 2, 4, & 6.

**Diagnosis** Compound unit with a short bowed blade, a sub-rectangular platform and an extremely large sub-circular escutcheon.

**Description** The blade is short, fairly thin, deep and slightly bowed. The bowing continues into the carina which extends to the posterior of the platform as a stout nodose ridge. The blade denticles are compressed at the anterior end but become progressively more rounded and node-like posteriorly. The platform is approximately rectangular, one diagonal being occupied by the carina. At each end of the other diagonal stands a large node, the nodes being joined to the carina by a transverse ridge which is more prominent on the inner half of the platform. Basally the platform walls are flared to form aborally a large sub-circular escutcheon. The aboral edge of the blade is grooved,
grooved, the groove extending across the escutcheon as a shallow trench. A transverse depression occurs in the escutcheon below the nodes and their connecting ridge.

**Occurrence** Upper Limestone, Glencart, Dalry.

**Holotype** J. S. Colln., H.M.G.S., Edinburgh. R.S.10942.

**Remarks** The specimen figured is of the type considered by Branson & Mehl to represent a primitive stage in the development of *Gnathodus*. It resembles spathognathodids such as *S. commutatus* Branson & Mehl in which the escutcheon is posterior and the blade is without a conspicuous anterior denticle. Its occurrence so high in the succession precludes its being ancestral to gnathodids with a greater platform development but the supposition that *Gnathodus* developed from early forms of *Spathognathodus* via forms such as *G. cruciformis* seems reasonable.

**Gnathodus smithi** sp. nov. Plate XI figs. 1, 3, 5 & 7.


**Diagnosis** *Gnathodus* with a very asymmetrical platform greatly enlarged on the outer side into a low nodose lobe.

**Description**/
Description. The blade is moderately long, deep and bowed, and continues across and beyond the platform as a stout transversely ribbed carina. The blade denticles are large, compressed and fused and highest towards the anterior of the blade. The platform is, on the inner side, high narrow and parapet-like and bears transverse ribs, while on the outer side it is shorter, low and distended into an almost semi-circular lobe ornamented with nodes. These nodes may be irregular but usually tend to have a concentric arrangement. A trench separates the inner parapet from the carina and continues down the anterior edge of the platform separating it from the blade. The inner parapet wall is essentially vertical. In profile the platform is arched and the blade aborally straight. Aborally the blade is narrow and grooved, the groove widening and deepening posteriorly and continuing across the escutcheon as a trench. The escutcheon occupies the whole aboral surface of the platform and the posterior extension of the carina and is deepest anteriorly. The outer part varies from rounded to sub-rectangular in outline, while the inner margin extends a little way at right angles to the blade then continues posteriorly as an undulose line.

Occurrences/
Occurrences
Upper Limestone, Glencart, Dalry.
Upper Limestone, Linn Spout Quarry, Dalry.
Upper Limestone, Monkcastle Glen, Kilwinning.
Castlecarry Limestone and shales, Joppa and Bilston Burn.

Holotype (figs. 1, 3, 5) J. S. Colln., H.M.G.S., Edinburgh. S.870.

Remarks
Included in this species are a number of forms closely similar in configuration but differing in the oral ornamentation of the outer side of the platform. This ornamentation ranges from irregular nodes through more or less arcuate lines of nodes almost to arcuate ridges. There is some variation too in the inner wall of the platform. In most forms it is essentially vertical and straight to slightly waved while in some it is inclined and markedly waved, all gradations between these two being present. There appears to be no correlation between variation in ornament and variation in platform wall and since the known range of this species is extremely short it is considered inadvisable to differentiate other species or sub-species on the basis of these two characters. The extreme of wall undulation is illustrated by the specimen in fig. 7. A close similarity exists between G. smithi and G. postulosus Branson & Mehl, but the latter has a more rectangular outer lobe bearing a definite line of nodes close to the carina; features not present/
present in G. smithi. G. liratus Youngquist & Miller differs from this species in having a platform with a narrower nodose inner side. G. mosquensis Pander has a narrower, less asymmetrical platform.

The genus GNATHODUS has been variously interpreted. Pander's description (1856, p. 33) reads:

"In the marls of the lowest strata of the Mountain Limestone in the Tula and the higher Moscow Governments well-preserved, jaw-like fossils occur; which, by their form and the configuration of their base are distinguished from those so far described but which are closely joined to them by their microscopic structure. On a high thin plate, consisting of double walls, small denticles arise in one row and give it the appearance of being bordered with a denticulate margin. Below at one side [end] these plates diverge strongly and form a cavity while at the opposite [end] they still remain close together. This cavity, which represents the pulp cavity is extended laterally [lengthwise] - Tab. 2a, fig. 10b and provides for each denticle, as would be expected, an ascending continuation."

Pander figures two lateral and an aboral view (Tab. 2a, figs. 10, 10a, 10b). Fig. 10c is an enlargement of a blade fragment.

In Smith's paper (1900) Hinde described Scottish Carboniferous conodonts; among them Polymathus (Gnathodus) mosquensis Pander thus including Gnathodus in Polymathus Hinde/
Hinde 1879, a genus erected to receive a heterogeneous group of diverse conodonts found closely crowded together in a small patch of the Conodont Bed in the Genesee Shale; Hinde considering them to be the remains of one animal.

Bryant (1921) considered that the genus *Polymathus* should be restricted to include only tuberculated and rugose plates similar to those discovered in the type specimen as he considered Hinde's specimen included several genera. He discussed (pp. 22-23) the affinities of *Gnathodus* and described a new species, commenting:

"This genus, transitional between the narrow-based pectinate forms like *Prioniodus* and the broad-based tuberculated tritorial plates of *Polymathus* has hitherto been known by a solitary species described by Pander from the marl in the vicinity of Moscow. It illustrates the progressive adaption of the basal portion of the plate into a grinding tritor. In *Polymathus* this transformation is complete, the pectinate ridge either disappearing or being confined to a crest projecting beyond the tritor.

"A form very close to *Gnathodus mosquensis* occurs in the Conodont bed and I propose to name this species, the first to be discovered in this country, *Gnathodus americanus*.

"For about one half of its length the base expands and curls upward like a withered leaf. Its upper surface bears a number of prominent tubercules. Surmounting the base is a long thin ridge of flat coalesced teeth unequal in height. The cavity beneath the base is centrally located, of the usual lozenge shape and much smaller than in *Gnathodus mosquensis."
Bryant's figure (Plate VII, fig. 5), a lateral view, does not show the aboral surface which is the most diagnostic feature in distinguishing the gnathodids from polygnathids. The upcurled edges of the platform "like a withered leaf" and the lozenge shape of the escutcheon indicate closer affinity to Polynathus than to Gnathodus.

Ulrich & Bassler (1926) failed to formulate a satisfactory definition of Gnathodus although Roundy (1926) found that the genus was abundant in the Barnett shale (Mississippian of Texas) and described a new species G. texanus and a variety bicuspidus (p. 12, Pl. II, figs. 7a-8b and 9a, 9b respectively). He stated that (p. 12): "Gnathodus seems to be essentially a Carboniferous genus".

Holmes (1928, p. 37) referred Hinde's Polynathus dubius (1879, p. 363, Pl. 16, fig. 15) to Gnathodus but Branson & Mehl (1933b, p. 153) consider the specimen to be a Spathognathodus.

Schmidt (1934) extended Gnathodus to include bar and blade forms found in natural assemblage with platform types which he considered were similar to Gnathodus mosquensis. From the figures Schmidt's specimens appear to be non-carinate and suggest reference to Spathognathodus or Idiognathodus. Rhodes/
Rhodes (1952, p. 887) reaches the same conclusion.

Branson & Mehl (1938, p. 144) quote Pander's description and give a revised description:

"Jaw pieces consisting of a thin, straight or slightly curved spathodus-like [spathognathodus-like] blade which at the posterior end is expanded into a more or less hemispherical, thin-walled cup, opening aborally; the blade extending across the oral surface of the cup as a low nodose or denticulate carina that terminates on the cup or a short distance behind it; oral edge of blade sharply crenulate through the growth of laterally compressed, partly fused denticles; oral surface of cup ornamented by nodes that tend to align themselves into ridges which typically radiate from the cup."

They remark that:

"Although the tendency toward radial ornamentation is not evident in all the gnathodids this character and the nearly equal cross diameters of the cup seem to be the most trustworthy means of separating the group from the less typical streptognathodids which they resemble and some of the highly modified spathodids [spathognathodids] which have posteriorly placed, expanded navels and accessory denticles on the expansion at one side of the blade."

They describe (p. 145) and figure two species G. perplexus (Pl. 34, fig. 24) and G. delicatus (Pl. 34, figs. 25, 26, 27).

Ellison (1941, p. 127) stated that Gnathodus differs from Streptognathodus in having a carina usually prominent along the whole length of the platform and in having no accessory lobes on the platform. In addition the ornamentation of Gnathodus may become radial and at the/
the same time the platform becomes sub-circular in outline.

After a long discussion of Gnathodus Youngquist & Downs (1949, pp. 163-5) refer to this genus specimens which cannot be accommodated within the limits of Idiognathodus and Streptognathodus and interpret Gnathodus as having the blade continued across the platform as a nodose or solid ridge to the posterior end and in some cases posteriorly beyond the platform proper. Aborally the platform is broadly excavated and is asymmetrical, one side being much extended laterally. They consider an oral view is usually essential to differentiate Gnathodus, Streptognathodus and Idiognathodus.

Pander's definition and figures are inadequate by the omission from both, of the oral surface of the platform and this has led to subsequent confusion in the interpretation of the genus.

Pander's description is wide enough to include Streptognathodus and Idiognathodus but reference to his figures (Tab. 2a, figs. 10 and 10a), which show a carina higher than the platform edge, indicates that these are distinct genera since Idiognathodus has no carina and the carina of Streptognathodus, situated in the oral trench,
is not visible in lateral view.

The examination of over 200 specimens, all of which are too prominently carinate to be referred to *Streptognathodus* leads the author to agree with the interpretation of *Gnathodus* given by Youngquist & Downs.

**Genus IDIOGNATHODUS Gunnell 1931**

More or less bilaterally symmetrical dental units with a transversely ribbed platform and an anterior blade traceable on to the platform as a suppressed carina. Lateral, nodose, accessory lobes common at the anterior end of the platform.

*Idiothodus linguiformis* sp. nov. Plate XI figs. 2, 4, 6.

**Diagnosis** *Idiothodus* with one accessory lobe on the outer side and two on the inner side; platform arched; blade short and deep.

**Description** The platform is long, arched and transversely ribbed. Anteriorly its ribbed surface narrows and becomes sulcate on each side of the posterior continuation of the blade. At this point accessory lobes are developed, that on/
on the outer side bearing four nodes, while on the inner side one has five nodes and the other, one. The blade is short, highest anteriorly and aborally straight and the platform side-walls are concave. Aborally the blade is narrow and grooved and the platform is broadly excavated to form a large more or less symmetrical escutcheon.

**Occurrence** Skipsey's Marine Band, Craigmark and Motherwell.

**Holotype** W. J. C. Colln.

**Remarks** This species resembles *I. magnificus* Stauffer & Plummer but is more slender and symmetrical and has fewer and smaller accessory lobes.

**Idiognathodus magnificus**? Stauffer & Plummer

Plate XII fig. 1.

1932 *Idiognathodus magnificus* Stauffer & Univ. Texas Bull. 3201, Plummer p. 46, Pl. 4, figs. 8, 18, 20.

**Remarks** A single fragmentary specimen from Skipsey's Marine Band, Craigmark differing from *I. linguiformis* in breadth, ribbing and the greater development of anterior accessory lobes on the platform and resembling *I. magnificus*.

**Idiognathodus spp.**

Plate XII figs. 2, 3.

**Remarks** Two fragmentary specimens referable to *Idiognathodus*.
Idiomathodus were found in the shales of No. 4 Marine Ironstone at Joppa. The specimen in fig. 2 has a long, slender platform typical of early Pennsylvanian species. That in fig. 3 shows marked thickening of all structures and the transverse rugosities of the platform appear to be almost worn away. Thickening and wear together suggest senility of the specimen.

Genus POLYGNATHODELLA Harlton 1933

Compound units with an elongate platform, orally flat or trenches, transversely ribbed and with a blade extending anteriorly from the outer side of the platform: no vertical differentiation at union of blade and platform.

Polygnathodella tenuis sp. nov. Plate XII figs. 4, 6.

Diagnosis Polygnathodellas with an extremely narrow platform trenched throughout the length: blade shorter than the platform, straight and uniform in height.

Description The platform is strongly arched anteriorly, is long, slender and high and has a median trench moderately deep anteriorly but shallowing posteriorly. The parapets bear transverse ridges throughout and the outer parapet is extended.
extended anteriorly as a fairly short, thin, denticulate blade. The blade is of uniform height and is aborally straight. The inner platform wall is slightly concave while the outer wall is vertical except near the base where it is widely flared. The aboral edge of the blade bears a median groove confluent with the large asymmetrical escutcheon which occupies the whole aboral surface of the platform.

**Occurrences** Skipsey's Marine Band, Craigmark, Motherwell, Burnfoot and Palacecraig.

**Holotype** W. J. C. Colln.

**Polysgnathodella spp.**

- Plate XII fig. 5.
- Plate XIII fig. 1.

**Remarks** Most of the specimens of *Polysgnathodella* obtained from Skipsey's Marine Band were *P. tenuis*. Two fragmentary specimens with much broader less deeply trenched platforms were recovered. The specimen in fig. 5 resembles *P. fossata* Branson & Mehl but differs in having a concavity towards the anterior end of the inner side of the platform. The other specimen is relatively longer, straighter and more slender.

**Occurrences** Skipsey's Marine Band, Craigmark (fig. 5) and Burnfoot (fig. 1).

**Genus STREPTOGNATHODUS**/
Genus STREPTOGHATHODUS Stauffer & Plummer 1932

Bilaterally symmetrical compound dental units with an elongate platform medianly trenched. Part or the whole of the length of the trench is occupied by a carina which continues posteriorly from the blade.

Streptogathodus minimus sp. nov. Plate XIII figs. 2, 4, 6.

Diagnosis Very small Streptogathodus with a high slender platform; trench shallow, carinate throughout.

Description The gently arched platform is symmetrical, very slender and has feebly nodose parapets separated by sulci from a low, slightly sinuous carina which runs the whole length of the platform. The blade is short, almost uniform in height, and aborally straight. The side walls of the platform are vertical except at the base where they are slightly flared. Aborally the blade is grooved, the groove expanding into a long, elongate escutcheon occupying the underside of the platform and the posterior end of the blade.

Occurrences Shales of Marine Ironstone 1, 2, 3 and 4, Millstone Grit, Joppa, Midlothian.

Holotype W. J. C. Colln.

Remarks/
Remarks. This species closely resembles S. tenuis Youngquist & Downs in oral aspect but differs in having less arching, deeper platform walls and a more uniform blade. S. delicatulus Youngquist & Heezen has a rather broader posterior termination and a higher blade.

*Streptognathodus parallelus* sp. nov. Plate XIII figs. 3, 5.

Diagnosis. *Streptognathodus* with a high, slender parallel sided platform carinate in the anterior half.

Description. The platform is high, gently arched and slender and has parapets parallel to near the posterior end where they converge rapidly. The median groove is occupied by a low carina which extends about half the length of the platform and then bends outwards to merge with the outer parapet. The blade is slightly longer than the platform, of uniform height and aborally straight. The platform walls are vertical but towards the base flare out to accommodate on the aboral surface a large, elongate, sub-symmetrical escutcheon. Anteriorly the escutcheon merges into the aboral groove of the blade.

Occurrences. Shales in Marine Ironstones 1, 2, 3 and 4, Millstone Grit, Joppa, Midlothian.

Holotype.
Holotype  W. J. C. Colln.

Remarks  This species has affinities to S. symmetricus Youngquist and Heezen but differs from that species in lacking a row of nodes between the carina and the outer parapet.
XI SCOLECODONTS

Introduction

The literature of conodonts contains many examples of confusion between conodonts and scolecodonts. There is a broad similarity of form between the two groups but they differ markedly in detail of form, in colour and in composition. Scolecodonts are hollow, silico-chitinous, highly lustrous, opaque, black or very occasionally dark brown, frequently hook-like and, except for the apices of denticles, have smooth curving outlines. They occur most frequently in shales, but are also found in sandstones, and sporadically in limestones. They are very similar to the jaws of recent polychaetes, having changed only slightly since Silurian times, and so are of little value stratigraphically. Eller (1942b) is of the opinion that they are ecologically significant, their most abundant occurrence in shales paralleling the favoured habitat of present day polychaetes.

A few forms obtained from the base of the Lower Limestone Group are figured for comparison with conodonts.

History

The major contributions on scolecodonts are those of/
of Hinde (1879a and 1882), Eller (1934a & b, 1938 and 1942a) and Stauffer (1933 and 1939). According to Eller (1934a) the first known paper is that of Grinnell (1877, Amer. Jour. Sc., 3rd series, vol. 14). Hinde (1882) attributes the first diagnosis of these fossils as annelid jaws to Angelin, quoting a letter dated June 19th, 1864, from Prof. Angelin to Prof. Lindström at Stockholm. However, this diagnosis was not published.

Figured descriptions of scolecodonts are few and only four specimens from the Scottish Carboniferous have been described. (Hinde 1879a). Most of the specimens described in the literature are from Devonian and earlier formations and little appears to be known of the post-Devonian occurrence of scolecodonts.

**Systematic Descriptions**

Phylum ANNELIDA

Class CHAETOPODA

Sub-Class POLYCHAETA

Genus ARABELLITES Hinde 1879

*Arabellites scoticus*
**Arabellites scoticus** Hinde

**Plate XV fig. 1.**

1879a *Arabellites scoticus* Hinde *Q. J. G. S.*, vol. 35, p. 386, pl. 20, fig. 24.

**Description** The jaw is sickle-shaped, anteriorly rounded and posteriorly truncate. The upper edge bears nine posteriorly inclined denticles set at about 70° to the main plane of the unit the anterior dentine being larger than the others. The edge opposite to that bearing the denticles is extended in the anterior half into a long backward curving spur which has a slight concavity on its anterior margin. The whole unit is slightly concave inwards (orally) and the convex outer surface has a large depressed muscle scar at the junction of the denticulate bar and the posteriorly directed spur. A smaller depression is visible at the base of the first dentine.

**Occurrence** Shales below 1st Abden Limestone, Kinghorn, Fife.

**Arabellites sp.**

**Plate XV fig. 2.**

**Description** The jaw unit is three times longer than deep, is obliquely truncate posteriorly and has anteriorly a stout, hook-like fang inclined inwards from the plane of the main part of the unit. The posterior third of the upper or oral edge is parallel with the base and bears six small sharp denticles/
denticles. The attachment scar is U-shaped, is situated on the outer side and extends forwards from the posterior margin half the length of the row of small denticles.

**Occurrence** 1st Abden Shales, Kinghorn, Fife.

**Genus ILDRAITES Eller 1936**

**Ildraites sp.**

**Plate XV fig. 3.**

**Description** The jaw is long, fairly slender and has a stout curved anterior fang whose apex stands well above the line of the posterior denticles. Immediately posterior to the fang the oral edge is very slightly concave. Posteriorly it bears a series of small denticles and extends beyond the aboral margin. The posterior end is a deep crescent-shaped bight. A rounded muscle scar occupies the outer surface from this bight to below the first of the posterior denticles.

**Occurrences** Shales below 1st Abden Limestone, Kinghorn, Fife.

Shales 2 ft. below North Greens Limestone, Bilston Burn, Midlothian.

**Remarks** Ildraites resembles Arabellites but differs in having a deep posterior bight. This specimen has in addition/
addition a more gently tapered fang and a thinner anterior bar.

Ildraites sp. Plate XV fig. 4.

Description The jaw is approximately triangular and has rounded anterior and posterior ends. The base is extended into a short, broad-based spur. The anterior denticle is fairly large and recurved and is followed by fourteen posteriorly inclined denticles which occupy the upper edge and extend round the posterior end which is bowed outwards. A muscle scar is present at the junction of the spur with the main part of the jaw.

Occurrence Shales below 1st Abden Limestone, Kinghorn, Fife.

Genus LUMBRICONEREITES Ehlers 1868

Lumbriconereites sp. Plate XV fig. 5.

Description The unit comprises a long slightly curved bar with a backwardly directed lateral spur at about its mid-length. The anterior end of the bar is produced into a/
a short, stout, up-curved denticle. A row of small
denticles posteriorly inclined and arranged into a gentle
sigmoid curve occupies the length of the bar which is
posteriorly blunt. The side of the bar opposite to that
with the spur has a narrow lateral flange in the posterior
third of its length.

**Occurrence**  Shales below 1st Abden Limestone, Kinghorn, Fife.

### Lumbriconereites sp.

**Plate XV fig. 6.**

**Description**  The units are curved in two planes and are
approximately triangular. The bar bears anteriorly a short,
stout re-curved denticle followed posteriorly by six to
eight small denticles arranged in a row along one side of
the bar. An up-curved lateral spur occupies the anterior
quarter length of the other side of the bar.

**Occurrences**  Shales below 1st Abden Limestone, Kinghorn, Fife.

Shales 2 ft. below North Greens Limestone, Bilton Burn, Midlothian.

### Nereidavus sp.

**Plate XV fig. 7.**

**Description**  The jaws are long and stout and have a
stout/
stout up-curved anterior denticle not in the same plane as the rest of the unit. A row of minute denticles occupies the posterior third of the oral edge. On the outer lateral edge and extending half the length of the row of denticles is a triangular flange. This flange directed outwards and upwards is characteristic of the genus. It extends very slightly beyond the posterior margin which is obliquely truncate.

**Occurrences**

- Shales below 1st Abden Limestone, Kinghorn, Fife.
- Shales below 2nd Abden Limestone, Kinghorn, Fife.
XII SUMMARY OF RESULTS AND STRATIGRAPHIC CONCLUSIONS

1. Conodonts are rare in the Scottish Carboniferous Limestone but are slightly more abundant in the lower part of the Scottish Millstone Grit.

2. Seventeen genera and 53 species (including one new genus, Dalryvella, and 21 new species) of conodonts are recognised and described.

3. Apart from Gnathodus carinatus, confined to the Lower Limestone Group, and G. smithi, indicative of the upper part of the Upper Limestone Group, conodonts have been found unsuitable for stratigraphic discrimination within the Carboniferous Limestone.

4. Two genera, Idiognathodus and Streptognathodus, diagnostic of the Pennsylvanian of N. America first appear near the horizon of the well-known palaeontological break in the lower part of the Millstone Grit thereby strengthening the evidence for correlating this break with the American Mississippian/Pennsylvanian boundary.
5. The range of *Apatognathus* must be extended from the top of the Devonian to near the top of the Upper Limestone Group.
XIII ACKNOWLEDGEMENTS

The research embodied in this thesis was carried out under the supervision of Professor Arthur Holmes and Dr. G. Y. Craig. To Professor Holmes I am indebted for constructive criticism and helpful suggestions, especially in the preparation of the typescript. I acknowledge guidance from and discussion with Dr. Craig and am most grateful for his encouragement at those times when every sample of a series proved barren of conodonts.

I am under obligation to Dr. F. W. Anderson and Dr. C. J. Stubblefield for their assistance in giving me access to Geological Survey Collections, and also to Dr. Ethel D. Currie of the Hunterian Museum, Glasgow, for providing some samples of Skipsey's Marine Band.
The samples collected and investigated are listed below in descending stratigraphic order for each locality. Those marked with an asterisk (*) contained conodonts. National Grid References are given.

**Locality A**  Bilston Burn, Midlothian.
Grid Reference 1" Sheet 32  275647 to 269649.

1. *Castlecary Limestone roof shale.*
2. *Castlecary Limestone shaley parting*
3. Shale overlying Extra Limestone
4. Shale underlying Extra Limestone
5. Lyoncross Limestone
6. Shale underlying Index Limestone
7-9 Lingula band and shales 2 ft. to 2 ft. 6 ins. above No. 1 Black Band Ironstone.
10. Shale 1 ft. above Johnstone Shell Bed.
11-15 (No. 13*) Bilston Burn Limestone
16,17 Upper and Lower Vexhim Limestones
18-21 (No. 19*) North Greens Limestone
22,23 *Shales 2 and 3 ft. below North Greens Limestone*
24 Sandy shale 20 ft. below North Greens Limestone
25/
25  Sandy limestone 200 ft. above Gilmerton Limestone
26-27 Calcereous shale 20 and 30 ft. below sandy limestone
28  Massive sandstone 10 ft. above Gilmerton Limestone
29-30 Shales 2 ft. above and 2 ft. below Gilmerton Limestone
31  Thin sandstone rib 26 ft. above Bone Bed Limestone
32-36 Shales 25, 15, 10, 5 and 3 ft. above Bone Bed Limestone
37  Shale 9 ins. above Bone Bed Limestone
38-41 Shales 1 to 6 ins. above Bone Bed Limestone
42  Bone Bed Limestone
43  Bilston Burn Bone Bed
44  Shales 6 ins. below Bone Bed

<table>
<thead>
<tr>
<th>Locality B</th>
<th>Kinghorn - Kirkcaldy Shore Section, Fife. Grid Reference 1&quot; Sheet 40 2787</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Roof of 2nd Kininny Limestone</td>
</tr>
<tr>
<td>2</td>
<td>Roof of 1st Kininny Limestone</td>
</tr>
<tr>
<td>3,4</td>
<td>Seafield Tower Limestone (middle and roof)</td>
</tr>
<tr>
<td>5</td>
<td>× 2nd Abden Limestone (roof)</td>
</tr>
<tr>
<td>6</td>
<td>Top of 2nd Abden Shale</td>
</tr>
<tr>
<td>7</td>
<td>× Base of 2nd Abden Shale</td>
</tr>
<tr>
<td>8,9</td>
<td>1st Abden Limestone (middle and roof)</td>
</tr>
<tr>
<td>10</td>
<td></td>
</tr>
</tbody>
</table>
10. Shale 6 ins. above Abden Bone Bed
11. * Abden Bone Bed
12. * Shale 6 ins. below Bone Bed

**Locality C**  
Bathgate, West Lothian.  
Grid Reference 1" Sheet 31  985695

1. Top of Petershill Limestone
2. 3 ft. below top of Petershill Limestone
3. * Shaley parting within Petershill Limestone
4. Shales underlying Petershill Limestone
5. W. Kirkton Limestone (shaley parting)
6. E. Kirkton Limestone (shaley parting)

**Locality D**  
Kilsyth, Stirlingshire
Da Corrie Burn  
Grid Reference 1" Sheet 31  684786

1. * Shale overlying Blackhall Limestone
2. Roof of Blackhall Limestone
3. Shale 6 ft. above Hurlet Limestone
4. * Roof of Hurlet Limestone
5. * Shale 4 ft. below Hurlet Limestone
6. Shale 2 ft. above Coral Limestone
7. Coral Limestone
8. Shale 3 ft. below Coral Limestone

*Denotes Near Burnhead Farm*
Locality Db  Near Burnhead Farm  
Grid Reference 1" Sheet 31  682781

1-3 (No. 1³)  Top Hosie Limestone

1-3  Shale 2 to 3 ins. below Top Hosie Limestone
5  Shale 12 ins. below Top Hosie Limestone  
6  Shale 21 ins. below Top Hosie Limestone
7,8  Posidonia band 22 to 24 ins. below Top Hosie Limestone

Locality Dc  Campsie Glen  
Grid Reference 1" Sheet 30  611800

1  Shale 30 ft. from top of Cementstone Group
2  Shale 32 ft. from top of Cementstone Group

Locality E  Cat Craig, South of Dunbar, East Lothian.  
Grid Reference 1" Sheet 33  716733

1  Shales 8 ft. above Skateraw Middle Limestone
2  Shales 4 ft. above Skateraw Middle Limestone
3  Shales 3 ft. above Skateraw Middle Limestone
4  Shales 2 ft. above Skateraw Middle Limestone
5  Shales 6 ins. above Skateraw Middle Limestone
6  Shales 2 to 3 ins. above Skateraw Middle Limestone
7  Shales immediately overlying Skateraw Middle Limestone
8  Roof of Skateraw Middle Limestone

9/
9. Shaley parting in the Skateraw Middle Limestone
10. Shale immediately below Skateraw Middle Limestone
11. Roof of Long Craig Upper Limestone
12. Shaley parting in Long Craig Upper Limestone
13. Base of Long Craig Upper Limestone

**Locality F** Port Seton Shore Section, E. Lothian
Grid Reference 1" Sheet 33 4176

1. Millstone Grit, base of Upper Marine Bed
2. Shales 7 ft. above Castlecary Limestone
3. Castlecary Limestone
4. Sandy shale underlying Castlecary Limestone
5. Roof of Arden Limestone
6,7. Shale 2 to 4 ins. below Arden Limestone
8. Shale 6 ft. above Extra Limestone
9,10 (No.10*) Roof of Extra Limestone and Extra Limestone
11. Shale 1 in. above Index Limestone
12. Index Limestone
13. Shale 2 ins. below Index Limestone

**Locality G** Joppa Shore Section, Midlothian
Grid Reference 1" Sheet 32 316735 to 320736

1. Millstone Grit Marine Ironstone No. 4 shaley part
2. Shale between Ironstones 3 and 4
3/
3  Millstone Grit Marine Ironstone No. 3 shaley part
4  Millstone Grit Marine Ironstone No. 2 shaley part
5  Millstone Grit Marine Ironstone No. 1 shaley part
6  Black shale 1 ft. above Castlecary Limestone
7  Roof of Castlecary Limestone
8,9,10,11 Three feet of shales within the Castlecary Limestone
12 Shale 3 ins. below Castlecary Limestone
13,14,15 Shales 170, 230 and 250 ft. below Castlecary Limestone

Five samples of Skipsey's Marine Band from Burnfoot, Craigmark, Motherwell (2) and Palacecraig were investigated and found to carry conodonts. Two samples from the Corrie Limestone, Arran, were found to be barren as were two from the Burdiehouse Limestone, one from Limestone No. 2 at Middleton and one from the shales below the Lugar Sill.

John Smith Collection  Principal Localities

Upper Limestone Group
Monkcastle Glen, Kilwinning  1" Sheet 22  291473
Glencart, Dalry  1" Sheet 22  319493
Linn Spout, Dalry  1" Sheet 22  283483
Stacklawhill, Stewarton  1" Sheet 22  371441

Lower/
Lower Limestone Group

Law, Dalry 1

Birkhead, Dalry 1

The Hawthorn Limestone, Glenbuck, Muirkirk, Ayrshire 6

Ponnie Water Douglas; The Ponnie Water crosses several limestone bands and Smith's labels do not indicate from which the specimens were extracted.
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Heezen, Bruce C., (1948, Nov.) Some Pennsylvanian conodonts from Iowa: *Jour. Paleont.*, vol. 22, no. 6, pp. 767-773, pl. 118.


PLATE I

Fig. 1. *Apatognathus geminus* (Hinde) Outer lateral view. R.S.10943 Linn Spout, Dalry.

Fig. 2. *A. geminus* (Hinde) The holotype, oral view. S.891 Glencart, Dalry.

Fig. 3, 4. *A. porcatus* (Hinde) (3) The holotype, S.892 Monkcastle. (4) Aboral view of another specimen. Skateraw Middle Limestone, Dunbar.

Fig. 5. *Euprioniodina angulata* (Hinde) The holotype, inner lateral view. S.885 Glencart, Dalry.

Fig. 6. *Hibbardella brevialata* sp. nov. The holotype, postero-lateral view. R.S.10931 Law, Dalry.

Fig. 7. *H. crai* sp. nov. The holotype, posterior view. S.884 Birkhead, Dalry.

All figures X 25

PLATE II

Fig. 1. *Hindeodella complex* (Hinde) The holotype, inner lateral view. S.890 Glencart, Dalry.

Fig. 2. *H. curta* sp. nov. The holotype. Shales 4 ft. above Skateraw Middle Limestone, Dunbar.

Fig. 3. *H. distorta* sp. nov. The holotype, inner lateral view. R.S.10932 Linn Spout, Dalry.

Fig. 4,5. *H. tenuis* sp. nov. (4) The holotype, outer lateral view. S.894 Birkhead, Dalry. (5) A fragment. S.895.

Fig. 6. *H. sp.* S.880 Monkcastle, Kilwinning.

All figures X 25
Fig. 1-3  *Hindeodella* spp. (1) S.879 and (2) S.878 Monkcastle, Kilwinning. (3) S.893 Birkhead, Dalry.

Fig. 4.  *Ligonodina complectens* sp. nov. The Holotype, inner lateral view. S.882 Law, Dalry.

Fig. 5.  *L. erecta* sp. nov. The holotype, inner lateral view. S.883 Glencart, Dalry.

Fig. 6,7.  *L. peracuta* (Hinde) (6) The holotype. (7) The same in transmitted light. S.887 Law, Dalry.

Fig. 8.  *L. tulensis* (Pander) Inner lateral view. S.881 Glencart, Dalry.

All figures X 25.
Fig. 1. **Ligonodina ultima** sp. nov. The holotype. R.S.10933 Hawthorn Limestone, Muirkirk.

Fig. 2. **L. sp.** North Greens Limestone, Bilston Burn.

Fig. 3. **Prioniodus brevis** sp. nov. The holotype, inner lateral view. R.S.10934 Law, Dalry.

Fig. 4. **P. peracuta** (Hinde) The type specimen, inner lateral view. S.888 Law, Dalry.

Fig. 5,6. **Trichinodella sp.** Lateral and posterior views of a fragmentary specimen.

All figures X 25
Fig. 1,2. *Dalryvella dalryensis* gen. et sp. nov.
(1) Inner lateral view of the holotype.
S.873 Upper Limestone, Dalry.
(2) Outer lateral view of the paratype.
R.S.10935 Monkcastle, Kilwinning.

Fig. 3. *D. convexa* (Hinde) S.872 Monkcastle, Kilwinning.

Fig. 4. *D. robusta* sp. nov. The holotype, inner lateral view. R.S.10936 Law, Dalry.

Fig. 5,6. *D. spp.* Inner lateral views of two specimens. (5) R.S.10937 Monkcastle, Kilwinning. (6) Shale above Skateraw Middle Limestone, Dunbar.

All figures X 25
PLATE VI

Fig. 1. metalonchodina convexa (Hinde) Inner lateral view. S.874 Monkcastle, Kilwinning.

Fig. 2. M. sp. A fragmentary specimen from Skipsey's Marine Band.

Fig. 3. ozarkodina dubia (Hinde) The holotype, inner lateral view. S.867 Birkhead, Dalry.

Fig. 4, 5. O. sp. Skipsey's Marine Band, Motherwell.

All figures X 25
PLATE VII

Fig. 1,2. *Spathognathodus commutatus* Branson & Mehl. Inner lateral and oral views. Skateraw Middle Limestone, Dunbar.

Fig. 3. *S. currieae* sp. nov. The holotype, outer lateral view. Skipsey's Marine Band, Motherwell.

Fig. 4,6. *S. exodentatus* sp. nov. The holotype, outer lateral view and oral view. Shales 6 ins. below Bilston Burn Bone Bed.

Fig. 5. *S. longifossatus* sp. nov. The holotype, inner lateral view. S.876 Linn Spout, Dalry.

All figures X 25
Fig. 1. *Spathognathodus minutus* ? Ellison. Shales 4 ft. above Skateraw Middle Limestone, Dunbar.

Fig. 2, 3. *S. pusillus* sp. nov. Syntypes, outer lateral view. Shales 2 ins. above Skateraw Middle Limestone, Dunbar.

Fig. 4. *S. scitulus* (Hinde). One of the syntypes, outer lateral view. S.875, Glencart, Dalry.

Fig. 5. *Subbryantodus planidorsalis* sp. nov. The holotype, inner lateral view. R.S.10938, Glencart, Dalry.

Fig. 6, 7. *Cavusgnathus inflexa* sp. nov. The holotype, oral and inner lateral views. R.S.10939, Law, Dalry.

All figures X 25
PLATE IX

Figs. 1, 3, 5. *Cavusgnathus navicula* (Hinde).
The holotype, oral, inner lateral and aboral views. S.871 Ponniel Water, Douglas.

Figs. 2, 4, 6. *Gnathodus carinatus* sp. nov.
2, 6. The holotype, oral and outer lateral views. R.S.10940 Birkhead, Dalry.
4. A specimen showing full development of the flared outer lip of the platform wall. Shales above Bilston Burn Bone Bed Limestone.

All figures X 25
PLATE X

Figs. 1,3,5. *Gnathodus clavatus* sp. nov.
The holotype; oral, outer lateral and aboral views.
R.S.10941 Birkhead, Dalry.

Figs. 2,4,6. *G. cruciformis* sp. nov.
The holotype; oral, inner lateral and aboral views.
R.S.10942 Glencart, Dalry.

All figures X 25
PLATE XI

Figs. 1, 3, 5. *Gnathodus smithi* sp. nov.

The holotype; oral, outer lateral and aboral views.

S.870 Monkcastle, Kilwinning.

Fig. 7

*G. smithi*. A specimen illustrating the extreme of undulation of the inner platform wall.

R.S.10945 Glencart, Dalry.

Figs. 2, 4, 6. *Idiognathodus linguiformis* sp. nov.

2, 4. The holotype; oral and outer lateral views.

6. Aboral view of another specimen.

Skipsey's Marine Band, Craigmark.

All figures X 25
PLATE XII

Fig. 1. *Idiognathodus magnificus*? Stauffer & Plummer. Oral view of an incomplete specimen. Skipsey's Marine Band, Craigmark.

Figs. 2, 3. *I. sp*. No. 4 Marine Ironstone, Millstone Grit, Joppa. Fig. 3 is considered to be a senile specimen.

Figs. 4, 6. *Polygnathodella tenuis* sp. nov. The holotype; oral and inner lateral views. Skipsey's Marine Band, Craigmark.

Fig. 5. *P. sp*. An incomplete specimen. Skipsey's Marine Band, Craigmark.

All figures X 25
PLATE XIII

Fig. 1  Polygnathodella sp. Oral view of an incomplete specimen. Skipsey's Marine Band, Burnfoot.

Figs. 2, 4. Streptognathodus minimus sp. nov. 6. The holotype; oral, inner lateral and aboral views. No. 4 Marine Ironstone, Millstone Grit, Joppa.

Figs. 3, 5. S. parallelus sp. nov. The holotype; oral and outer lateral views. No. 1 Marine Ironstone, Millstone Grit, Joppa.

All figures X 25
PLATE XIV

Fig. 1. Cusp of a prioniodid conodont (X 40) showing evidence of repeated breakage and regeneration.

Fig. 2. Tip of (1) much enlarged.

Fig. 3. Hindeodella sp. X 20. Showing inserted peg-like appearance of denticles.

Fig. 4. Blade of Gnathodus sp. (X 40) showing growth lamellae and cone-in-cone structure along each dentine axis.

Fig. 5. Anterior end of (4) much enlarged.

Fig. 6. Posterior end of Lonchodus sp. (X 40) showing regeneration of the last and second last denticles. In the second last dentine the cone axis is offset anteriorly in the regenerated part.

Fig. 7. Ligonodina peracuta (Hinde) X 40. Showing the cone axis passing through cellular areas (dark).

Fig. 8. A bar fragment (X 40) showing an early stage in the regeneration of a broken dentine. The change of slope from the old stump to the growing point is marked.

All figures in transmitted light
Fig. 1. Arabellites scoticus Hindo. Views of attachment side (Upper specimen) and oral side.

Fig. 2. Arabellites sp. Inner lateral view of hooked jaw unit.

Fig. 3. Ildraites sp. Inner and outer lateral views of hooked jaw units.

Fig. 4. Ildraites sp. Attachment side of a triangular type.

Fig. 5. Lumbriconereites sp. Oral aspect of a main jaw unit.

Fig. 6. Lumbriconereites sp. Oral and lateral (upper specimen) views of triangular type.

Fig. 7. Nereidavus sp. Inner (upper specimen) and outer lateral views of hooked jaw units.

All specimens figured are from the shales below the 1st. Abdan Limestone, Kinghorn, Fife.

All figures X 25