LOWER CARBONIFEROUS CONODONT FAUNAS FROM RAVENSTONEDALE, CUMBRIA

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ABSTRACT. Conodont faunas from the Lower Carboniferous, Courceyan–Holkerian Stages, of Ravenstonedale are described. Three zones, the *Taphrognathus*, *Cloghergnathus*, and *Cavusgnathus* Zones, are recognized in the Chadian–Holkerian strata and one fauna, Fauna A, in the mid-Courceyan. These zones and the Fauna are correlated with the standard British Stages and with the American classic sections. The faunas are typical of the shallow water facies of the Lower Carboniferous and are dominated by the genera *Taphrognathus*, *Clydagnathus*, *Cloghergnathus*, and *Cavusgnathus*, which characteristically occur in intertidal and shallow subtidal environments. These shallow-water faunas are joined by deeper-water immigrants only in the Arundian but, even at this level, they are the dominant elements, indicating only a slight water depth increase. The absence of the deeper-water genera *Gnathodus* and *Siphonodella* adds difficulty to the correlation of this succession with goniatite-bearing sequences, but correlation with the Avon Gorge and with shallow-water facies in the north of England is possible. Three species, *Apatognathus asymetricus*, *A. scandalenis*, and *Cloghergnathus carinatus* are proposed as new taxa.

THIS account of the conodont faunas of the Lower Carboniferous succession of Ravenstonedale is a documentation of one aspect of a succession which in recent years has become increasingly important to the stratigraphy of the Carboniferous period as a whole. The special significance of Ravenstonedale is, however, long standing, since it falls within the area designated by Garwood (1913, p. 451) as his type area for the Lower Carboniferous of the north of England. Garwood (1907, 1913) had produced a zonation, based primarily upon corals and brachiopods, which was a complement to the slightly earlier and very influential work of Vaughan (1905) in the Bristol area. Vaughan had designated the Lower Carboniferous as 'Avonian' in view of 'the completeness of the sequence in the Avon section' (1905, p. 264) and had further produced the well-known and much used zonal scheme based, he supposed, upon the evolutionary lineages of corals and brachiopods. Garwood (1913) recognized the great importance of Vaughan's paper and consequently included a correlation of his zones with those of Vaughan (Garwood 1913, p. 452).

This faunal zoning proved to be outstandingly successful. Indeed, in the opinion of Ramsbottom (1973, p. 568) the advance of Carboniferous stratigraphy was for some time ironically hampered by this very fact, since it appears to have induced a period when very little attention was paid to the many other aspects of the Lower Carboniferous sequence, in particular to details of lithology and their interpretation. Vaughan's zonal scheme along with Garwood's correlation for the north of England, was the foundation upon which Dinantian stratigraphy was based for sixty years, until it was superceded by a series of divisions based upon major cycles of deposition (Ramsbottom 1973). These cycles coincide very closely with the six new stages proposed by George, Johnston, Mitchell, Ramsbottom, Sevastopulo, and Wilson (1976) which are designed to be applied throughout Britain.

One consequence of the re-examination of the Dinantian rocks was that Ramsbottom (1973) was able to show that, far from being complete, the Avon Gorge succession contains four major non-sequences, and as a result large parts of the succession of the north of England are not able to be directly correlated with Vaughan's type area or zonal scheme. In addition, other biozonations based upon the Avon Gorge succession must necessarily be as incomplete as the coral/brachiopod zonation. One such scheme is that of Rhodes, Austin, and Druce (1969) in which they established fourteen conodont assemblage zones, the three highest of which were actually based upon the

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north crop of the South Wales coalfield rather than upon the Avon Gorge. Substantial revision of this zonal scheme has, however, since (Austin 1973) been necessary, with the result that whilst the Brigantian (part of three conodont assemblage zones) and Courceyan (six assemblage zones plus a non-sequence) are usefully subdivided, the whole of the interval from just below the top of the Asbian down to a horizon within the Chadian is occupied by the *Cavusgnathus/Apatognathus* assemblage zone, non-sequences, or horizons with no conodonts (see George *et al.* 1976, Table 1).

The present study in Ravenstonedale was initiated in an attempt to provide a Dinantian conodont sequence from an area in which the succession has been demonstrated to be much more complete than that of the Avon Gorge (Ramsbottom 1973, p. 595).

STRATIGRAPHY

At its outset the Carboniferous period presented in the North-west Province a landscape of probably some considerable relief, dominated by rocks of Ordovician and Silurian age. During Dinantian times this landscape was gradually overwhelmed by a major transgression, evidence for which can be seen in the progressive overlap of Carboniferous strata on to Lower Palaeozoic and thereby giving rise to an increasing hiatus at the base of the Carboniferous succession. Complete submergence was not achieved until Asbian times, and as a result, within the North-west Province the local base of the Carboniferous succession varies in age from Courceyan to Asbian.

Deposition of the relatively thick (approx. 1500 m) Dinantian succession of Ravenstonedale began with local subsidence in a region known as the Stainmore Trough or Gulf, which opened to the east and was bounded to the north, west, and south by the positive massifs of the northern Pennines and the Lake District. Subsidence appears to have begun earlier in this trough than elsewhere and to have continued throughout Dinantian times. The Ravenstonedale area thus provides the most complete Dinantian succession within the North-west Province, with what appears to be an almost continuous record of sedimentation from Courceyan to Namurian. Readers are referred to Johnson and Marshall (1971) for further details on the regional setting of the Ravenstonedale area.

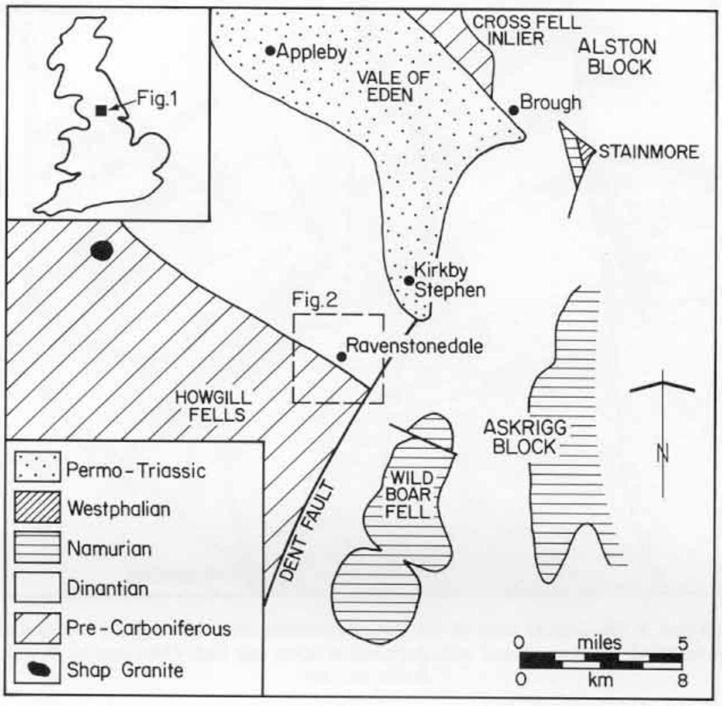
The present outcrop of this succession strikes north-westwards from the Dent Fault near Ravenstonedale, towards Penrith (text-fig. 1) on the southern side of the Vale of Eden. The regional structure is relatively simple, with gentle dips predominantly in a north to north-easterly direction. Natural stream exposure is generally good, and when combined with other natural exposures, road-cuttings, and the numerous small quarries, provides an almost complete record of the succession, except near its base, where much of the detail is obscured by an extensive deposit of glacial drift. The problems associated with the lower part of the succession were amply outlined by Holliday, Neves, and Owens (1979) in their account of a shallow borehole programme undertaken near Ravenstonedale over the period 1975 to 1978.

Working in collaboration with Holliday *et al.* the present authors have recently described the conodont faunas from the exposed part of the Pinskey Gill Beds (Varker and Higgins 1979) which form the lowest unit of the succession. These beds, which lie unconformably upon steeply inclined Silurian Bannisdale Slates and beneath the felspathic conglomerate, were shown by Holliday *et al.* (1976) to be 45–50 m in total thickness, of which only approximately 15 m near the base are exposed. The conodont faunas indicate an age of mid-Courceyan, i.e. late K or Z on the coral/brachiopod scheme, for the base of the Dinantian succession in Ravenstonedale.

The overlying felspathic conglomerate, which is also poorly exposed, was calculated by Johnson and Marshall (1971, p. 267) to be 36·4 m in thickness in Thackthwaite Gill. However, since neither of the boundaries of the horizon are well exposed and Holliday *et al.* (1976, p. 349) have shown them to be gradational with no major breaks in deposition, calculations of thickness can only be approximate. Holliday *et al.* (1976, p. 348) estimated the cumulative thickness from their borehole evidence to be around 42 m and interpreted the felspathic conglomerate as a continental interlude between the marine Pinskey Gill Beds and the overlying marine Stone Gill Beds. Capewell (1955) considered both the Pinskey Gill Beds and the felspathic conglomerate to be the lateral equivalents of the much-thicker basal beds which occur to the north-west, where they reach 274 m in thickness in the Lowther Valley area.

Above the felspathic conglomerate there are the Stone Gill Beds, which consist predominantly of limestone but also include thin (usually less than 1 m) siltstone and shale/mudstone horizons, which are usually calcareous. The lower part of this sequence and its junction with the conglomerate is not exposed but Holliday *et al.*

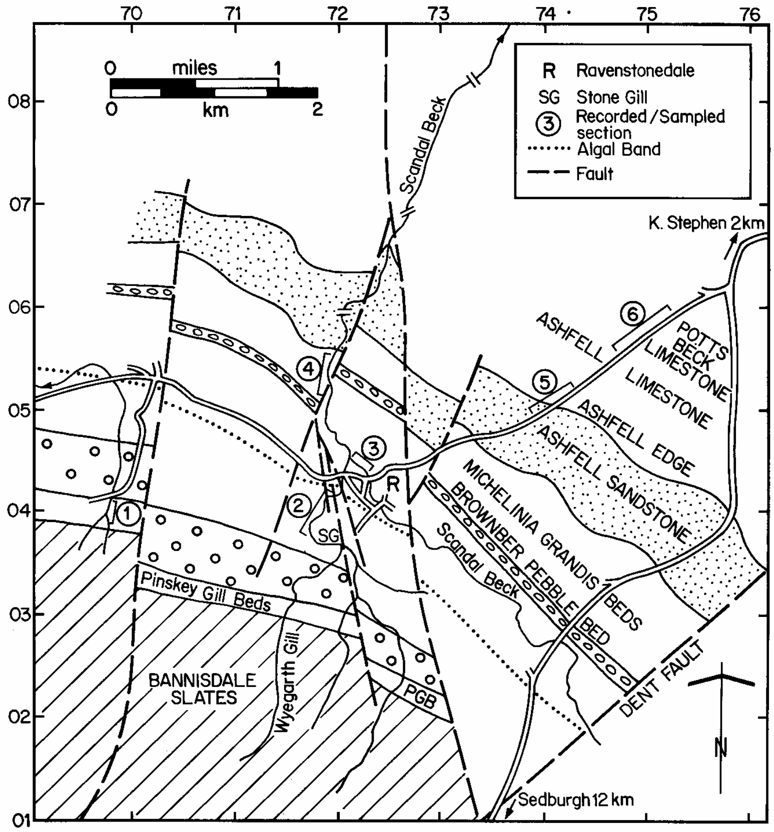
(1976, pp. 349, 350) estimated the thickness of the unexposed beds to be only slightly in excess of 42 m from borehole evidence. Virtually all of the remaining part of the Stone Gill Beds is exposed in Stone Gill itself, where they have been recorded and sampled, at intervals not exceeding 3 m, by the present authors (section 2, text-figs. 2, 3). The sequence includes a great variety of limestone lithologies, although calcite mudstones predominate and large parts of the succession have suffered some dolomitization. This part of the Dinantian succession also includes several of the marker bands described by Garwood (1913), in particular the *Vaughania* Band and the *Palaeechinus* Bed, both of which occur near the base of the exposed succession.



TEXT-FIG. 1. Location of the Ravenstonedale Area.

The overlying Coldbeck Beds begin at the *Spongiostroma* Band of Turner (1950) and extend up to a nodular algal band which outcrops beneath Coldbeck bridge at Ravenstonedale (NY 7209 0435). These beds, which are also predominantly fine grained limestones, may be distinguished from the Stone Gill Beds by their sparser fauna and the occurrence of several nodular algal layers. The algal layer described by Turner (1950) may be one of these, since it appears to be slightly lower stratigraphically than the band taken by Ramsbottom (1974, p. 52) to mark the top of the unit. Exposure of the Coldbeck Beds in Stone Gill is almost complete and once again conodont samples were taken at intervals not exceeding three metres (section 2, figs. 2, 3). It is, however, likely that these samples do not fully represent the Coldbeck sequence since Turner (1950, pp. 30, 35) presented evidence which suggested that approximately 30–35 m of beds had been removed from this stream section by faulting.

The Stone Gill Beds and the Coldbeck Beds were considered by Ramsbottom (1973, p. 574) to represent the transgressive and regressive phases of his first major cycle of the Dinantian, and they were both consequently included in the Courceyan Stage by George *et al.* (1976). An inconsistancy was, however, noted by the latter authors (1976, p. 38) in that foraminifera from the Stone Gill Beds included forms typical of the V_{1a} of Belgium, i.e. Chadian, not Courceyan. Holliday *et al.* (1979, p. 354) considered the then available

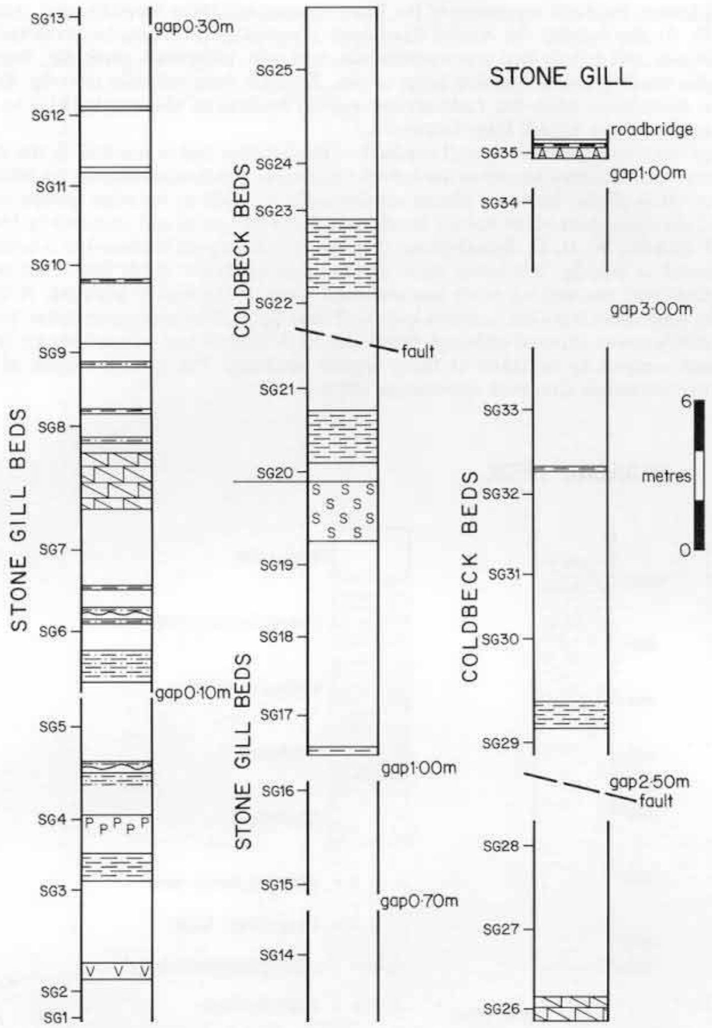


TEXT-FIG. 2. Geological map of the Ravenstonedale area showing the location of the sampled sections (Based with permission upon one inch GEOLOGICAL SURVEY SHEET No. 40)

palaeontological evidence for the position of the Chadian/Courceyan boundary to be inconclusive but concluded on sedimentological grounds that the boundary should be lower than indicated by George *et al.* and placed it, with reservation, high in the felspathic (Shap) conglomerate. On this basis, the whole of the Stone Gill/Coldbeck succession would be of Chadian age.

The succession continues with the Scandal Beck Limestone, which was considered by George *et al.* (1976, p. 38) to represent the whole of the Chadian Stage. These authors placed the top boundary of the unit, and stage, in an unexposed part of the sequence some 15 m below the Brownber Pebble Bed and indicated a total thickness for the unit of approximately 100 m. Johnson and Marshall (1971, p. 265) considered the same interval to be closer to 125 m in thickness. The Scandal Beck Limestone was sampled for conodonts only from approximately 10 m of partly dolomitized bioclastic limestone and calcite mudstone which occur near the base of the unit. It is this sequence which outcrops at the confluence of Stone Gill and Scandal Beck (section 3, text-fig. 2), which is represented in text-fig. 4.

The Brownber Pebble Bed, which forms a useful marker horizon in the region as an approximation for the base of the Arundian Stage, is 4 to 6 m in thickness and consists of calcareous sandstone with quartz pebbles, particularly in its upper part. Above the pebble bed the Arundian succession of Ravenstonedale may be conveniently divided into two parts, the *Michelinia grandis* Beds and the overlying Ashfell Sandstone. There are considerable variations in the published thicknesses attributed to these units. Turner (1950, p. 33) described the *M. grandis* Zone as consisting of 'nearly 150 feet (*c.* 46 m) of well bedded, somewhat iron-stained

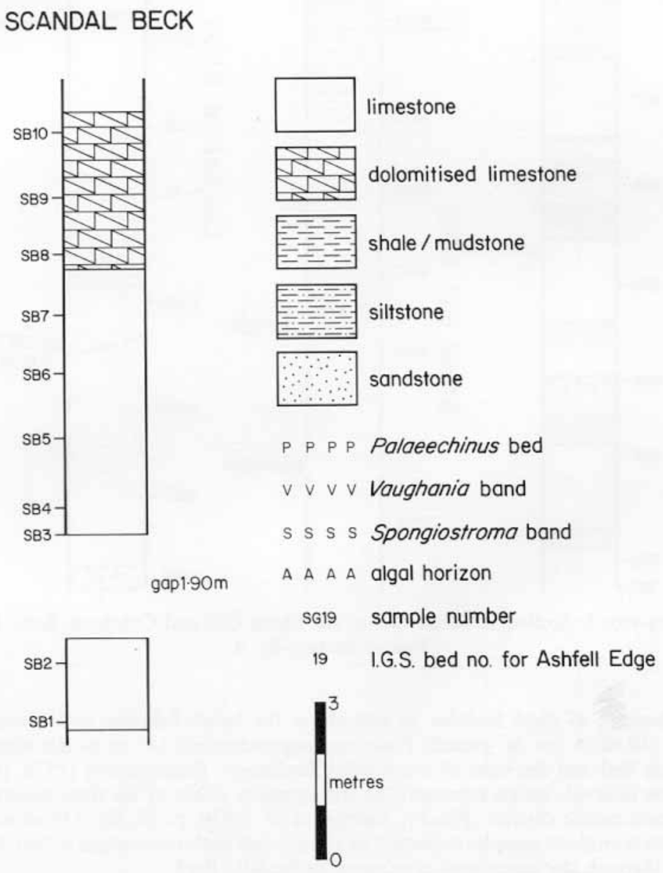


TEXT-FIG. 3. Section in Stone Gill of the Stone Gill and Coldbeck Beds. For legend see text-fig. 4.

limestones with a horizon of chert nodules 30 feet above the base'. Johnson and Marshall (1971, p. 265), however, allocated 110 m to the *M. grandis* Zone and approximately 145 m to the whole interval between the Brownber Pebble Bed and the base of the Ashfell Sandstone. Ramsbottom (1974, p. 55) indicated that the beds of this same interval, which represent the transgressive phase of his third major cycle, reach about 240 m in the Ravenstonedale district. Finally, George *et al.* (1976, p. 38, fig. 11) allocated a thickness of about 130 m. The ten conodont samples collected by the present authors (section 4, text-fig. 2) were collected at regular intervals through the succession as exposed in Scandal Beck.

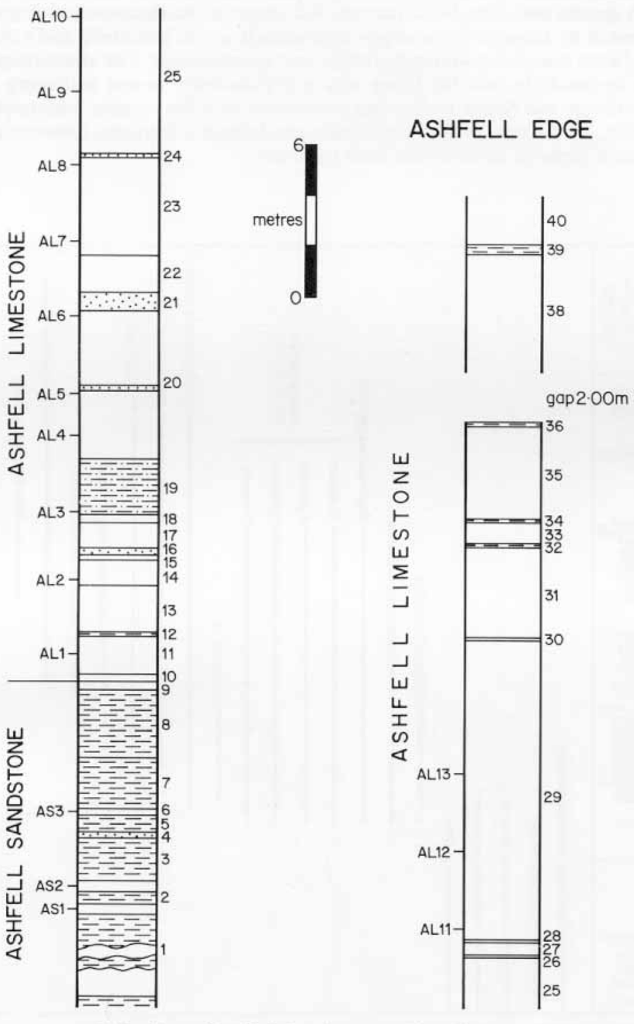
The Ashfell Sandstone is reported to reach 170 m in thickness in the Ravenstonedale area (Ramsbottom 1974, p. 57) but it does thin rapidly southwards. Only the top 13·25 m have been examined in the present study at the well-known roadside exposures of the Ravenstonedale/Kirkby Stephen road, Ashfell Edge (section 5, text-fig. 2). At this locality the Ashfell Sandstone is represented by massive, false-bedded sandstone with slump structures, soft purple and green mudstones, and thin, sometimes lenticular, limestones, several of which are highly fossiliferous, containing large, *in situ*, dendritic coral colonies (text-fig. 5). Turner (1950, p. 34) considered these latter beds, the *Lithostrotion martini* horizon of Garwood (1913) to be confined to the immediate vicinity of the Ashfell Edge locality.

The Arundian/Holkerian boundary is well exposed at this locality and is marked by the incoming of the predominantly limestone sequence known as the Ashfell Limestone, which represents the whole of the Holkerian Stage. The lowest 60 m of this unit was almost continuously exposed in the road section on Ashfell Edge where, along with the upper part of the Ashfell Sandstone, it was measured and recorded by Dr. I. C. Burgess, Mr. M. Mitchell, and Dr. W. H. C. Ramsbottom (Institute of Geological Sciences) in September 1972. The sequence represented in text-fig. 5 is based upon their measured section (with their kind permission), but unfortunately recent civil engineering work has obscured some of the higher horizons. A total of thirteen conodont samples were taken from the horizons indicated (text-fig. 5). The upper part of the Ashfell Limestone sequence is not continuously exposed although exposures, both natural and in quarries, are frequent enough to allow conodont samples to be taken at fairly regular intervals. The total thickness of the Holkerian succession on Ravenstonedale Common approaches 200 m.



TEXT-FIG. 4. Section of Scandal Beck Limestones seen in Scandal Beck and Legend for text-figs. 3–5.

The Asbian Stage is represented in this region by two main divisions, the Potts Beck Limestone (new name George *et al.* 1976, p. 40) and the overlying Knipe Scar Limestone. Only the Potts Beck Limestone has been sampled for conodonts in the present study, from a series of quarries on the north-west side of the Ravenstonedale/Kirkby Stephen road (section 6, text-fig. 2). According to George *et al.* (1976) this limestone is only found in the Stainmore Trough around Kirkby Stephen, in the I.G.S. Borehole at Raydale, and in the River Clough near Sedbergh. Elsewhere there is a considerable non-sequence between the Holkerian and Asbian. The Potts Beck Limestone forms the youngest stratigraphic horizon in this conodont study and was the only limestone which did not yield faunas.



TEXT-FIG. 5. Section of Ashfell Sandstone and Ashfell Limestone seen in road cutting at Ashfell Edge.

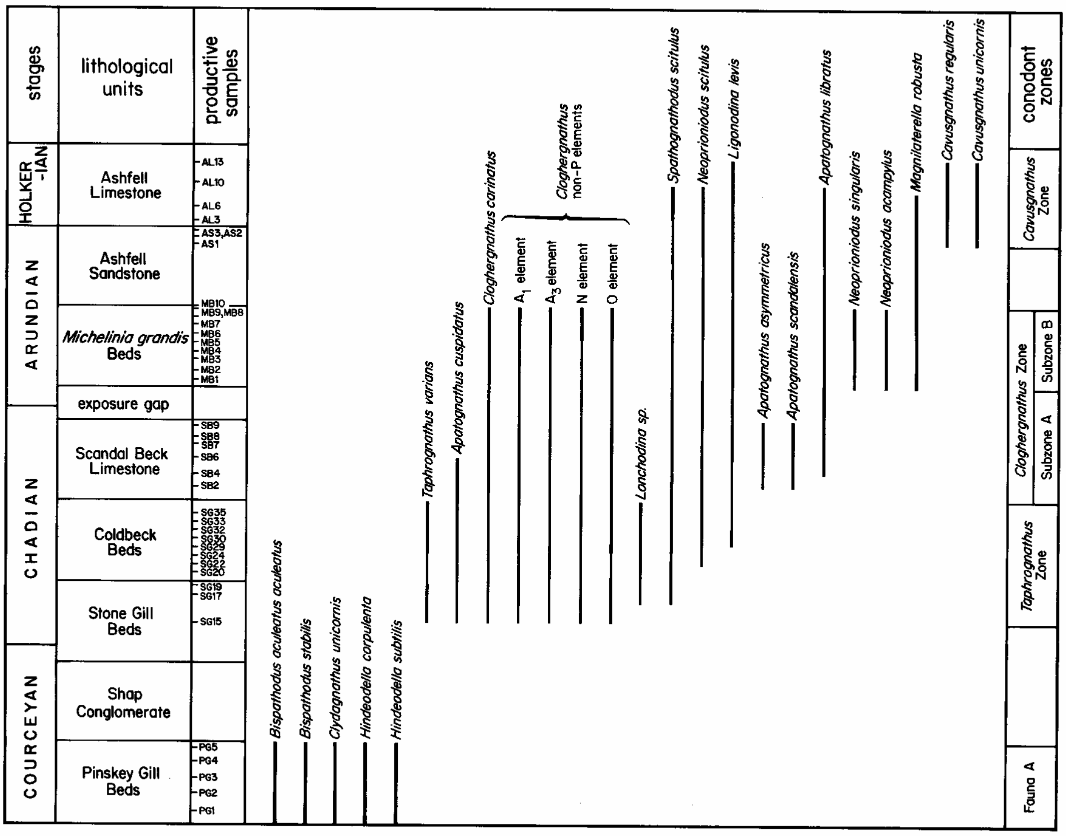
CONODONT FAUNAS

A sequence of four conodont faunas is recognizable in the Ravenstonedale succession. However, because the element ranges of the lowest fauna are incompletely known this is not named as a formal zone. The upper three zones are from an almost completely exposed and continuous sequence and are named and defined with a greater degree of certainty (see text-fig. 6).

Fauna A

The elements of Fauna A have recently been described by Varker and Higgins (1979). They occur in the outcrop section of Pinskey Gill and a series of dolomites and dolomitic limestones in the Pinskey Gill Borehole at depths between 33 and 36 m. The fauna probably typifies the whole of the Pinskey Gill Beds, but is so impoverished in both species and abundance that the full range of the elements is not known.

The fauna is dominated by ***Bispathodus aculeatus aculeatus*** (Branson and Mehl) and ***Clydagnathus unicornis*** Rhodes, Austin and Druce together with hindeodellids and ozarkodinids. The association of these forms led Varker and Higgins to conclude that the fauna was mid-Courceyan in age belonging to late K or early Z Zones of the Avon Gorge and South Wales, and correlating with the ***costatus costatus/Gnathodus delicatus*** Zone of Rhodes, Austin, and Druce (1969). Sevastopulo and Johnston (personal communication) would place the fauna firmly in the Z-Zone in terms of the Irish sequence.



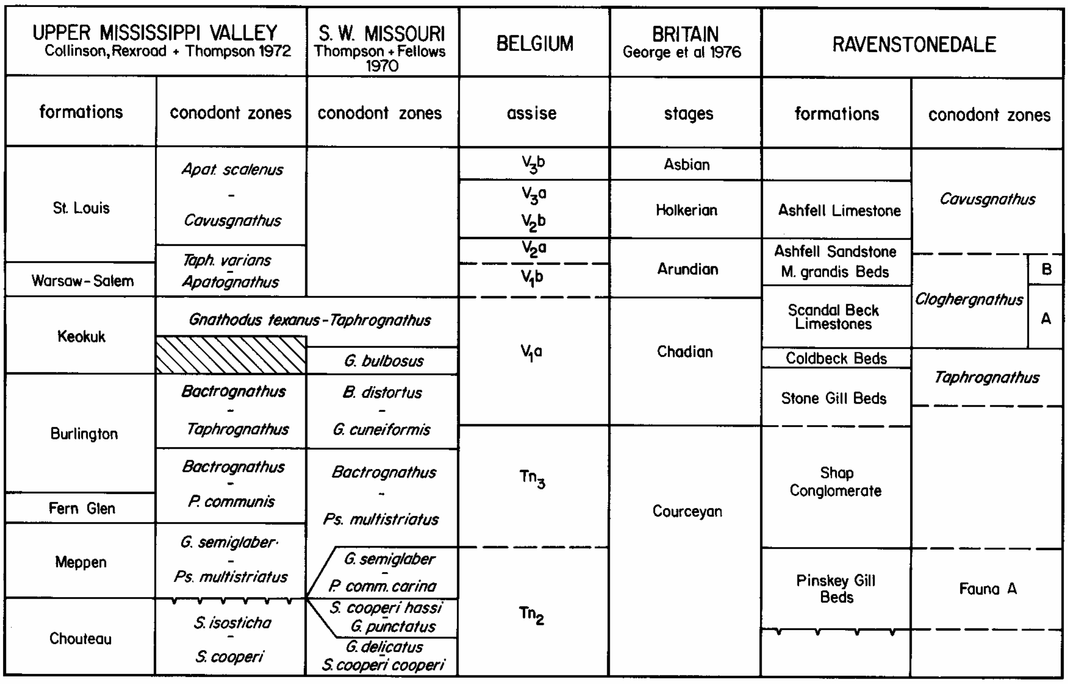
TEXT-FIG. 6. Stratigraphical ranges of conodont species in the Lower Carboniferous of the Ravenstonedale area.

Taphrognathus Zone

This is a partial range zone occurring in the upper part of the Stone Gill Beds and in the Coldbeck Beds. The Shap Conglomerate sequence above the Pinskey Gill Beds and the lowest part of the Stone Gill Beds do not contain conodonts. Faunas first appear some 40 m above the base of the exposed section in Stone Gill and continue up to the top of the Coldbeck Beds at Coldbeck Bridge.

The fauna remains impoverished in species, but is somewhat richer in abundance than that of the Pinskey Gill Beds. It is characterized by *Taphrognathus varians* Branson and Mehl, *Cloghergnathus carinatus* sp. nov., *Spathognathodus scitulus* (Hinde), *Apatognathus cuspidatus* Varker, and a variety of non-platform elements. *T. varians* is probably the best-known species for it has a very wide distribution. In the Upper Mississippi Valley and Missouri (Collinson, Rexroad, and Thompson 1972) it characterizes the middle part of the Valmeyeran Series (Upper Osage/Lower Meramec) ranging from the Keokuk to the lower part of the Upper St. Louis Formations. It is also known from Australia (Jenkins 1974) in strata which Jenkins concluded were of early Viséan age. *Taphrognathus* has also been recorded from Britain in the Main Algal Limestone of Roxburghshire (Rhodes *et al.* 1969), where it is of early Viséan age. Finally it occurs in Ireland (Austin and Mitchell 1975) again in the early Viséan. *Cloghergnathus* also occurs with *Taphrognathus* in Ireland as does *Spathognathodus scitulus*. *S. scitulus* is characteristic of the St. Louis Formation, Upper Valmeyeran in the Upper Mississippi Valley, where it overlaps the range of *Taphrognathus* although the closely related species *S. coalescens* occurs earlier and coexists with the greater part of the range of *Taphrognathus* (fig. 7).

The *Taphrognathus* Zone correlates broadly with the *Bactrognathus-Taphrognathus* Zone which occurs in the upper part of the Burlington Formation of the Upper Mississippi Valley. In Europe this fauna is uncommon but does occur in Ireland (Austin and Mitchell 1975) with the characteristic early Viséan *Mestognathus beckmani* and it was given a lower Viséan age. George *et al.* (1976) referred the Stone Gill Beds and the Coldbeck Beds to the late Courceyan, but the presence of V_{1a} foraminifera (Ramsbottom 1977) clearly indicates an early Viséan age for these sediments, and they are now referred to the Chadian (Ramsbottom 1977).



TEXT-FIG. 7. Correlation of the Ravenstonedale conodont and sedimentary sequence with the Belgian Assises and the North American conodont sequences.

Taphrognathus sp. also occurs in the Lower Windsor Group of Nova Scotia (von Bitter 1976) although its occurrence with *Cavusgnathus* spp. probably indicates a younger age than the *Taphrognathus* Zone of Ravenstonedale.

Cloghergnathus Zone

This assemblage zone occurs in the Scandal Beck Limestone and the *Michelinia grandis* Beds. Every sample has yielded a fauna although none of them are abundant.

The characteristic species present are *Cloghergnathus carinatus*, *Spathognathodus scitulus*, *Apatognathus asymmetricus*, and *A. scandalensis*. The appearance of *Magnilaterella robusta* and *Neoprioniodus singularis* at the base of the *Michelinia grandis* Beds allows the subdivision of this zone into two subzones: a lower one with *Cloghergnathus*, *Apatognathus asymmetricus*, and *A. scandalensis*, and an upper one with *Neoprioniodus singularis* and *Magnilaterella robusta*. Both of the latter species are known to have longer ranges elsewhere and their appearance within the zone may well be due to environmental change at the base of the *Michelinia grandis* Beds. The fauna of the zone is not distinctive and is merely an interregnum between the disappearance of *Taphrognathus* and the appearance of *Cavusgnathus*.

This interval compares closely to the *Taphrognathus varians–Apatognathus* interval in the Upper Mississippi Valley (Collinson *et al.* 1972) which occupies the Warsaw, Salem, and lower St. Louis Formations. In Ireland (Austin and Mitchell 1975) there is a broad zone between the top of the Lower Carboniferous Shale (C_2S_1) with *T. varians*, and the upper Calp Limestone (D_1), with *Cavusgnathus* sp., of which the lower part would correspond to the *Cloghergnathus* Zone.

George *et al.* (1976) dated the Scandal Beck Limestone (Subzone A) as Chadian and the *Michelinia grandis* Beds (Subzone B) as Arundian. According to George *et al.* (1976) this part of the sequence is largely missing in the Avon Gorge or is represented by non-conodont bearing strata (Austin 1973).

Cavusgnathus Zone

The Cavusgnathus Zone includes the highest beds of the Ashfell Sandstone and at least the lowest beds of the Ashfell Limestone. The fauna includes *Cavusgnathus regularis* and *C. unicornis*, *Neoprioniodus scitulus*, *Spathognathodus scitulus*, *Magnilaterella robusta*, and *Apatognathus libratus*.

This fauna correlates with that of the *Apatognathus scalenus–Cavusgnathus* Zone of the Upper Mississippi Valley (Collinson *et al.* 1972) which occurs in the Upper St. Louis Formation. However, as Austin (in Austin and Mitchell 1975) has pointed out, there is a breccia between the Upper and Lower St. Louis Formation with some condensation of faunas. This may account for the absence of the major gap between the disappearance of *Taphrognathus* and the appearance of *Cavusgnathus* which occurs in the Ravenstonedale sequence. This zone compares well with the lower part of the *Cavusgnathus–Apatognathus* Zone of the Avon Gorge (Austin 1973) (text-fig. 8).

The Ashfell Sandstone is included in the upper part of the Arundian and the Ashfell Limestone in the Holkerian by George *et al.* (1976).

Influence of environment on the conodont faunas

The influence of the depositional environment on the conodont animal in the Palaeozoic generally is readily apparent from a perusal of the symposium volume on conodont palaeoecology (Barnes 1976), and in the Lower Carboniferous in particular from the work of Austin (1976) and von Bitter (1976). There is a clear distinction between extremely shallow-water faunas seen in the Windsor Group of Nova Scotia (Globensky 1967; von Bitter 1976) and Ravenstonedale and the basinal faunas of the same age in Spain (Higgins and Wagner Gentis, in press) and in Germany (Bischoff 1957; Voges 1959). Other faunas show mixing of both shallow-water and basinal types, and Austin (1976) has attempted to show typical associations of this type. Although these differences are normally ascribed to a depth control on the conodont animal, there may be also an element of provincialism as suggested by Austin (1976), for the type of fauna seen in Ravenstonedale appears to have a restricted geographical distribution. In view of the growing evidence of environmental control of the conodont animal it is important to know whether the faunal changes in the Ravenstonedale sequence reflect evolutionary or environmental changes, or both.

Clydagnathus, occurring in dolomites and dolomitic limestones in Pinskey Gill is, according to Austin (1976), found in dolomites and oolites in littoral/deltaic and offshore neritic facies only,

STAGES George et al 1976	AVON GORGE: George et al 1976, Kellaway & Welch 1955	AVON GORGE: Rhodes, Austin & Druce 1969, Austin 1973	RAVENSTONEDALE conodont zones this paper	
Holkerian	Upper Clifton Down Limestone	*Cavusgnathus* - *Apatognathus*	*Cavusgnathus*	
Holkerian	(hatched)	(hatched)	*Cavusgnathus*	
Arundian	Lower Clifton Down Limestone	*Cavusgnathus* - *Apatognathus*	*Cavusgnathus*	
Arundian	Upper Clifton Down Mudstone	no conodonts	*Cloghergnathus*	B
Arundian	Goblin Coombe Oolite	no conodonts	*Cloghergnathus*	B
	(hatched)	(hatched)	*Cloghergnathus*	B
Chadian	Lower Clifton Down Mudstone	no conodonts	*Cloghergnathus*	A
Chadian	Gully Oolite	*Mestognathus beckmanni* -	*Cloghergnathus*	A
Chadian	Sub-Oolite Bed	*Polygnathus bischoffi*	*Cloghergnathus*	A
Chadian	(hatched)	(hatched)	*Taphrognathus*	
Courceyan	Black Rock Limestone	*G. antetexanus* *P. lacinatus*		
Courceyan	Black Rock Limestone	*P. lacinatus* - *Ps. longiposticus*		
Courceyan	Black Rock Limestone	*Bispathodus costatus costatus* - *G. delicatus*	Fauna A	
Courceyan	Lower Limestone Shale	poor exposure *S. cf robustus* *B. aculeatus*		
Courceyan	Lower Limestone Shale	*Siphonodella* - *P. inornatus*		
Courceyan	Shirehampton Beds	*Pa. variabilis* - *P. inornatus*		

TEXT-FIG. 8. Comparison of the conodont zonation of Ravenstonedale with that of the Avon Gorge.

and is typically supratidal. Sandberg (1976), in his study of late Devonian biofacies, concluded that *Clydagnathus* is abundant in offshore banks and lagoons of shallow brackish to normally saline banks commonly occurring with algae.

Taphrognathus, according to Austin has a similar distribution to that of *Clydagnathus*, and von Bitter (1976) came to a similar conclusion in relating *Taphrognathus* to his Biofacies II which occurred in inner shelf and reefoid environments.

Apatognathus and *Spathognathodus scitulus* generally occur together and were suggested by Austin (1976) to be an association which occurred in the littoral/delta front, offshore neritic, and back reef lagoonal facies. Von Bitter grouped these two with his Biofacies II association.

Cavusgnathus has a similar shallow-water origin to *Taphrognathus* according to Austin (1976), von Bitter (1972, 1976), and Merrill and Martin (1976).

Cloghergnathus is a relatively new genus and its distribution is poorly known, but it does occur in the Windsor Group of Nova Scotia (Globensky 1967; von Bitter 1976) where it would probably be placed in von Bitter's biofacies II, and it also occurs in Ireland (Austin and Mitchell 1975) where it occurs in association with *Taphrognathus*.

The majority of the platform conodonts in these faunas are asymmetric: *Clydagnathus unicornis* and all species of *Cavusgnathus* are right-sided whereas *Cloghergnathus carinatus* is both left and right sided and *Taphrognathus varians* often shows a tendency towards asymmetry. The asymmetry appears to be associated with shallow-water environments, but is not restricted to these environments. *Cavusgnathus*, for example, may occur in basinal environments (Higgins 1975), and so may *Apatognathus* but in small numbers only. They are only dominant in shallow-water faunas. Similarly, the basinal faunas of this age, dominated by the symmetrical or highly ornamented platform elements, may occur on the margins of the shallow-water zones mixed with asymmetric elements. Von Bitter recorded the presence of simple gnathodids in his biofacies II, and more complex gnathodids occur with cavusgnathids and apatognathids in his deep-water biofacies III. In the Ravenstonedale sequence such mixing occurs rarely, indicating the extreme shallowness of the water. *Neoprioniodus singularis*, which is a common basinal species, occurs as an uncommon component of the *Michelinia grandis* Beds but its origin is known to be earlier in basinal sequences and it must be regarded as a deeper-water immigrant into a dominantly shallow-water environment.

Thus *Clydagnathus*, *Cloghergnathus*, *Taphrognathus*, *Cavusgnathus*, and *Apatognathus* are environmentally controlled to a high degree, occurring typically in littoral and lagoonal facies but ranging into offshore infratidal facies. The faunas in which they occur are restricted in both variety and abundance. Their persistent occurrence throughout the Ravenstonedale sequence is a reflection of the persistence of this facies in the area, and has enabled us to study the development of these unusual faunas through a long sequence. The proposed zones, although fundamentally environmentally controlled, are of biostratigraphic usage within this type of environment.

Neoprioniodus singularis, on the other hand, is clearly of only local value as a stratigraphic marker and merely reflects the major transgression which occurred at the base of the *Michelinia grandis* Beds (see also Leeder in discussion of George 1978) and brought with it immigrant faunas into the area.

In broad outline the changes in the conodont faunas occur both at stage boundaries and at the cycle boundaries of Ramsbottom (1973, 1977), although the two do not exactly coincide. The boundary between the *Taphrognathus–Cloghergnathus* Zones is coincident with the algal horizon at the top of the Coldbeck Beds which, according to Ramsbottom (1973, 1977), is the boundary between two cycles. Similarly the boundary between Subzones A and B of the *Cloghergnathus* Zone coincides with the Chadian–Arundian boundary although the exact horizon of the boundary is thought to be unexposed (George *et al.* 1976). The beginning of the *Cavusgnathus* Zone coincides with the appearance of the first limestone above the sandstone beds of the Ashfell Sandstone. These occur in a few metres of shales immediately below the base of the Ashfell Limestone which is taken as the boundary between the Arundian and Holkerian Stages, and the boundary between cycles 3 and 4 of Ramsbottom (1973).

With the exception of the Subzone B fauna, all the conodont faunas are of a shallow-water type and they occur throughout the cycles in the Chadian, through the lower part of the Arundian, and reappear at the top of the Arundian. The general distribution of the faunas supports the attribution of the beds to the stages of George *et al.* (1976), but the similarity between the faunas is probably due to the position of the Ravenstonedale area during Lower Carboniferous times at the head of a shallow gulf where a change of sea level to bring in sandstone or algal horizons led to the absence of conodonts rather than a change in the type of fauna.

SYSTEMATIC DESCRIPTIONS

All type and figured material has been lodged in the micropalaeontological collection, Department of Geology, University of Sheffield.

Genus *Apatognathus* Branson and Mehl

Type species. Apatognathus varians Branson and Mehl, 1934

Apatognathus asymmetricus sp. nov.

Plate 19, figs. 7, 9

Holotype. Pl. 19, fig. 7. R21.

Horizon. Scandal Beck Limestone, sample SB9.

Diagnosis. Anterior process, laterally thickened, half the height of the posterior process which is thin. Denticles on posterior process fused and twice the height of those on the anterior process.

Description. Processes unequal, diverging at about 40°. Strongly inwardly curved. Anterior process low, laterally thickened with a shelf on the upper edge, and maintaining its height to the extremity. Up to ten denticles on the oral surface whose inclination increases towards the cusp. The denticles are small, laterally compressed, and are incurved. They are discrete for about half their length.

Posterior process thin, but high, up to twice the height of the anterior process and the inner face is strongly convex. The denticles are twice as high as those of the anterior process and are fused for most of their length. They are strongly laterally compressed and decrease in height towards the extremity of the process. The denticles are slightly incurved.

Cusp is twice the height and width of the posterior bar denticles. The adjacent posterior bar denticle is fused to its posterior edge, but it is largely free on its anterior edge due to the small size of the anterior process denticles.

The cavity is triangular and is situated on the inner face of unit below the cusp. The processes are grooved on the aboral side.

Comparison. This species most closely resembles *Apatognathus cuspidatus* from which it differs in lacking lateral thickening on the posterior process and having more strongly fused denticles. It differs from *A. scandalensis* in having lateral thickening on the anterior process.

Apatognathus libratus Varker

Plate 19, fig. 12

1967 *Apatognathus? libratus* Varker pp. 134, 135, pl. 18 figs. 3, 6, 8, 9, 12, 13.

Remarks. This is an extremely large specimen, but its major characteristics conform to the diagnosis of *Apatognathus libratus*. The main difference lies in the width of the process beneath the cusp which is twice as broad as in other figured specimens of this species.

Apatognathus scandalensis sp. nov.

Plate 19, fig. 10

Holotype. Pl. 19, fig. 10, R18.

Horizon. Scandal Beck Limestone, sample SB8.

Diagnosis. A wide angled, almost symmetric, *Apatognathus* with thin processes and denticles on the anterior process which are highest near, but not at, the cusp. The denticles on the anterior process are twice the height of those on the posterior process.

Description. The processes diverge at about 50° and are strongly inwardly curved. The unit is slender and thickening of the processes only occurs close to the cusp, where a slight shelf is formed.

The anterior limb is slightly longer than the posterior and is strongly curved inwardly. It is higher than the posterior limb and bears up to thirteen laterally compressed denticles which rise to a point about one-third from the cusp. The denticles are sharply pointed and are flatter on the outer than the inner side and are discrete for more than half their length. The posterior process is about two-thirds the length of the anterior process and is inwardly curved about the same amount. Only slight thickening occurs near the cusp. Up to ten denticles occur on its oral surface and these are only half the height of the largest anterior process denticles and are subequal.

The cusp is twice the height and width of the largest denticle on the processes, and is laterally compressed more strongly on the outer than the inner side. It is discrete for more than half its length and is sharply pointed. It is slightly curved inwards.

A shallow triangular pit occurs at the base of the cusp and is situated on the inner face rather than aborally. It is continued along the processes as barely discernible grooves.

Comparison. Apatognathus scandalensis most closely resembles *A. cuspidatus* but differs in having a less strongly inclined and a smaller cusp and a larger angle between the processes.

Genus *Cavusgnathus* Harris and Hollingworth, 1933

Type species. Cavusgnathus altus Harris and Hollingworth, 1933

Cavusgnathus regularis Youngquist and Miller

Plate 18, figs. 12, 13

1949 *Cavusgnathus regularis* Youngquist and Miller, p. 169, pl. 101, figs. 24, 25.

Remarks. The generally short and compact form and the regular denticulation of the blade of this species are present in the Ravenstonedale specimens, but there are some differences from previously described examples. The principal difference is the length of the fixed blade which extends up to half the length of the platform and is larger than that normally found on specimens of this species.

EXPLANATION OF PLATE 18

All figures ×60

Figs. 1-11. *Cloghergnathus carinatus.* P. element. 1, oral view of specimen from the Stone Gill Beds, sample SG19, specimen R29, transitional to *Taphrognathus varians.* 2, 7, oral and outer lateral views of holotype, specimen from the Scandal Beck Limestone, sample SB2, specimen R30. 3, inner lateral view of a specimen from the Stone Gill Beds, sample SG19, specimen R32. 4, oral view of a young specimen from the Coldbeck Beds, sample SG32, specimen R31. 5, outer lateral view of a young specimen from the *Michelinia grandis* Beds, sample MB10, specimen R35. 6, 10, outer lateral and oral views of a specimen from the Scandal Beck Limestone, sample SB9, specimen R33. 8, 9, 11, aboral, outer lateral and oral views of a specimen from the Coldbeck Beds, sample SG32, specimen R34, specimen transitional to *Taphrognathus varians.*

Figs. 12, 13. *Cavusgnathus regularis.* Oral and inner lateral views of a specimen from the Ashfell Sandstone, sample AS1, specimen R36.

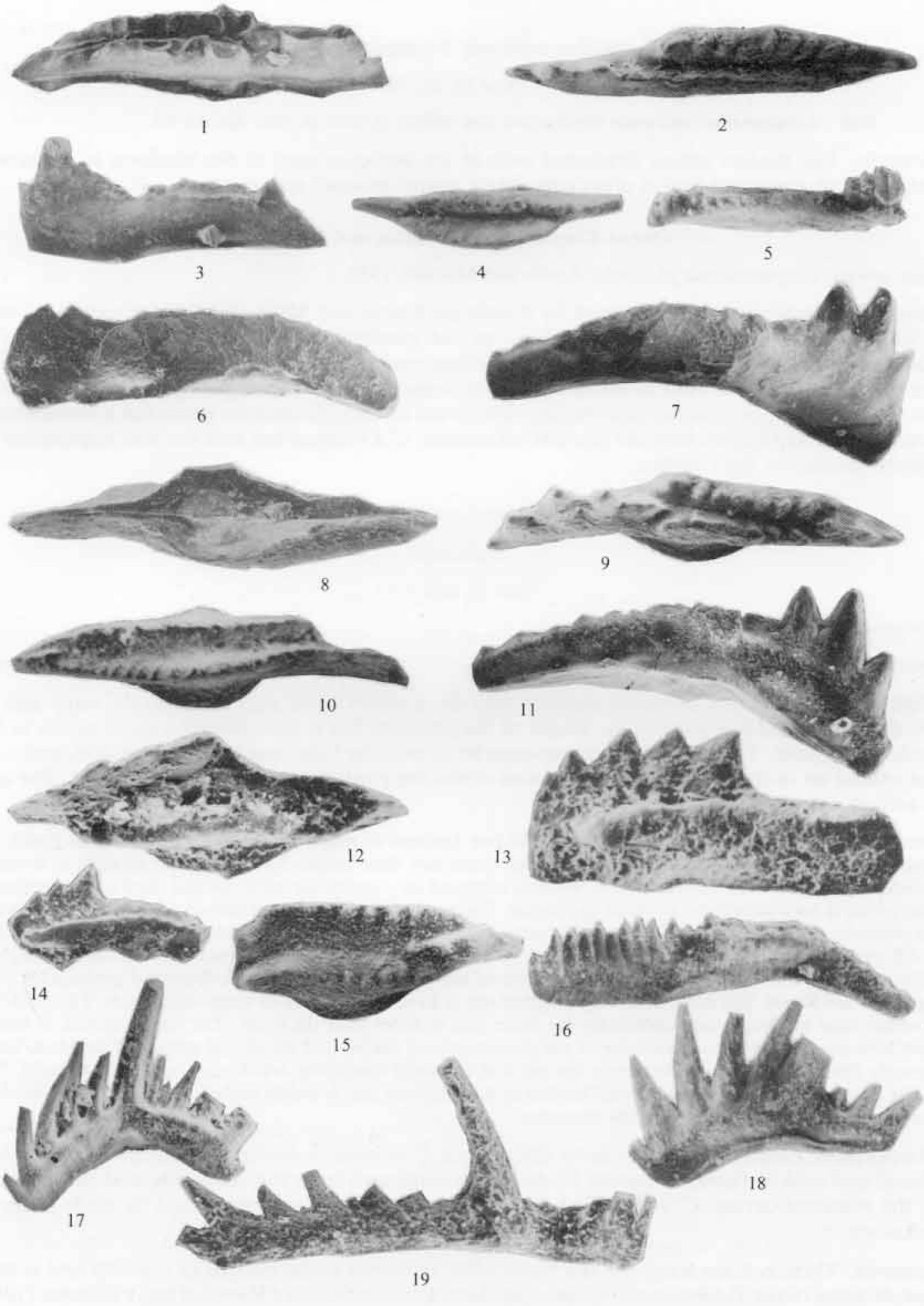
Fig. 14. *Cavusgnathus unicornis.* Inner lateral view of a specimen from the Ashfell Sandstone, sample AS1, specimen R38.

Figs. 15, 16. *Taphrognathus varians.* Oral and inner lateral views of specimens from the Stone Gill Beds, sample SG19, specimens R37, R39.

Fig. 17. *Lonchodina* sp. Inner lateral view of specimens from the Coldbeck Beds, sample SG33, specimen R27.

Fig. 18. O element of *Cloghergnathus carinatus.* Inner lateral view of a specimen from the Coldbeck Beds, sample SG32, specimen R14.

Fig. 19. A_1 element of *Cloghergnathus carinatus.* Inner lateral view of a specimen from the Coldbeck Beds, sample SG31, specimen R3.



HIGGINS and VARKAR, Lower Carboniferous conodonts

Cavusgnathus unicornis Youngquist and Miller

Plate 18, fig. 14

1949 *Cavusgnathus unicornis* Youngquist and Miller, p. 619, pl. 101, figs. 18–23.

Remarks. The median carina developed only in the posterior part of the platform is prominent only in large specimens and is often completely absent in small specimens.

Genus *Cloghergnathus* Austin and Mitchell

Type species. Cloghergnathus globenskii Austin and Mitchell, 1975.

Remarks. Cloghergnathus was named by Austin (in Austin and Mitchell 1975) for specimens with a lateral blade which does not extend on to the platform as a high, crested structure as in *Cavusgnathus*. The blade may occupy a sub-median position whilst remaining connected to one of the platform sides and such forms are probably transitional to *Taphrognathus*. Its characteristics are those of *Clydagnathus* Rhodes, Austin, and Druce an early Courceyan genus but a considerable stratigraphic gap occurs between the last occurrence of *Clydagnathus* and the first appearance of *Cloghergnathus* in the Chadian.

Cloghergnathus carinatus sp. nov.

P element

Plate 18, figs. 1–11

Holotype. Pl. 18, figs. 2, 7. R30.

Horizon. Scandal Beck Limestone, sample SB 2.

Diagnosis. A right- and left-sided element with the anterior blade developed on the inner side of the unit. A central trough runs the length of the platform but is occupied by a short carina in the posterior quarter. The blade is short, one-quarter to one-third the length of the platform, and does not extend on to the platform. It is extended above the platform and is convexly curved. The unit is arched.

Description. The anterior blade consists of up to five denticles of which the largest is in the centre giving the blade a convex outline. The denticles are free for about half their length. The platform is straight to strongly curved and bears a deep median trough which is occupied by a carina for up to the last third of the platform. The carina is very prominent in small specimens. The inner parapet is curved and commonly does not reach the posterior end of the unit and is continued anteriorly as the blade, although the curvature of some specimens is difficult to determine because the blade may be outwardly curved. In a few specimens the blade is slightly offset and, whilst it originates from the inner side of the platform, it occupies a sub-central position on both right and left forms. The oral surface of the platform is covered by nodes or transverse ridges. The platform is widest near midlength and commonly the inner side is wider than the outer. The unit is arched in lateral view both the oral and aboral surfaces of the platform being curved and the aboral surface of the blade being strongly downturned. The curvature is less marked in young specimens which may be almost straight. The cavity occupies the whole of the aboral surface of the platform and is widest slightly anterior to its mid-point tapering to both the anterior and the posterior.

Comparisons. Cloghergnathus carinatus differs from *C. globenskii* Austin and Mitchell by its arched aboral and oral surfaces, its convex blade, which originates from the inner side, and the presence of the posterior carina. *C. rhodesi* is left-sided, does not possess a carina, and its blade shape is unknown.

Remarks. There is a tendency for the blade of *C. carinatus* to be median in position and it may include some of the *Taphrognathus–Cavusgnathus* transition forms of Rexroad and Collinson (1963; especially fig. 24, p. 111). Austin (in Austin and Mitchell 1975) has argued that *Cloghergnathus* is not intermediate between *Taphrognathus* and *Cavusgnathus* but is an offshoot of the former genus in which the blade, although lateral, does not extend on to the platform. In this respect *Cloghergnathus* mirrors *Adetognathus* which is probably a younger homeomorph, or which may prove to be the same genus when its full range is known. All figured specimens of *Cloghergnathus* have a low blade or one which rises gradually as in *C. carinatus* none of them have the typical cavusgnathoid blade. In addition, all known species of *Cloghergnathus* are either right- and left-sided or only left-sided, whereas *Cavusgnathus* species are all right-sided. *C. carinatus* is also similar to *Clydagnathus darensis* but differs in having a larger basal cavity.

Cloghergnathus non-platform Elements

O element

Plate 18, fig. 18; Plate 19, fig. 4

1957 *Ozarkodina compressa* Rexroad, p. 36, pl. 2, figs. 1, 2.

Remarks. The Ravenstonedale specimens have the prominent apical denticle of the paratype but have a smaller number of denticles on the processes than is usual in this element. However, it is thought to fall within the variability of the element.

N element

Plate 19, fig. 18

1941 *Prioniodus varians* Branson and Mehl, p. 174, pl. 5, figs. 7, 8.
1957 *Prioniodina varians* (Branson and Mehl), Bischoff, p. 49, pl. 5, fig. 35.
1957 *Neoprioniodus varians* (Branson and Mehl), Rexroad, p. 35, pl. 2, fig. 10.

Remarks. Von Bitter (1976) named *Neoprioniodus camurus* Rexroad as the Ne element in his multi-element reconstruction of *Cavusgnathus windsorensis*. He also figured a similar form in his reconstruction of the non-P elements of *Cavusgnathus* sp. from the Pennsylvanian (1972, pl. 9, fig. 5). Baesemann (1973) figured a similar neoprioniodontid in his reconstruction of *Adetognathus* (pl. 2, figs. 26, 35). No form comparable to *N. camurus* occurs in the Ravenstonedale samples where the only neoprioniodontids are *N. varians*, *N. acampylus*, and *N. scitulus*.

A_1 element

Plate 18, fig. 19; Plate 19, fig. 20

1953 *Hindeodella ensis* Hass, p. 81, pl. 16, figs. 19–21.
1960 *Hindeodella tenuis* Clarke, p. 8, pl. 1, figs. 10, 11.

Remarks. There are two variants in this element. One is typified by *Hindeodella tenuis* and *H. ensis* and is the more common of the two. This has a long posterior process with alternating denticles and a long, often inwardly curved anterior bar commonly with non-alternating denticles which are as large as the large posterior bar denticles. The other variant is shorter and arched with a cusp which is as long as the posterior process, and has non-alternating denticles of which the posterior process denticles increase in size posteriorly.

A_3 element

Plate 19, figs. 5, 6, 8

Description. A robust unit consisting of two massive lateral processes, a large cusp, and a slender posterior process. The cusp is large, slightly curved posteriorly, and has a triangular cross-section with sharp posterior and lateral edges. Its surface is covered with fine discontinuous striations. The posterior bar is incomplete, appears to be narrow, and has an oval cross-section.

The lateral processes are massive, bar-like with a square cross-section, and almost in the same plane. They are as long as the main cusp and slightly inclined downwards. The denticles on the oral surface, up to five in number, are large, increasing in size towards the extremities of the processes, and are flattened in an antero-posterior direction. The largest denticle is approximately half the size of the cusp.

The aboral side of the unit is grooved, and the grooves meet forming a small triangular pit beneath the cusp.

Remarks. This form most closely resembles *Hibbardella ortha* Rexroad, the primary difference being the shallow angle between the processes. It is also much more massive than *H. ortha* but this is a characteristic shared by specimens of all species in the Ravenstonedale faunas and is most likely due to the shallow-water environments in which the fauna occurs.

Genus *Magnilaterella* Rexroad and Collinson

Type species. Magnilaterella robusta Rexroad and Collinson 1963.

Magnilaterella robusta Rexroad and Collinson

1940 *Lonchodina* sp. Branson and Mehl, p. 171, pl. 5, fig. 10 only.
1956 *Metalonchodina*? sp. Elias p. 124, pl. 4, fig. 3.
1963 *Magnilaterella robusta* Rexroad and Collinson, pp. 14-17, pl. 1, figs. 4, 5, 9.

Remarks. Typically *Magnilaterella robusta* has a prominent bevel on the inner side of the lateral process. However, Rexroad and Collinson (1965) did include specimens without the bevel which have the characteristic denticulation on the lateral process.

At the present time the multi-element species to which *M. robusta* belongs is unknown.

EXPLANATION OF PLATE 19

All figures ×60

Figs. 1-3. *Lonchodina* sp. Inner lateral views of specimens from the Coldbeck Beds. Fig. 1 from sample SG33, specimen R1; fig. 2 from sample SG31, specimen R2; fig. 3 from sample SG33, specimen R40.

Fig. 4. O element of *Cloghergnathus carinatus*. Inner lateral view of a specimen from the Coldbeck Beds, sample 29, specimen R26.

Figs. 5, 6, 8. A_3 element of *Cloghergnathus carinatus*. Posterior views of specimens from the Coldbeck Beds, sample 29, specimens R9-11.

Figs. 7, 9. *Apatognathus asymmetricus*. 7, inner lateral view of holotype from the Scandal Beck Limestone, sample SB9, specimen R21. 9, inner lateral view of a specimen from the Scandal Beck Limestone, sample SB7, specimen R20.

Fig. 10. *Apatognathus scandalensis*. Inner lateral view of holotype from the Scandal Beck Limestone, sample SB8, specimen R18.

Figs. 11, 13, 19. *Apatognathus cuspidatus*. Inner lateral views of specimens from the Scandal Beck Limestone, fig. 11 (SB7), specimen R16 and fig. 19 (SB2), specimen R17, and Coldbeck Beds sample SG33, specimen R15.

Fig. 12. *Apatognathus libratus*. Inner lateral view of a specimen from the Ashfell Sandstone, sample AS1, specimen R19.

Fig. 14. *Spathognathodus scitulus*. Outer lateral view of a specimen from the Ashfell Sandstone, sample AS1, specimen R5.

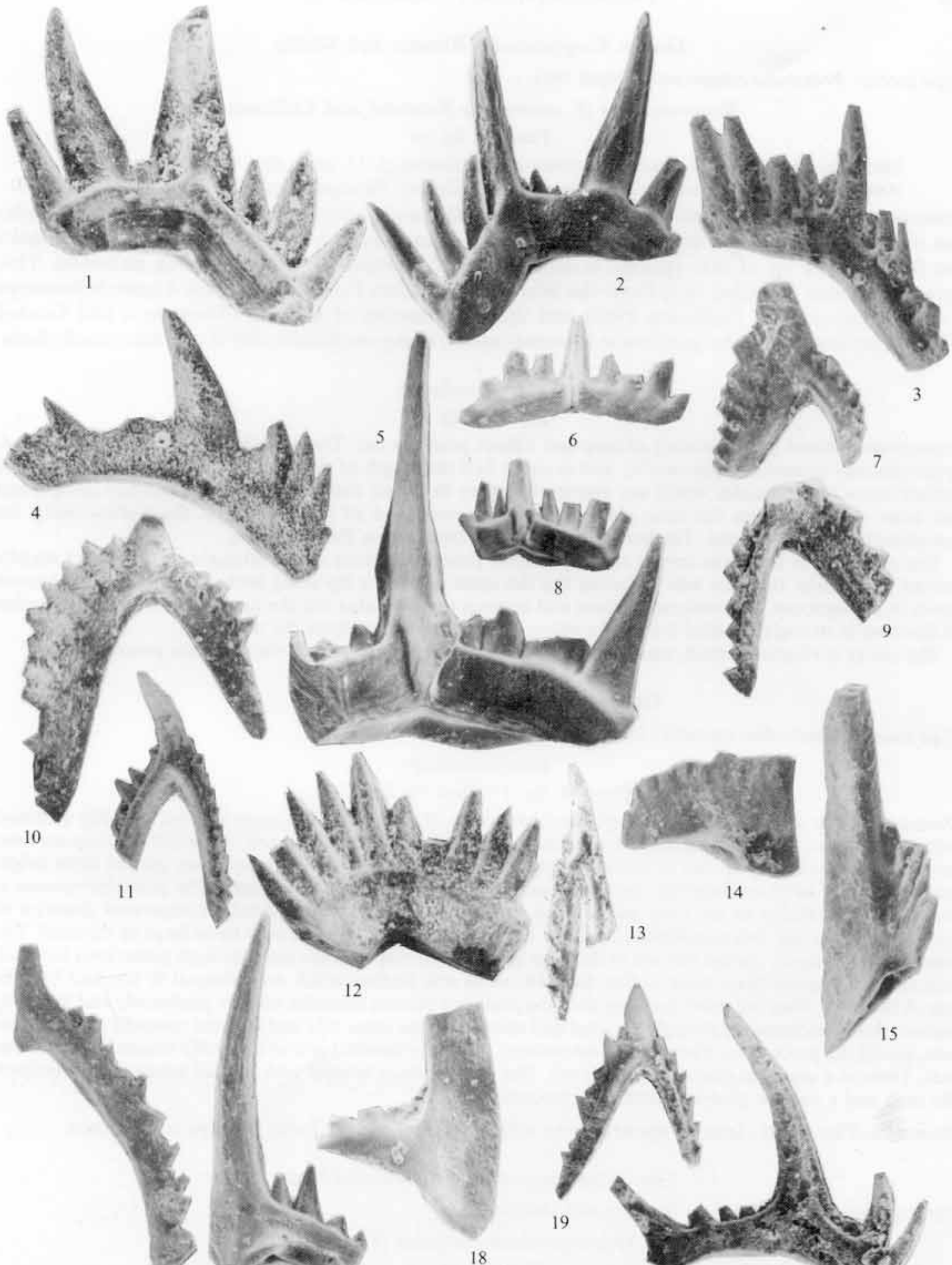
Fig. 15. *Neoprioniodus singularis*. Inner lateral view of a specimen from the *Michelinia grandis* Beds, sample MB2, specimen R8.

Fig. 16. *Neoprioniodus* cf. *acampylus*. Inner lateral view of a specimen from the *Michelinia grandis* Beds, sample MB2, specimen R13.

Fig. 17. *Neoprioniodus* sp. Inner lateral view of a specimen from the Coldbeck Beds, sample SG29, specimen R7.

Fig. 18. N element of *Cloghergnathus carinatus*. Inner lateral view of a specimen from the Scandal Beck Limestone, sample SB9, specimen R12.

Fig. 20. A_1 element of *Cloghergnathus carinatus*. Inner lateral view of a specimen from the Coldbeck Beds, sample SG29, specimen R24.



HIGGINS and VARKAR, Lower Carboniferous conodonts

Genus *Neoprioniodus* Rhodes and Muller

Type species: Prioniodus conjunctus Gunnell 1931.

Neoprioniodus cf. *acampylus* Rexroad and Collinson

Plate 19, fig. 16

1965 *Neoprioniodus acampylus* Rexroad and Collinson, p. 11, pl. 1, figs. 25–27.
1968 *Neoprioniodus acampylus* Rexroad and Collinson, Thompson and Goebel, p. 37, pl. 3, fig. 2.

Remarks. This specimen conforms to the general outline and description of *Neoprioniodus acampylus* but differs in possessing a more robust posterior process which is laterally thickened, and it lacks the flaring inner lip of that species. It differs from *N. camurus* Rexroad in being unbowed. This species has been recorded only from the Warsaw and Salem Formations of the Upper Mississippi Valley (Rexroad and Collinson 1965) and the Meramacian of Indiana (Thompson and Goebel 1968). It occurs at a similar position in Ravenstonedale being confined to the *Michelinia grandis* Beds.

Neoprioniodus sp.

Plate 19, fig. 17

Description. Robust unit consisting of cusp and a short posterior bar. The posterior bar is laterally thickened, approximately square in cross-section, and is about half the length of the cusp, but is not complete. Its oral surface bears four denticles which are discrete for more than half their length and are laterally compressed but more strongly so on the inner side. They are incurved and of varying length, the highest being the penultimate one on the cusp. The bar is straight and is bevelled on the inner face.

The cusp is four times the length of the posterior process denticles and is strongly incurved and slightly curved posteriorly. Its outer side is convex but the inner side has a lip along both margins which continues down to the anticusp. The anticusp is short and appears to be pointed but the tip is broken. The aboral edge of the cusp is strongly bevelled but the bevelling does not continue down the anticusp.

The cavity is elliptical, small, and is continued as a faint groove beneath the posterior process.

Genus *Lonchodina* Ulrich and Bassler

Type species: Lonchodina typicalis Ulrich and Bassler 1926.

Lonchodina sp.

Plate 18, fig. 17; Plate 19, figs. 1–3

Description. The unit includes both right and left forms; it is bowed. The cusp is large, laterally flattened with sharp edges, strongly inwardly curved, and posteriorly inclined and curved. Typically the cusp narrows gently towards the oral tip but in some specimens the base is very wide. The processes are the same height and length and both are laterally thickened but the height is twice the thickness. The posterior process is almost at right angles to the cusp and its oral surface bears three to six laterally compressed denticles of variable size, but the two penultimate ones are the largest and one of them may be as large as the cusp. The denticles are inwardly curved and are in the same plane as the cusp, but are more strongly posteriorly inclined. The anterior process bears three to five denticles on its oral surface which are subequal in size and half the size of the cusp. They are more founded than the posterior process denticles and are posteriorly and inwardly curved. Both processes are strongly bevelled and striated on the inner side and inclined inwardly on the upper side, giving the processes a triangular cross-section. The inner bevelled side is markedly striated on the lower half. There is a small lip over the basal cavity. The aboral side is narrow with a small triangular pit beneath the cusp and a narrow groove beneath the processes.

Remarks. The multi-element apparatus to which this distinctive form belongs is unknown.

Genus *Spathognathus* Branson and Mehl

Type species: *Spathodus primus* Branson and Mehl 1941.

Spathognathodus scitulus (Hinde)

Plate 19, fig. 14

1900 *Polygnathus scitulus* Hinde (part), p. 343, pl. 9, figs. 9, 11 only.
1949 *Spathognathodus scitulus* (Hinde) Youngquist and Miller, p. 622, pl. 101, fig. 4.

Remarks. Austin and Rhodes recorded a fused cluster consisting of one specimen of *Spathognathodus scitulus* and four specimens of *Apatognathus* sp. from the Lower Carboniferous of the Avon Gorge. Undoubtedly the forms have a similar range and commonly occur in the same samples. Baesemann (1973) described a multi-element species, *Ozarkodina minuta* which includes a P element, *S. minutus* which is very similar to *S. scitulus*. Similarly, von Bitter (1976) suggested that *S. cristulus*, also morphologically similar to *S. scitulus*, could be the P element of his *Ellisonia* sp. apparatus. However, neither Baesemann's nor von Bitters's accompanying element are present in the Ravenstonedale sequence, and the Austin and Rhodes model may be the more likely for the *S. scitulus* apparatus.

Genus *Taphrognathus* Branson and Mehl

Type species: Taphrognathus varians Branson and Mehl 1941.

Taphrognathus varians Branson and Mehl

Plate 18, figs. 15, 16

1941 *Taphrognathus varians* Branson and Mehl p. 182, p. 6, figs. 27–33, 35–40.

Remarks. A short carina occurs in the posterior quarter of the median sulcus which occurs on a few but not the majority of previously figured specimens of this species. At the present time such specimens are included within *Taphrognathus varians*.

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