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ENVIRONMENTAL CONTROLS OF BRIGANTIAN CONODONT-DISTRIBUTION : EVIDENCE FROM THE GAYLE LIMESTONE OF THE YOREDALE GROUP IN NORTHERN ENGLAND[1]

R.B. DAVIES[2], R.L. AUSTIN[3] & D. MOORE[3]

(7 figures, 2 tables and 2 plates)

ABSTRACT. The Gayle Limestone, the second limestone formation of the Yoredale Group on the Askrigg Block of the North of England, has been mapped across its outcrop area on a scale of 1:10,560. Ten rock types have been defined on the basis of field and petrological characteristics. For each rock-type, the faunas, bioclast and/or grain contents and diagenetic history, have been described. Investigation of the individual rock-types permits interpretation of the overall environment of the Gayle Limestone. 1570 identifiable conodont elements are recorded from the Gayle Limestone and related to the rock types. The proximity of shelf to basin, availability of nutrients and interactions of wave-energy, water-depth and shelf topography had considerable influence on conodont distribution. *Gnathodus girtyi, G. homopunctatus* and *Lochriea commutata* (offshore conodonts) dominate the faunas of the Gayle Limestone. *Gnathodus bilineatus* has been recovered only from the deeper part of the lagoon. *'Synclydognathus'* was able to inhabit some environments inimical to the majority of conodonts apart from *Cavusgnathus.* The sparsity of *Cavusgnathus* in the Gayle Limestone is related to the absence of agitated, euryhaline environments. *Idioprioniodus* and *Kladognathus*-type apparatuses seem to have been moderately common.

KEY WORDS: Carboniferous, Brigantian, N. England, sedimentary petrology, conodonts.

RESUME. Contrôle par l'environnement de la distribution des conodontes Brigantien : évidences dans le Calcaire de Gayle du Groupe de Yoredale dans le nord de l'Angleterre. Le Calcaire de Gayle, la deuxième formation calcaire du Groupe de Yoredale, sur le bloc Askrigg dans le Nord de l'Angleterre, a été cartographié au travers de son aire d'affleurement à l'échelle du 1:10.560. Dix types de roches ont été définis sur la base de caractéristiques pétrographiques et de terrain. Pour chaque type de roches, les faunes, le contenu en bioclastes et/ou en grains et l'histoire diagénétique ont été décrits. L'étude des types de roches individuels permet l'interprétation de l'ensemble de l'environnement du Calcaire de Gayle. 1570 éléments identifiables de conodontes ont été isolés du Calcaire de Gayle et des types de roches associés. La proximité de la plateforme et du bassin, la disponibilité des nutrients et les interactions entre niveau d'énergie des vagues, profondeur de l'eau et topographie de la plateforme avaient une influence considérable sur la distribution des conodontes. *Gnathodus girtyi, G. homopunctatus* et *Lochriea commutata* (conodontes offshores) dominent les faunes du Calcaire de Gayle. *Gnathodus bilineatus* a été récolté seulement dans la partie plus profonde du lagon. '*Synclidognathus*' était capable d'habiter dans quelques environnement qui rebutaient à la majorité des conodontes à l'exception de *Cavusgnathus.* La rareté de *Cavusgnatus* dans le Calcaire de Gayle est liée à l'absence d'environnements euryhalins agités. Les appareils de *Idioprioniodus* et du type *Kladognathus* semblent avoir été modérément communs.

MOTS-CLES: Carbonifère, Brigantien, Nord de l'Angleterre, pétrologie sédimentaire, conodontes.

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[1] *Manuscript received and accepted January 1994.*

[2] *B.P. Exploration, 900 East Benson Boulevard, Anchorage, Alaska, USA.*

[3] *Department of Geology, The University, Southampton, SO9 5NH, UK.*

1. INTRODUCTION

The IUGS Subcommission on Carboniferous Stratigraphy has established a number of projects, one of which is concerned with a chronostratigraphic boundary in the late Viséan (see *Newsletter on Carboniferous Stratigraphy*, volume 10, 1992). The appearance of the conodont species *Gnathodus bilineatus* has been proposed as a potential marker horizon of world-wide extent. In Great Britain *G. bilineatus* first appears in Asbian rocks (Sevastopulo & Varker, 1985; Riley, 1992), but it is a facies controlled species being relatively abundant in basinal facies and relatively rare in occurrence within shelf environments On the advice of Dr A T S Ramsey (University of Cardiff) promising Asbian limestones of deeper water aspect from South Wales were collected and processed with the intention of contributing at Liège to the discussion on Project Group 3 - a chronostratigraphic boundary in the late Viséan. Despite the sedimentological evidence of an original deeper water depositional environment for the Asbian samples collected from South Wales only a few conodont fragments have been obtained from the 12 kilograms of rock processed.

Analysis of conodont distribution from the Gayle Limestone of the Yoredale Group in the North of England is presented in this paper which suggests that the interaction of wave-energy and depth, in particular the relationships between surge base and shelf bathymetry, appears to have exerted a controlling influence over conodont distribution. Conodont zonations proposed for the region on the basis of successive shelf faunas are considered to be only of local importance. The few conodonts of 'basinal aspect', such as *G. bilineatus*, which encroached into the shelf environment are more likely to assist international correlations. Conodont faunas of equivalent age represent the responses of conodont animals to a variety of environmental settings. Such responses will be elucidated only after recognition of separate environmental settings, by means of detailed sedimentological analyses such as that reported by Davies (1981) on the Gayle Limestone.

The Gayle Limestone is first referred to by that name in the Ingleborough Memoir (Dakyns *et al.*, 1890). Phillips (1836) had included the Gayle Limestone with the 'Mountain Limestone', the term he used for the underlying Great Scar Limestone. Although Dakyns *et al.* (1890) named the Gayle Limestone, they did not describe the formation, nor show it on their maps, and it has tended to be ignored by later workers, except in the type area of Upper Wensleydale (Hudson, 1924; Moore, 1958). However, its presence outside of the type area was recognised by Hallett (1966) and by Burgess & Mitchell (1976). The Gayle Limestone has been identified and mapped over most of the western half of the Askrigg Block, wherever it outcrops (Davies, 1981). The study area (Fig. 1) has been divided into five sub-areas for easier description of the Gayle Limestone. These sub-areas are Wensleydale and its tributaries, Dentdale and the north-west, Upper Ribblesdale and the south-west, Wharfedale and its tributaries, and Malham Moor and the south (Fig. 2). Wensleydale (Fig. 2) is the type area for the Yoredale Group (Moore, 1958 and Fig. 3). The locations of measured sections are shown in Fig. 4 and Table 1. Thickness variations in the Gayle Limestone are indicated in Fig. 5. Conodonts from the Gayle Limestone have been reported by Varker (1964, 1967, 1968) Rexroad and Varker (1992) and Rhodes *et al.* (1969). Burnett (1987) details conodont CAI over the Askrigg Block. Fig. 6 indicates the location of the conodont samples of the current study. Hallett (1970) reported foraminifera and algae from the Yoredale "Series" Group.

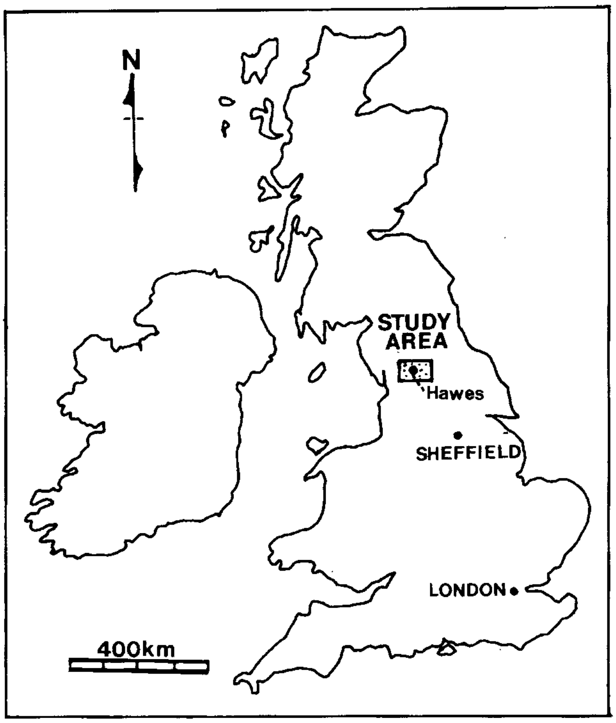

Fig. 1.- Map of Northern England, showing study area and the Yorkshire Dales National Park (stippled).

The type section of the Gayle Limestone is at Gayle Force and upstream through Gayle village, in Duerley Beck (SD 872893). It is not an easy section to measure, and various estimates of the thickness have been given. Walker (1964) and Rhodes *et al.* (1969) both quote a thickness of 57 feet (17.3m), although both their figured sections contradict this. The true thickness is of the order of half this, being 7.9 m (see also Varker, 1968). The underlying Gayle Shale is well exposed, with a sharp, flat contact between it and the Gayle Limestone. The lowest 2.35m

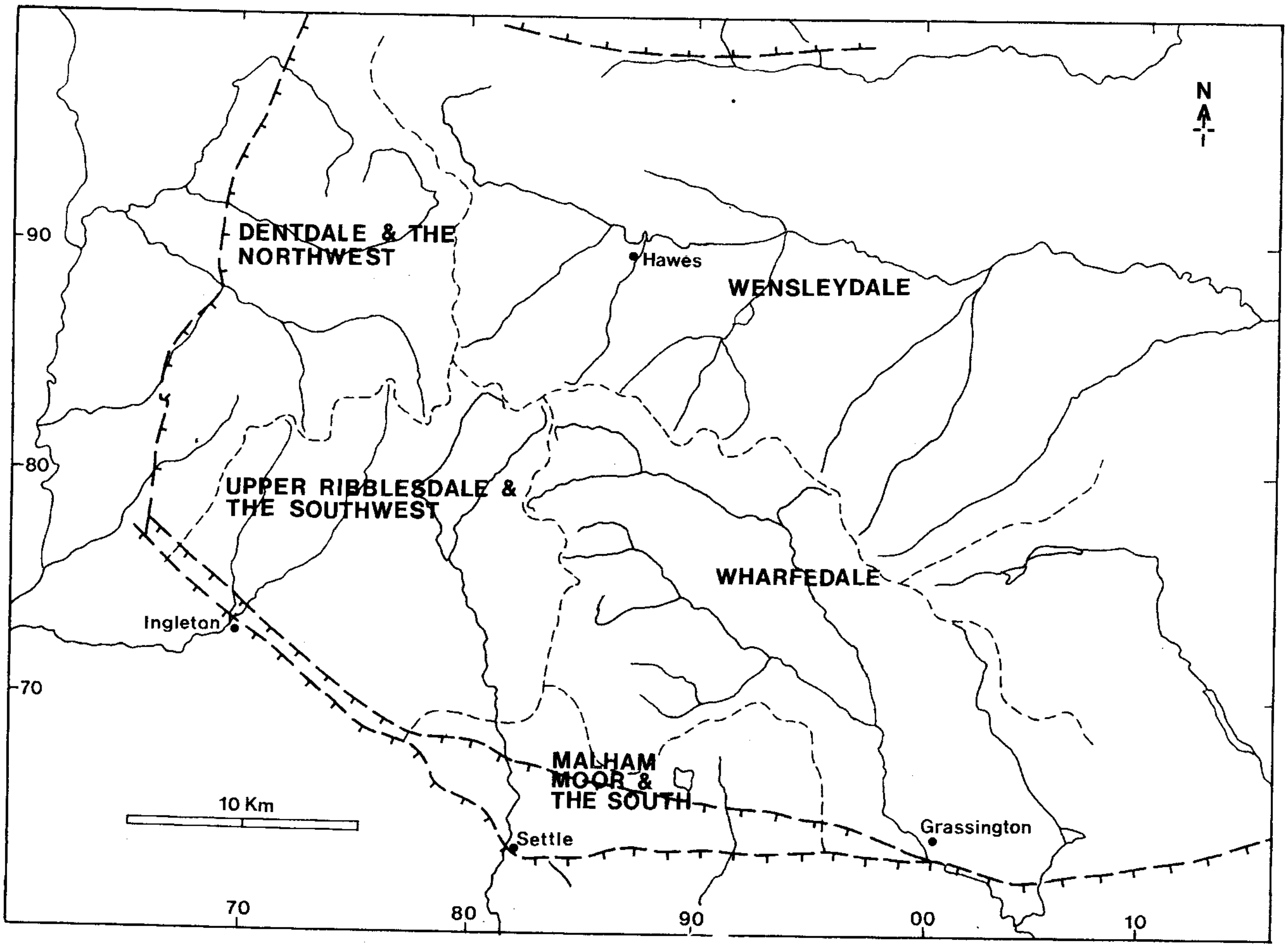

Fig. 2.- Map showing regions used for descriptions of the Gayle Limestone.

of the Gayle Limestone are of medium bedded (10-30 cms), dark calcilutites, with undulose shaly partings. *Gigantoproductus* is common, usually in life-position. Smaller brachiopods, solitary and compound corals also occur. Two beds of pale grey calcilutite succeed these beds. They total 2 m. There are cross sections of brachiopods on the top of the upper pale calcilutite, often in clusters of 6-10. They include *Gigantoproductus*. The next 80 cm consists of three beds of calcilutite, the middle bed containing abundant *Lithostrotion junceum*. These limestones are overlain by a thin bed of shale, in turn overlain by a 90 cm bed of unsorted crinoidal calcarenite. The topmost 1.55 m is of medium-bedded dark calcilutites, containing individual crinoid columnals, brachiopod and bryozoan fragments. Algal coatings, paler than the matrix, are more common in the top few beds. Nearly all good outcrops are in stream sections. There are few quarry sections. Usually, the Gayle Limestone lies at a prominent break of slope and is substantially masked by superficial deposits, both till and alluvium. Outcrops tend to be sparse in consequence. This is not true of the southern part of the area where the Gayle Limestone is more like the underlying Kingsdale Limestone, and overlying Hardraw Scar, Simonstone and Middle Limestones, in lithology and thus the Gayle Limestone is not at the prominent break of slope. Although the Dinantian Subsystem of the north of England is most reliably dated by goniatites (Bisat, 1924), they are very sparse in the Yoredale Limestones. Hence a zonation based on corals and brachiopods has been used (Garwood, 1913). The *Girvanella* Bed was taken as a convenient marker for the D_1/D_2 boundary, although the presence of the D_2 zonal coral *Lonsdaleia floriformis* in the lower half of the Hawes Limestone shows this to be inaccurate (Burgess & Mitchell, 1976). In terms of the Dinantian regional stages (George *et al.*, 1976) the D_1/D_2 boundary equates to the Asbian - Brigantian Stage boundary. Therefore all the Dinantian cyclothems of the Yoredale Group constitute the Brigantian Stage in the Askrigg Block (see George *et al.*, 1976, figs. 10.11). The distinctive *Osagia* nodules (oncoids) of the *Girvanella* Bed have proved a reliable and useful guide to the succession at many localities, dividing the Hawes Limestone into an upper and lower half (Moore, 1958; Burgess & Mitchell, 1976). Above the Upper Hawes Limestone, and usually separated from it by thin clastics, lies the Gayle Limestone.

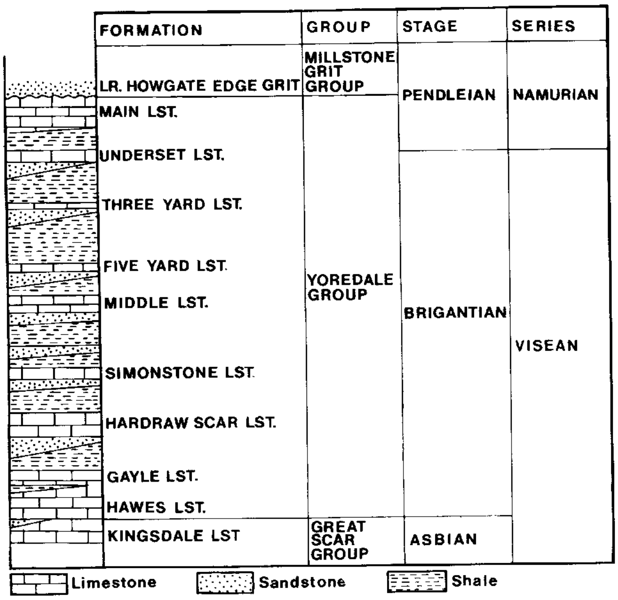

Fig. 3.- Lithostratigraphy of the Yoredale Group in the Askrigg Block.

2. DESCRIPTION, DISTRIBUTION AND ENVIRONMENTAL INTERPRETATION OF THE ROCK-TYPES OF THE GAYLE LIMESTONE

The carbonate rock-types of the Yoredale Group on the Askrigg Block have been described in detail by Moore (1958), who recognised twelve types of limestone based on hand specimen and field characteristics. He described four major types: pure calcite mudstones, crinoidal calcite mudstones, crinoid debris limestones and crinoid reef limestones. The remaining eight types consisting either of fossil additions to the above (algae, bryozoa, corals, brachiopods), non-carbonate additions (sand or mud), or post-depositional modifications (bioturbation or diagenesis). Moore described the crinoid debris limestones as dominating the type area, although others (Garwood & Goodyear, 1924; Black, 1950) have assumed that dark, fine grained limestones were most abundant. All these papers essentially predate the birth of modern carbonate petrography (Folk, 1959; Dunham, 1962 expanded by Embry & Klovan, 1972; Füchtbauer, 1974) and recent comprehensive studies (Flugel, 1982, Tucker & Wright, 1990; Bathurst, 1975, Peryt, 1983; Reading, 1986; Scholle *et al*, 1983; James & MacIntyre, 1985 and Friedman, 1969). In the Gayle Limestone, crinoid ossicles and columnals are the most abundant bioclasts. In some calcarenites and calcirudites, the skeletal parts of other phyla occur sporadically. The dark limestones are more varied because brachiopods, corals, bryozoans, molluscs and foraminifera all make significant contributions to the sediments, both as bioclasts and as *in situ* biostromes. Algae occur sporadically but abundantly as bioclast-cored oncolites and have also been identified in the form of tiny fragments visible only in thin section. Non-skeletal grains are generally sparse in the Gayle Limestone: intraclasts are sometimes important; faecal pellets have not been identified with certainty, although pelletoids (Milliman, 1974) of similar dimensions do occur; ooliths have not been found. Carbonate mud is a very important constituent of many of the limestones, forming the matrix in all calcilutites and in the mud-supported calcarenites. The origin of this lime mud is not revealed by petrographic examination, its grain size of 4µm or less making for considerable difficulties in thin-section manufacture. The sources of lime mud are the subject of an extensive literature, (e.g. Purdy 1963a, 1963b; Matthews, 1966; Stockman *et al.*, 1967; Land, 1970). Scholle & Kling (1972) stressed the poor comparison between recent lime 'muds' and ancient micrites, which have grain sizes of <4µm.

The main constituents of the carbonate rocks of the Gayle Limestone combine in different proportions to give distinct rock-types. These rock-types fall into two broad groups, roughly comparable with Moore's (1958) two dominant limestone types and with two of the facies of Ramsbottom (1973).

I. Dark, thin bedded calcilutites (Moore's crinoidal calcilutites)

II. Pale, thicker bedded, crinoidal limestones, mostly calcarenites (Moore's crinoid debris limestones).

The first group compares lithologically with Ramsbottom's dark, thinner bedded bioclastic limestones, although their faunal content of spirifers, lithostrotionids and lonsdaleids is more appropriate to the pale, thicker bedded, bioclastic limestones of Ramsbottom (1973). His pale limestones are lithologically comparable to the second group of the Gayle Limestone. Their bioclast-content is dominated by crinoid debris. It is possible to sub-divide the pale, crinoidal limestones on the basis of whether the ossicles form a framework, or are supported in a mud matrix. This gives two sub-groups: IIa - Crinoidal calcilutites and IIb - Crinoidal calcarenites. The clastic members of the Gayle Limestone are treated separately as III - Fine sands and IV - Shales.

Davies (1981) defined 10 rock types on the basis of field and petrological characteristics (see also Plate 1). For each rock-type, the faunas, bioclast and/or grain contents and diagenetic history were described. Sources were proposed for bioclasts and clastic grains. Investigation of the individual rock-types permitted interpretation of the overall environment of the Gayle Limestone. A biogenic produced shoal along the fault controlled southern margin of

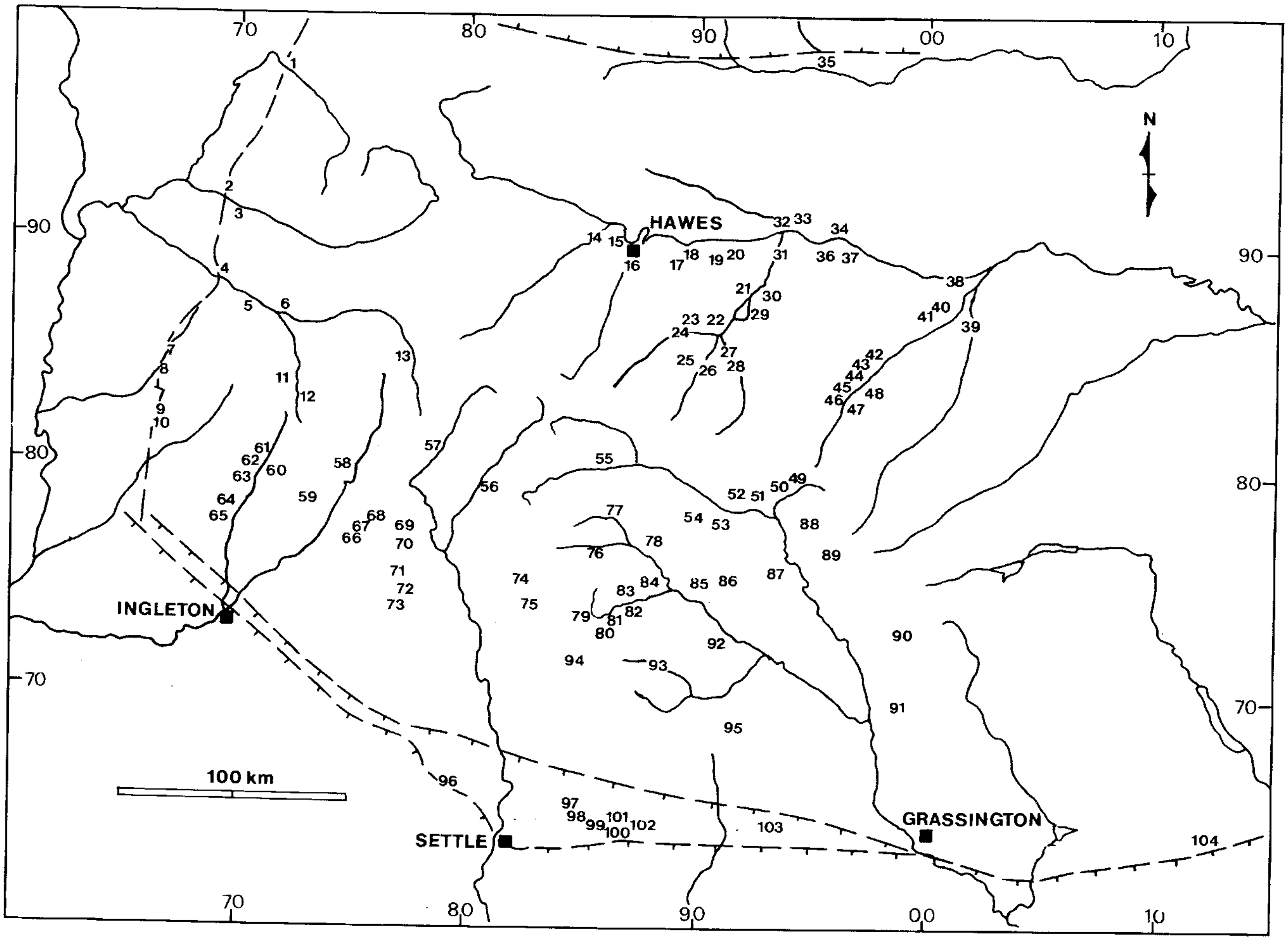

Fig. 4.- Location of measured sections through the Gayle Limestone (Davies, 1981).

the shelf separated the Pennine Basin from a shelf lagoon in which deposition of predominantly carbonate mud was taking place (Fig. 7). A description of the Gayle limestone lithologies and their environmental interpretation summarising the work of Davies (1981) has been deposited with the British Library, Boston Spa, Yorkshire, U.K. as supplementary Publication No. 90327 (Davies, Austin and Moore, 17 pages). Copies may be purchased from the British Library, Document Supply Centre, Boston Spa, Wetherby, West Yorkshire LS23 7BQ. Prepaid coupons for such purposes are held by many technical and university libraries throughout the world.

3. CONODONT FAUNAS OF THE GAYLE LIMESTONE

The conodont faunas of the Gayle Limestone have been studied previously by Varker (1964), who collected from the type section (Duerley Beck) at approximately 0.3 m (= 1 ft.) intervals. He identified 43 species of conodonts as belonging to 17 genera. Of these, 13 species were represented by single specimens. *Gnathodus* was the dominant genus, forming 41% of the identified elements, and 26% of the total fauna. Two-thirds of the gnathodids were of the species *G. girtyi*, and the remaining third was dominated equally by *G. homopunctatus* and *Lochreia commutata*. The second most abundant genus was *Synclydognathus ('Apatognathus')*, forming 13% of the total. Rhodes *et al.* (1969) made limited collections from the Yoredale Group for comparison of its conodont faunas with those obtained from the South-West Province of the British Isles. Only one of their samples was taken from the Gayle Limestone; it contained no conodonts diagnostic of any of their conodont zones, although Rhodes *et al.* assigned the formation to the *Mestognathus beckmanni - Gnathodus bilineatus* Assemblage Zone. For the purposes of the present study, it was thought unnecessary to collect from the type-section of the Gayle Limestone, as Varker's meticulous work had already established the conodont faunas at that locality. A number of rock-types have been identified in the Gayle Limestone. Examples of each, from various localities across the Askrigg Block, have been digested for conodonts. The position of samples are shown in Fig. 6. Significant differences in the conodont faunas have been recognised. These have been interpreted in terms of the overall environmental frame-

Table 1.- Location of measured sections through the Gayle Limestone (Davies, 1981).

1.	River Rawthey	SD 719974	53.	Bouther Gill	SD 909777
2.	Gt.Dovecote Gill	SD 696920	54.	Hagg Beck	SD 898780
3.	River Clough	SD 700912	55.	Beckermonds Scar	SD 857802
4.	Blea Beck	SD 694885	56.	Cam Beck	SD 805792
5.	Flintergill	SD 703867	57.	Intack	SD 788809
6.	Scotchergill	SD 720872	58.	Ivescar	SD 746799
7.	Short Gill	SD 670847	59.	Ellerbeck Gill	SD 730783
8.	South Barkin Gill	SD 668840	60.	Buck Beck	SD 715797
9.	Hazel Sike	SD 664820	61.	Back Gill	SD 711803
10.	Ay Gill	SD 664818	62.	Cluntering Gill	SD 710802
11.	Gastack Beck	SD 719836	63.	Yordas Gill	SD 703792
12.	Combe Gill	SD 728828	64.	Rowtings Caves Gill	SD 696781
13.	River Dee	SD 774850	65.	Thorney Rigg	SD 692774
14.	Widdale Beck	SD 856903	66.	near Gt. Douk Cave	SD 751767
15.	Spillian Green Sike	SD 864901	67.	Keld Bank Spring West	SD 754772
16.	Duerley Beck, Gayle	SD 871893	68.	Fairweather Spring West	SD 759775
17.	Burtersett village	SD 890894	69.	Shiver Spring	SD 772773
18.	Bursersett	SD 894896	70.	Washfold Spring	SD 773765
19.	Ray Gill Sike	SD 905894	71.	Alum Pot Beck	SD 769753
20.	Band Gill	SD 912895	72.	Fell Close Sike	SD 772743
21.	Countersett Quarry	SD 921881	73.	Farrers' Shooting Box	SD 768738
22.	Cow Pasture Sike	SD 906866	74.	Hull Pot Beck	SD 825749
23.	Ashgill Beck	SD 895863	75.	Hunt Pot Beck	SD 827740
24.	Bardale Beck	SD 894862	76.	Foxup Beck	SD 855765
25.	Naked Dale Gill	SD 894849	77.	Cosh Beck	SD 863779
26.	Raydale House	SD 902843	78.	Halton Gill Beck	SD 881769
27.	High Park Scar	SD 913852	79.	Lockey Beck	SD 855735
28.	Bank Wood, Cragdale	SD 914849	80.	Dawson Close	SD 859730
29.	Low Blean	SD 924871	81.	Dawson Close	SD 863733
30.	Little Ings Sike	SD 930877	82.	Dawson Close	SD 869735
31.	River Bain	SD 932897	83.	Upper Hesleden	SD 870745
32.	Grange Gill	SD 934912	84.	Hesleden Bergh	SD 878749
33.	Mill Gill	SD 943912	85.	Potts Beck	SD 902751
34.	Newbiggin Beck	SD 951983	86.	Crystal Beck	SD 914752
35.	Gunnerside Beck	SD 951983	87.	Step Gill	SD 935755
36.	Bingy Hill	SD 957898	88.	Buckden Beck	SD 949777
37.	Worton	SD 960897	89.	Cam Gill Beck	SD 959762
38.	Aysgarth Force	SE 012887	90.	Dowber Gill Beck	SD 989729
39.	Walden Beck	SE 020867	91.	New Close Allotments	SD 988697
40.	Tom Gill	SE 006874	92.	Little Scoska Moor	SD 910724
41.	Heaning Gill	SE 002872	93.	Darnbrook Beck	SD 884715
42.	How Sike	SD 974849	94.	Rainscar Pasture	SD 847714
43.	Odlin Holes Wood	SE 972846	95.	Parsons's Pulpit	SD 921687
44.	Mary Pasture Sike	SD 968843	96.	Buck Haw Brow	SD 794662
45.	Scar Top Sike	SD 965841	97.	Langcliffe Scar	SD 848652
46.	Foss Gill	SD 960836	98.	Settle Scar	SD 851647
47.	Myers Garth Gill	SD 969829	99.	Great Scar	SD 860644
48.	Newhouse Gill	SD 975837	100	Great Scar	SD 863643
49.	Cray Gill	SD 943794	101	West of Grizedales	SD 866646
50.	Crook Gill	SD 934793	102	Grizedales	SD 874642
51.	Hubberholme	SD 928788	103	Cow Gill	SD 932646
52.	Strans Gill	SD 917789	104	Coldstones Quarry	SE 124643

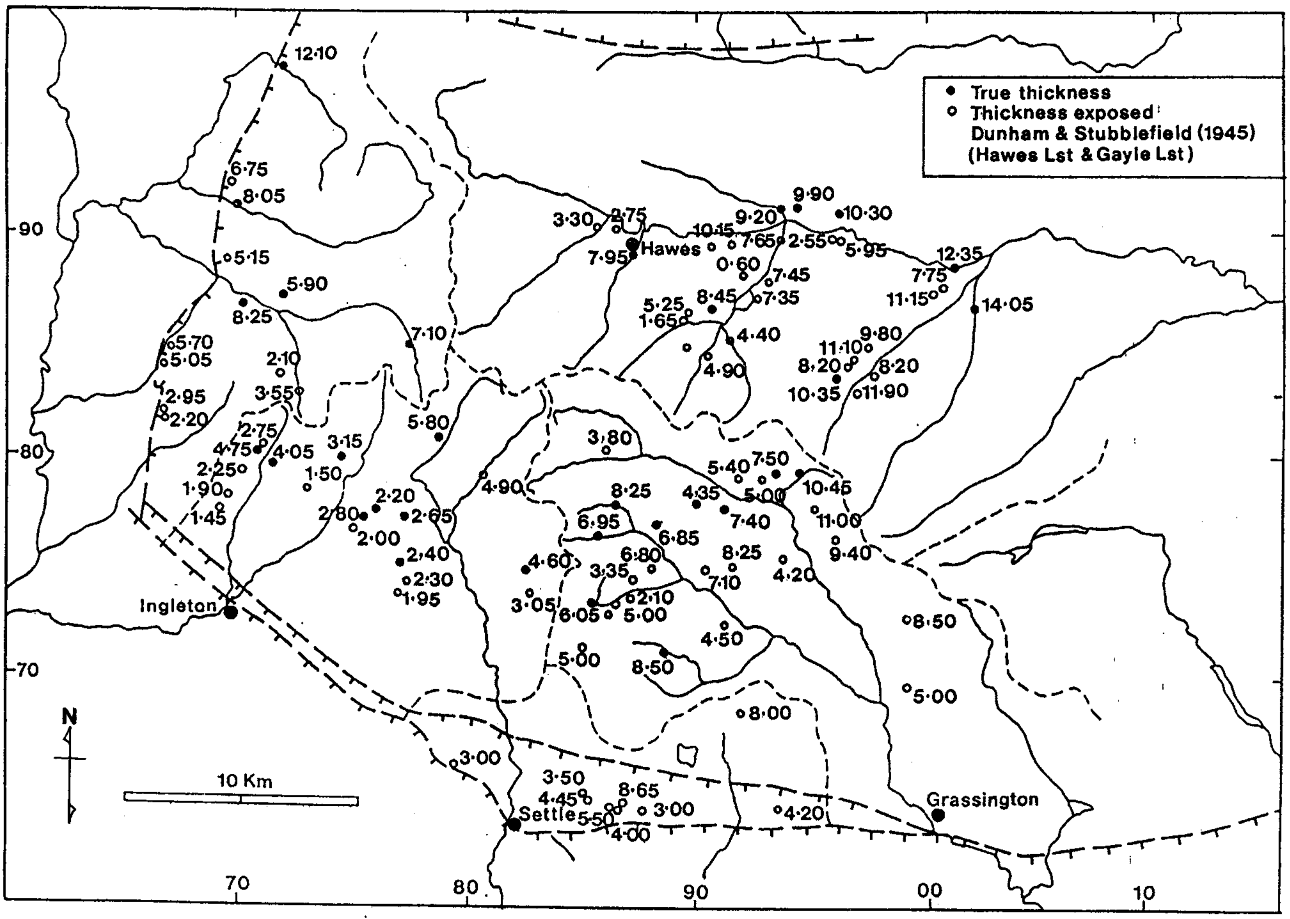

Fig. 5.- Thickness variations in the Gayle Limestone.

work of the shelf, as revealed by detailed mapping. This improves our understanding of the environmental factors which influenced conodont-distribution. A total of 3067 conodonts have been recovered from the Gayle Limestone. Of these 1570 were identifiable. The identifiable conodont faunas obtained are shown in Table 2. The occurrences and abundances of genera and selected important species of conodonts are discussed below, as are the faunas of the individual rock-types of the Gayle Limestone.

Abundances of conodonts range from 0 to 262 specimens per Kg, 2½ times the maximum abundance obtained by Varker (1968) from the type-section, comparable to the concentrations recovered by Varker from the top of the Three Yard Limestone in Weardale, but considerably less than the 600 conodonts per Kg recovered from the top part of the Three Yard Limestone in Swaledale. Of the samples of the Gayle Limestone taken for the present study, eight yielded faunas in excess of 100 specimens per Kg. These are from widely-spaced localities, including the River Clough in Garsdale, and Lockey Beck near Peny-y-Ghent. All these large faunas came from the top metre of the Gayle Limestone, some from the uppermost 25 centimetres. Varker (1968) recovered the largest faunas in the type section from approximately 0.9 m (= 3 feet) below the top, and found that conodont faunas diminished rapidly above that. Clearly, this is not a feature of all outcrops of the Gayle Limestone. The top beds of some sections contain much smaller conodont faunas. The two larger faunas obtained in the present study came from the top of the Gayle Limestone where it is considerably thinner than in Wensleydale. Abundances of 262 specimens per Kg and 199 specimens per Kg were present in samples collected in Hagg Beck and Buck Beck respectively. Two samples of the *Gigantoproductus*-bearing bedset yielded no conodonts. Samples of carbonate-cemented arenites also failed to yield conodonts, but proved difficult to dissolve completely in acetic acid. No shale samples were investigated. Several samples of the *Gigantoproductus*-bearing bedset and of the pale grey, crinoidal calcilutites contained only unidentifiable fragments. Preservation of the conodonts varies considerably. Many of the dark grey to black, algal calcilutites yielded well preserved specimens, but those of the poorly sorted crinoidal calcarenites and stem calcirudites were poorly preserved. The well sorted, clean washed calcarenites contain mainly broken specimens.

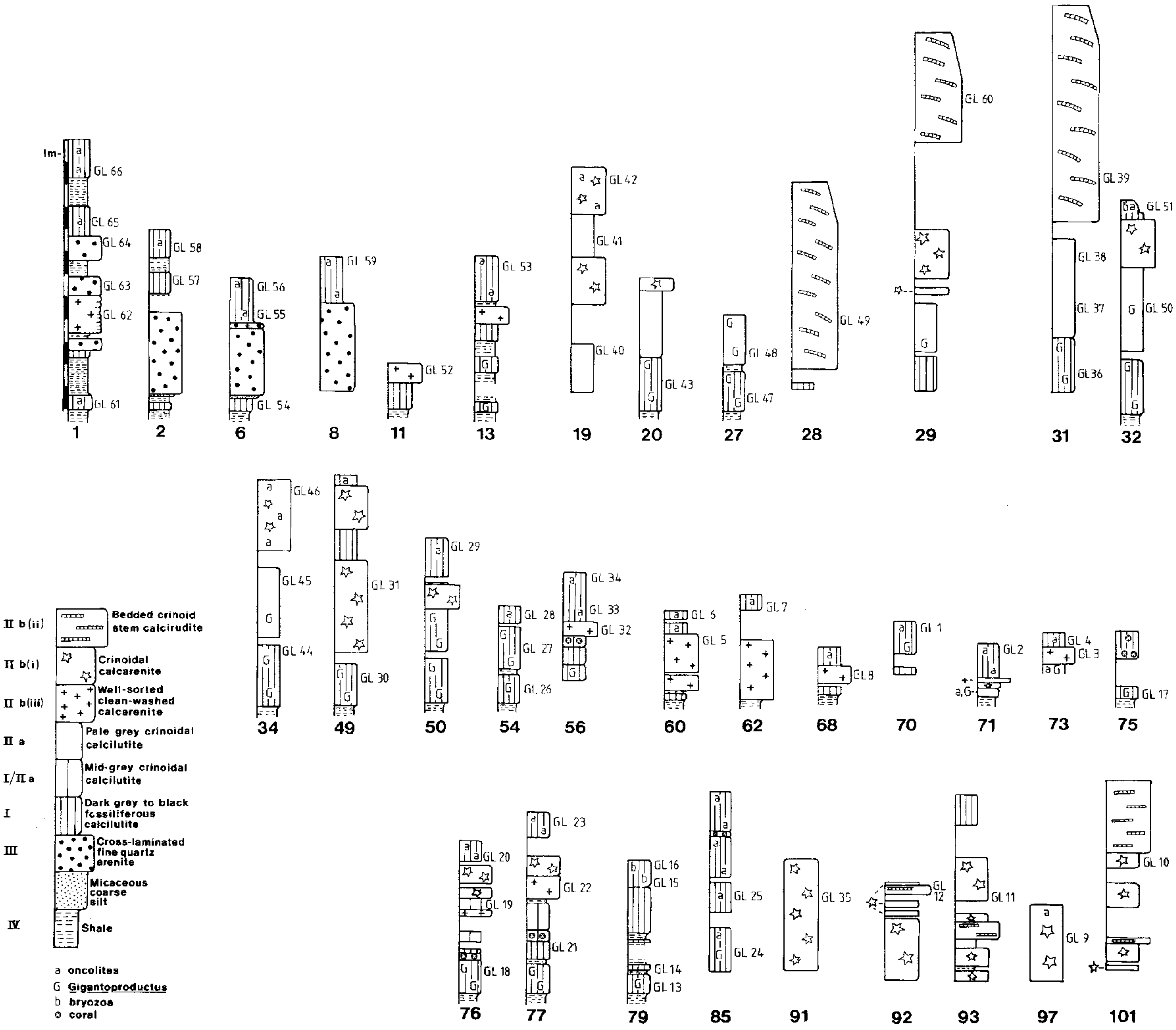

Fig. 6.- Horizons sampled for conodonts and their location (See Fig. 4).

3.1. THE GENUS *GNATHODUS*

A total of 664 Pa elements of *Gnathodus*, have been identified from the Gayle Limestone. A further 73 gnathodid Pa elements cannot be identified to species-level either for reasons of bad preservation or because of the presence of encrusting grains on their platforms. Of those identified, 383 specimens represent *G. girtyi*, 161 *G. homopunctatus*, 106 *G. symmutatus* and 14 *G. bilineatus bilineatus*. The dominance of *G. girtyi* is consistent with the results obtained by Varker (1964) but it forms a smaller proportion (41%) of the total gnathodid population. *G. girtyi* is present in all carbonate rock-types of the Gayle Limestone. It is the most abundant species in the algal calcilutites and, where these yielded the largest faunas, *G. girtyi* is usually twice as abundant as any other species, and occasionally even more dominant in a single sample. In contrast, only two Pa elements of *G. girtyi* have been recovered from the *Gigantoproductus*-bearing bedset. These are large, robust conodonts and thus unlikely to have been destroyed or removed from sediments found to contain smaller, delicate conodonts. *G. girtyi* is

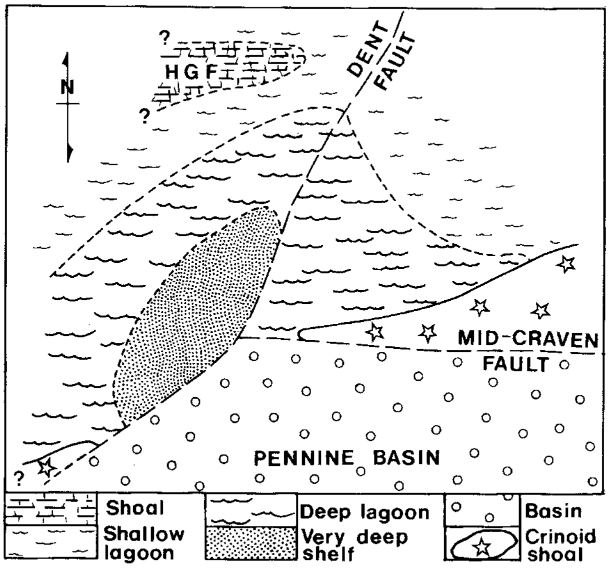

Fig. 7.- Configuration of the south-west corner of the Askrigg Block and surrounding areas during Gayle Limestone times, showing the shelf-edge crinoid shoal and suggested relative water-depths in the shelf lagoon and adjacent environments, based in the study of Davies (1981).

an important constituent of, but does not dominate, the conodont faunas of the pale grey, crinoidal calcilutites and the unsorted crinoidal calcarenites. The species was not recovered from the clear washed calcarenites of the Rawthey and Gastack Beck outcrops, but was present in all other samples of that rock-type. *G. homopunctatus* is the third most abundant species in the Gayle Limestone. It occurs most frequently in the algal calcilutites, in approximately one half to one third of the numbers of *G. girtyi* and in similar numbers to *L. commutata*. *G homopunctatus* has not been recovered from the *Gigantoproductus*-bearing calcilutites.

Pa elements of *Gnathodus symmutatus* are common conodont elements in the Gayle Limestone, present in all carbonate rock-types, although only one such element has been recovered from samples of well sorted calcarenite. The species is fairly common in the algal calcilutites, and is the most abundant species in the uppermost bryozoa-rich, dark calcilutite of the Lockey Beck outcrop.

Pa elements of *G. bilineatus bilineatus,* an important global zonal index, occur in relatively few numbers. The sparsity of this species in the Gayle Limestone is probably a result of environmental factors. The specimens recovered in this study are all from the southern half of the Askrigg Block, although Varker (1964) recorded it "as being rare" in the type-section. These results are consistent with Austin's (1974) suggestion that *G. bilineatus bilineatus* is indicative of deeper water, more basinal conditions. However, von Bitter (1976a) reported that *G. bilineatus bilineatus* is common only in intertidal carbonates of the Upper Windsor Group of Nova Scotia. In the Gayle Limestone, *G. bilineatus bilineatus* does not occur in the lower half, but conodont yields are poor from that interval.

3.2. THE GENUS *LOCHREIA*

This genus is represented by 191 Pa elements, of which 170 are of *Lo. commutata*, the second most abundant species in the Gayle Limestone. This species achieves its greatest abundance in the algal, dark calcilutites in which it occurs in similar numbers to *G. homopunctatus*. *Lo. commutata* is present in all carbonate rock-types of the Gayle Limestone, and was the only species recovered from the small, bryozoa-rich mounds of Grange Gill. Thirteen Pa elements of *Lo. nodosa* have been obtained, all from the upper half of the Gayle Limestone. Varker (1964) reported that the species occurred sparsely in the Gayle Limestone, but did not obtain it from lower horizons. The apparent absence of *Lo. nodosa* from the lower half of the Gayle Limestone may be the consequence of its first appearance (Cu111â) occurring after this part of the Gayle Limestone was deposited, or it may simply reflect the improbability of collecting it in the small samples processed. The topmost beds of the Gayle Limestone, from six separate outcrops, have yielded eight specimens of *Lochreia mononodosa*. The coincidence of the first appearance of *Lo. nodosa* and of *Lo. mononodosa* in the Gayle Limestone supports the suggestion that the base of the *Lo. nodosa* Zone of the German succession (Meischner, 1970) and that of the *Lo. mononodosus* Assemblage Zone of Britain (Rhodes *et al.*, 1969) are equivalent, as was implied by Austin (1973, Chart 1).

3.3. THE GENUS *CAVUSGNATHUS*

This genus is sparse in the Gayle Limestone, with only 18 Pa elements recovered, of which 11 occurred in a single sample, the well-sorted calcarenite of the Rawthey outcrop. These eleven specimens are fragmented, and only one can be unreservedly assigned to a species - *Cavusgnathus unicornis*. Of the remaining 7 specimens, 6 are also clearly assignable to *C. unicornis*. Two of these were recovered from the well-sorted calcarenite of Gastack Beck, two from the uppermost algal calcilutite of the Farrer's Shooting Box outcrop of Ingleborough, one from the 1.35 m algal calcilutite of the Rawthey section, and a further one from an unsorted crinoidal calcarenite, 5.5 m above the base of the Cray Gill outcrop. Varker (1964) recorded *Cavusgnathus* from the type section of the Gayle Limestone, but in the current study it has not been found in any sample collected in

Table 2.- Sample numbers, identified conodont elements and sample lithologies. Key to lithologies (left hand column). 1. Dark grey to black calcilutites algal bearing; 2. dark grey to black calcilutite *Gigantoproductus* bearing;. 3. dark grey to black calcilutite bryozoa bearing; 4. dark grey to black calcilutite; 5. bedded crinoidal stem calcirudite; 6. well-sorted clean-washed calcarenite. 7. crinoidal calcarenite; 8. cross-laminated fine quartz arenite; 9. plate grey crinoidal calcilutite with *Gigantoproductus*;10. pale grey crinoidal calcilutite; 11. mid grey crinoidal calcilutite.

LITHOLOGY	CONODONT ELEMENTS SAMPLE (GL)	*Cavusgnathus unicornis* (Pa)	*Cavusgnathus sp.* (Pa)	*Mestognathus sp.* (Pa)	*Synclydognathus libratus* (S)	*S. geminus* (S)	'*laeviposticus*' (Pb)	'*chauliodus*' (S)	'*petilus*' (S)	'*scalenus* (S)	*Synclydognathus sp.* (S)	*scitulus* (Pa)	*Hindeodus cristula* (Pa)	*Hindeodus cristula* (M)	*Synprioniodina microdentata* (M)	*Gnathodus bilineatus* (Pa)	*Gn. girtyi* (Pa)	*Gn. homopunctatus* (Pa)	*Gn. symmutatus* (Pa)	*Gnathodus sp.* (Pa)	*Lochriea commutata* (Pa)	*L. mononodosa* (Pa)	*L. nodosa* (Pa)	*Hibbardella acuta* (Sa)	*H. milleri* (Sa)	*H. pennata* (Sa)	*Hibbardella sp.* (Sa)	*Hindeodella cawdorensis* (Sc)	*H. germana* (Sc)	*H. ibergensis* (Sc)	*H. simplex* (Sc)	*Hindeodella sp.* (Sc)	*Neoprioniodus peracutus* (M)	*N. scitulus* (M)	*N. singularis* (M)	*Neoprioniodus cf. N. parvus* (M)	*Neoprioniodus sp.* (M)	*Ozarkodina collinsoni* (Pb)	*Oz. delicatula* (Pb)	*Ozarkodina sp.* (Pb)	*Ligonodina levis* (S)	*L. roundyi* (S)	*L. tenuis* (S)	*Ligonodina sp* (S)	*Lonchodina furnishi* (S)	*Lonchodina sp.* (S)	*Roundya barnettana* (Sa)	*Kladognathus macrodentatus* (S)	*Magnilaterella clarkei* (S)	*Ma. complectens* (S)	*Magnilaterella sp.*	*Subbryantodus subaequalis* (Pb)	*Geniculatus sp.*	NO. OF ELEMENTS
1	66										3	1					4	2			1																								1									12
1	65	1																3			1				1								1		1								1											9
8	64																																																					0
8	63																																																					0
6	62	1	0																																						1			1										13
1	61																															1	1																					2
5	60										1						1	2																			1		1					1	2									9
1	59			1		2	1	1			3						8	3		2	2	1						1					1								1							2						29
1	58								1		1	1					5	2		3	5								1					1			1	1		1	1				2							1		27
4	57																3	2													1						1							1										8
1	56					3	1				14	3					21	7	3		10	1	1		1								1		4				2		1								1				1	77
1	55					2		1			1	1					3	1	2		3		1										1											1										17
4	54							1							1		2	1	2		1											1																						9
1	53				1		2	1			1	4					9	6	1	1	2	1	1	1											4				2						1									38
6	52	2	1	3							2																						2							1				1										12
1:3	51																				2																																	2
9	50					1		1									1	1	2																				2					1	1									10
5	49							1			1						13	3	4	2	9		1						1			1			2		2								1									41
9	48																																																					0
2	47							2																																														2
7	46											1					2	1			1									1											1			1										10
9	45								1									4	1		3				1				1						1		1							1	1					1				16
2	44																																																					0
2	43																1																																					1
7	42																5	1			1												1							1				2								1		12
10	41								1		3	5					3		2	2	2			1									1	1	1																			22
9	40											1																				1					1																	3
5	39					1											6	4	1																1			1					1											17
10	38									1																							1								1													3
10	37											1							1		1																							1										4
2	36																																								1													1
7	35										2	3					2	2	1	4	8									1		1	1		2					1				2				1						31
1	34					2		2	1		4	1		1		1	34	15	8	6	1		3						2	1	1	3			4			1		2				1	3			1					1	105
1	33					2					1					1	1	2	1	1	1											1				1									2									14
6	32					1					2	1					4			2	2																													1				13
7	31	1															1		1		1																																	4
2	30																1		1																																			2
1	29					1	1				1						3			1	2														1				1	1														12
1	28					1	1								1		20	11	6	7	6			1					1	1	1	1	1		2			5	1	3	1		1					1	1					74
2	27																		1		1																															1		2
2	26																																															1						1
1	25										1								2		1											1																						5
1:2	24																																																					0
1	23					2		1			3						12	4	3	1	3		2						1			2			5			1	5			1	1			1	1							49
6	22					1		1									3	2		2															2		2																	13
4	21					2					1																											1										1						4
1	20						1				3		1			2	35	6		2	4		1								2		3		2		1		5	2	1							1						72
11	19								1		2	2		1			8	6	3	1	1				1								1	1	1		1		1				2		1									34
2	18																																																					0
2	17																																																					0
3	16															1	12	6	14	13	16				1	1	1		4			2	1		10		1	2	3	3	1	1	1		1					1				108
3	15															2	17	1	5	3	1			1						1			2	1	1		1		1		1			1				1						40
1	14				1	4	5	5		1						1	4	6	9	8	10	1							1	1					5				2						1									65
2	13			1					1			1																																										3
5	12										2										2																																	4
7	11					4		3				1					6	6	2		6													1	4				1															34
7	10														1		9	3	6		1								1			3	1		3		1		1			1			1									32
7	9					1		1			1						1	1	4	3	1													1	4			1		1				4	1									25
6	8			1		4	1				4	2	1			2	23	6	1	1	8												2		4		1		3	5	3	1			3				2	1				79
1	7							1				1					1	1			5														1																			12
1	6				1	7		7			9	1		1	1		55	21	8	6	15	3		1	1			1	3	1			1	1	3	2	4		4	5	3				1									170
6	5										1					3	2				1		1														1						1		1									15
1	4	2				4						1					3	4	1		8		1										1	1	1		1		2	1		1		1								1		34
6	3																6			1																	1																	7
1	2					1		2			6	3				1	27	15	4	1	15	1	1												4		1	2		4		1		1	1				1	2		1		95
1	1				1	1													1													1					1																	5

Wensleydale. The sparsity of *Cavusgnathus* in the shelf environments of the Gayle Limestone suggests that environmental factors exerted strong influence over the distribution of this genus. The specimens recovered are the largest conodont elements obtained from the Gayle Limestone, and they would have been the last to be removed by transportation or abrasion. Fourteen of the Pa elements of this genus were present in well-sorted calcarenites. Thus the robustness of the conodonts and their association with sediments deposited in higher energy environments suggest that *Cavusgnathus* preferentially inhabited more agitated environments. However, the well-sorted calcarenites are interpreted as representing reworking of carbonate sediments. Conodonts, particularly the robust *Cavusgnathus* Pa elements, could have been reworked with the other skeletal grains. Thus these occurrences of *Cavusgnathus* Pa elements in the Gayle Limestone may not record an indigenous fauna, but merely reflect the ability of the conodont elements to resist abrasion long after death. This would not preclude *Cavusgnathus* from the shelf environment of the Gayle Limestone, since four of the remaining six records come from other rock-types.

3.4. THE GENUS *MESTOGNATHUS*

Mestognathus is extremely sparse in the Gayle Limestone, only 6 Pa elements being recovered. Well-sorted calcarenites yielded four of these. Varker (1964) did not record *Mestognathus* from the Gayle Limestone. The sparsity of *Mestognathus* in the Gayle Limestone shows that it found some shelf environments to be unfavourable. Since the Pa elements are robust conodonts similar to those of *Cavusgnathus*, it may have had a similar distribution pattern. Unfortunately, too few specimens occur in the Gayle Limestone for any firm conclusions to be made.

3.5. THE GENUS *'SYNCLYDOGNATHUS'*

Varker (1967) found that *Synclydognathus* (formerly '*Apatognathus*') represented over 10% of the total conodont faunas of the Yoredale Group, and concluded that its distribution was facies-controlled. In the present study, 176 Pa, Pb and S elements of *Synclydognathus* have been obtained from the Gayle Limestone representing the species *S. geminus* and *S. libratus* (Varker, 1967; Rexroad and Varker, 1992). These include the discrete S elements '*Apatognathus*' *chauliodus* (31 specimens) 'A' geminus (47 specimens), *'A' libratus* (4 specimens) and *'A.' petilus* (6 specimens). The discrete Pb element *Ozarkodina laevipostica* (13 specimens) and the discrete Pa element *Polygnathus scitulus* (35 specimens). A further 73 fragmentary synclydognathids cannot be identified to species level. Unidentified elements include many fragments which also may be of synclydonathid origin. Rexroad and Thompson (1979) and Rexroad and Varker (1992) have reconstructed the *Synclydognathus* aparatus. The S and Pb elements of *Synclydognathus* are most abundant in the algal, dark calcilutes forming the top beds of the Gayle Limestone, but have been recovered from most rock types. The Pa element has a similar distribution, but unusually, is the most abundant species in a pale grey crinoidal calcilutite in the upper half of the Ray Gill Sike outcrop. Particularly well preserved S elements of *Synclyclognathus* were present in an algal calcilutite at the top of the *Gigantoproductus*-bearing bedset in Lockey Beck. It is noteworthy that two samples of bryozoa-rich calcilutites, from the uppermost 1.25 m at the same locality, did not yield synclydognathids despite conodont abundances of 55 and 168 specimens per Kg respectively. These results confirm that *Synclydognathus* was generally common in the shelf environment of the Gayle Limestone, as recognised by Varker (1967), but could be facies-restricted. The bryozoa-rich calcilutites in Lockey Beck probably represent reworked cores to stem calcirudite mounds, a localised, presumably very quiet environment, from which the synclydognathids may have been excluded. Unfortunately, none of the cores of the Gayle Limestone mounds are exposed.

3.6. THE GENUS *HINDEODUS*

Hindeodus cristulus, a multi-element skeletal apparatus (Ziegler, 1977) is represented by its Pa element (= '*Spathognathodus' cristulus*) and its M element (= *Neoprioniodus camurus*) in the Gayle Limestone. Only 2 specimens of the Pa element and 3 examples of the M element have been recovered. Also, there are no joint occurrences of Pa and M elements in the Gayle Limestone. The absence of oolites from the Gayle Limestone may explain the sparsity of *Hindeodus cristulus* in the latter formation.

3.7. RAMIFORM ELEMENTS

Very little attention has been paid to the responses of ramiform conodonts to environmental conditions. Nicoll & Rexroad (1975) referred to this aspect of conodont-distribution in the shallow shelf, Mississippian seas of central North America. Ramiform conodonts obviously responded to environmental influences. Many formed part of the same apparatuses as the elements, which are known to have restricted distributions. Other ramiform conodonts are parts of *Idioprioniodus*- or *Kladognathus* type apparatuses, composed exclusively of ramiform elements. Generally, ramiform conodonts are less robust than Pa elements and, in consequence, less likely to be preserved in identifiable form. For example, many Sc elements recovered from the Gayle Limestone cannot be identified, even to generic level. The diversity of conodont faunas of the Gayle Limestone is such that the recognition of apparatuses is difficult. Of 1570 identified conodonts, 989 are Pa elements. In the Gayle Limestone faunas, only 45 S elements including 13 Sd elements have been recovered. There are significantly fewer Pb (86 specimens) and M elements (148 elements) than Pa elements in the Gayle Limestone. The sparsity (71 specimens) of the individual elements of *Idioprioniodus* and *Kladognathus* may be due to their being less robust than the Pa elements of other apparatuses. However, an alterative explanation is that *Idioprioniodus* and *Kladognathus* lived in deeper water than did the majority of conodont organisms whose apparatuses contain Pa elements. However, the presence of *Idioprioniodus* and *Kladognathus* in the Gayle Limestone indicates that these multi-element genera were able to inhabit shallower waters during Brigantian times. Merrill & von Bitter (1976) concluded that *Idioprioniodus* was found in rocks deposited under low energy conditions. Such a response to environment may explain the occurrences of *Idioprioniodus* in the low-energy environment of the shelf lagoon represented by the Gayle Limestone.

4. ENVIRONMENTAL CONTROL OF CONODONT DISTRIBUTION IN THE GAYLE LIMESTONE

Stone (1991), on the basis of limited conodont faunas, has commented on environmental controls on Arundian conodonts. The sparsity of conodonts in the sediments now forming the lower half of the Gayle Limestone contrasts sharply with their much greater abundance in the upper half. Varker (1968) suggested that changes in the deposition-rates and changes in the abundance of conodont animals were the primary controls of conodont-distribution in the Yoredale Group Limestones. That the latter suggestion is correct is obvious, but the causes of the changes needs to be clarified. The former certainly had an influence, but its importance may have been exaggerated. The two largest faunas recovered in this study came from sections of less than average thickness, which supports the contention that a lower sedimentation rate is reflected in larger abundances of conodonts. However, this cannot be the sole control of conodont distribution in the Gayle Limestone for it would imply that the *Gigantoproductus*-bearing dark calcilutites accumulated many times more rapidly than the algal dark calcilutites. The former have conodont abundances which never exceed 10 specimens per Kg, whereas those of the latter may exceed 200 specimens per Kg. Higher sedimentation rates may be reflected in greater turbidity of the water body, and this factor could influence the distribution of the conodont animals.

The factors which may have influenced conodont-distribution in the Gayle Limestone can be grouped under three major headings (i) ambient environment (depth of water, wave energy, turbidity of water, water interchange rates, salinity variations, temperature) (ii) substrate (proximity to shoreline, overall environment of the shelf, relationship of environments to one another, influence of local substrates, if conodonts were nekkobenthic) and (iii) nutrition (availability of food, competition for food, susceptibility to predation). Many of these parameters are interrelated and cannot be considered singly. It is unlikely that any one was the sole control over conodont-distribution. Some, particularly depth, are rarely rigorously defined. Absolute depth below sea level can rarely be determined and is less significant than depth relative to surge base and wave base, which have considerable influence on substrate conditions and energy levels in the water column. Thus the influence of depth is closely related to wave-energy. Wave-energy can also have an intimate association with distance from shore and may induce stirring of bottom sediments to produce turbid water. Unfortunately, as with depth, wave-energy is not quantitatively defined. In consequence, it is usually considered in terms of important levels in the water column, notably the intertidal zone, surge-base and wave-base. These levels cannot be defined quantitatively for they are dependent on sea-floor topography. The environmental setting of the Gayle Limestone was such that, in the basin immediately to the south of the Askrigg Block, wave-base would have been at a greater depth than it was on the shelf, though not as deep as would have been attained in the open oceans of the time. A great deal of wave-energy was rapidly dissipated along the shelf edge in consequence of the abrupt shallowing, and even more in the crinoid thickets where the stems baffled the waves. This resulted in a sheltered area in the central part of the shelf where lime mud accumulated.

Lees (1975) has proposed that salinity and temperature are the prime controls of carbonate sedimentation on a world-wide scale. However, there is unlikely to have been much fluctuation in either salinity or temperature during deposition of the Gayle Limestone. Walker (1964) attempted to recognise salinity fluctuations in the Yoredale Group by measuring concentrations of boron. His results show that boron contents are generally highest in marine limestones and generally lowest in sandstones. The boron content also varies within individual limestone formations, including the Gayle Limestone. This might be taken to indicate salinity fluctuations, but the faunal evidence is in conflict. Throughout its thickness, the Gayle Limestone contains "normal marine fossils". Sessile echinoderms are exclusively marine in modern environments, and corals are most successful in salinities of 34-36‰ (Heckel, 1972). Crinoids were the primary source of bioclasts in the pale calcilutites and calcarenites of the Gayle Limestone. Corals, both solitary and colonial, were important faunal constituents of many dark calcilutites. The success of these two fossil groups in the Gayle Limestone is strong evidence for continuity of normal marine salinities on the shelf. Temperature is also unlikely to have shown much variation. Certainly shelf seas are warm (Bathurst, 1975), and water temperatures increase in association with shallowing. However, the Gayle Limestone was deposited on a shelf of near uniform depth, apart from a shoal along the shelf edge, and water temperatures therefore were presumably fairly constant. Thus temperature and salinity are unlikely to have had more than minor influence over conodont distribution in the Gayle Limestone.

Proximity to shore and the type of shoreline would influence many factors including energy and salinity. The Yoredale Group consists of the clastics of a large delta complex and shallow marine carbonates. During deposition of the lower half of the Gayle Limestone, the outermost, fossiliferous prodelta shales occasionally prograded into the area of carbonate deposition, but during deposition of the upper beds, the delta-front had been displaced a considerable distance to the north. This is shown by the widespread deposition of the Gayle Limestone and its northern equivalent, the Lower Little Limestone (Burgess & Mitchell, 1976). The shoreline was probably remote enough not to have influenced directly the distal shelf environments. Water discharged from the river mouth must have had more widespread effects. It would have diluted the sea, thus counteracting any tendency towards increased salinities at the least, and causing reduced salinities at most. The water carried in it suspended sediment of silt and clay sizes which were turbid in the river discharge and, to a lesser extent, in the underlying sea-water. Light penetration would be diminished wherever there were such turbid waters. Corals, bryozoans and crinoids all prefer non-turbid water, as they are suspension feeders (Heckel, 1972). The abundance of algal-coated grains in the Gayle Limestone indicates that adequate light- - penetration for photosynthesis existed at the shelf lagoon floor. Thus turbidity is believed not to have affected the conodont-bearing organisms of the Gayle Limestone.

The low diversity of conodont animals in the Gayle Limestone suggests that they were predators. The exact nature of their food source is unknown, although plankton seem a likely possibility. The recognition of a shelf edge has important implications on the availability of nutrients. Upwelling at the shelf edge is recorded in the contemporaneous Bowland Shale of Newton Gill, Long Preston (SD 851584) in the occurrence of rudite layers rich in phosphate nodules, implying phosphate-rich waters similar to those off Southern California at the present day. Presumably such upwelling would generate rich plankton blooms, the beginnings of the food chain. The depth of the Pennine Basin is uncertain, but probably in the range 1-2 Km, and the magnitude of upwelling cannot be determined. However, organic productivity in equatorial and subtropical belts is enhanced by upwelling along edges of continental shelves. In modern environments, such oceanic upwelling is particularly strong on the western sides of continents in the northern hemisphere and on the eastern sides in the southern (Selwood, 1978). Continental reconstructions for the Lower Carboniferous (e.g. Smith *et al.*, 1973) show the British Isles to lie just south of the equator, on the south-eastern side of a large continent. The Pennine Basin was of limited extent, separated from the contemporaneous ocean by the shelf areas of the English Midlands and Wales. Nonetheless, during the Dinantian Subperiod, this area lay in latitudes where upwelling was presumably important, and probably provided a rich source of nutrients to conodont animals inhabiting the near-surface layers of the basin and the adjacent shelf. The circulation of waters on the shelf, possibly in gyres radiating from tidal channels through the calcarenite shoals of the shelf-edge, may have played an important role in distributing the nutrients across the shelf, leading to wide distribution of the organisms exploiting the food supply. The abundance of crinoids along the shelf-edge is probably related to this nutrient supply. Competition for the nutrients between organisms may have been strong, but the amount supplied seems to have allowed successful exploitation by several fossil groups. The abundance of these would have attracted larger predators, of which fish and cephalopods are known, and were most likely to have included conodont animals in their diet. It seems likely that predation did not significantly reduce the numbers of conodont-elements which were included in the sediments.

The factors listed above, which have not been rejected as having significant influences on conodont-distribution, are wave-energy, depth, availability of nutrients, and the overall environmental setting of the shelf. The close links between wave-energy and depth have already been stressed. It is rarely possible to give values for depth, but the presence of stem-calcirudite mounds gives a minimum depth of 10 m, and a likely depth of 20 m, for the Wensleydale area during deposition of the top beds of the Gayle Limestone. Wave-base was very shallow because of the rapid decrease in energy across the shelf-edge. Tidal channels, believed to cut the crinoid meadows of the shelf edge, must have been subtidal, for the crinoids flanking them could not have survived unless totally immersed in water. The channels would have been the main routes for on-shelf flow during rising tides and off-shelf flow during falling tides. During the former, these channels would have been the means by which nutrient-rich waters flowed into the shelf lagoon. Thus energy, in the form of tidal flows, probably had an indirect influence on conodont distribution in the Gayle Limestone by controlling the availability of nutrients. The influence of depth is not obvious. The depth of water during deposition of the upper beds (10-20 m) allowed conodont animals to be fairly abundant in the shelf waters. However, although the overall depositional environment of the lower part of the Gayle Limestone does not appear to have been significantly different, conodont faunas are sparse in that interval. The nutrients were presumably available at the shelf-edge, but somehow failed to reach the interior parts of the shelf-lagoon. It is possible that the absence of stem calcirudite mounds at this level indicates slightly shallower waters which were inhabited by large sessile gigantoproductids. The spat of these gigantoproductids must have been extremely abundant in the shelf environment at this time. The nutritional requirements of this spat is unknown, but perhaps they were in direct competition for the food supply with the conodont animal. Local larger concentrations of conodonts in the lower part of the Gayle Limestone (e.g. in the algal calcilutite 1.05 m above the base of the Lockey Beck outcrop) may reflect slightly deeper areas of the shelf or proximity to a tidal channel. The shelf-edge shoal seems to have been a more effective barrier at this time, possibly because it was of lithified carbonate sediments and was thus interrupted by fewer tidal channels, therefore limiting the rate of water-interchange and thus the number of conodont animals able to find their way into the shelf lagoon. This seems a more reasonable hypothesis than Varker's (1968) proposal that sedimentation rate was one of the prime controls of conodont-distribution in the Yoredale Group.

The width of the shelf-edge shoal can be approximated as the width of crinoidal calcarenite, which is widest in the most easterly outcrops and narrows to a minimum in the south-west of the Askrigg Block (see Fig. 7). There is, moreover, an upward, northward expansion of the crinoidal calcarenite throughout its length. This shows striking similarity to the configuration of the shelf-edge shoal off Belize, described by Matthews (1966), where the wider parts of the shoal are associated with shallower lagoon waters than the narrower parts. It seems to suggest that the Gayle Limestone lagoon was deeper in the west of the Askrigg Block than in the east. Such a configuration would result in the production of lesser quantities of lime mud in the west than in the east, therefore generating thinner calcilutites in the lagoon and permitting more obvious terrigenous mud dilution. This matches precisely the thickness-variations in the Gayle Limestone calcilutites. There is another similarity between the modern Belize shelf and the Gayle Limestone - the absence of oolite shoals. One important difference suggests itself, the Belize shoal is covered by water varying from zero to 2 metres in depth; the Gayle Limestone shoal seems to have been significantly deeper than this to permit the crinoid thickets their optimum growth. Thus the Askrigg Block was submerged to a minimum depth of several metres over the shelf-edge shoals, below the optimum depth for oolith-formation (Newell *et al.*, 1960). The shelf lagoon was significantly deeper, probably deepest immediately inshore of the shoal, and deepened westwards across the Block. This gave a limited range of stenohaline environments in which the conodont animal could live. Those forms adapted to shallow-water, high energy environments are lacking.

It is suggested that the environmental setting of the Gayle Limestone was the primary control over its conodont faunas. The importance of an abundant food supply from the adjacent basin has been stressed, as has the presence of suitably deep water on the shelf. This is in agreement with a previous suggestion (Austin, 1976) that some parts of shelves had water depths which permitted conodont animals typical of basinal environments to exist within the shelf-environment. Westward-deepening of the Gayle Limestone lagoon, especially if it extended into even deeper waters on the west side of the Dent Fault, would provide a suitable deep shelf environment. It could also have made an end to the shelf-edge shoal, as in modern Belize (Matthews, 1966), thus permitting a virtual open connection along the west side of the Dent Fault with the Askrigg Block lagoon, and thus a gradual lifting of wave and surge-base, instead of the abrupt change which must have occurred along the eastern parts of the Askrigg Block. Such a configuration would not alone account for the sparsity of conodonts in the lower half of the Gayle Limestone and for their comparative abundance in the upper half. However, if the shelf edge shoal formed a continuous barrier during deposition of the lower beds, but there was an open connection to the Pennine Basin during deposition of the upper beds, then this would account for the vertical distribution of conodonts in the Gayle Limestone. Such a change in the extent of the shoal would have required depression of an area west of Ingleton at the present south-west corner of the Askrigg Block. Significantly, the deposition of fine quartz sands and clean washed calcarenites, which occur in the middle part of the Gayle Limestone, is interpreted as resulting from successive uplifts along the line of the Howgill Fells anticline. Contemporaneous tectonic depression of the area west of Ingleton would not only offer a possible mechanism for a change in the configuration of the shelf-edge shoal, but would have occurred during the relevant time period to account for the vertical distribution of conodonts in the Gayle Limestone. The occurrences of *Gnathodus*, and especially of *Gnathodus bilineatus bilineatus* (indicative of deeper-water, more basinal facies), in the conodont faunas of the Gayle Limestone, appear to confirm it. The abundance of some species of *Gnathodus* and *Lochriea* in the top beds of the Gayle Limestone, and the sparsity of forms such as *G. bilineatus bilineatus*, is significant. If gnathodids were basin-dwellers, as the faunas obtained by Higgins (1975) in the southern Pennines seem to indicate, then they occupied different ecological niches within that basin. Forms such as *G. girtyi*, *G. homopunctatus* and *L. commutata* must have been successful in the upper layers of the seas, though their maximum depth limits are unknown. Insurge of waters along the deeper water zone west of the Dent Fault brought these conodonts to shallower depths than normal.

G. bilineatus bilineatus, which either lived in slightly deeper waters or was simply less common than the other conodonts, is sparse in the Gayle Limestone faunas and restricted to the south-western part of the Askrigg Block, that is, to the deeper part of the lagoon. Shelf-associated genera found in sediments of agitated or euryhaline environments, such as *Cavusgnathus* and *Mestognathus* (Austin, 1976), occur sparsely in the Gayle Limestone. Encroaching basinal genera may have outcompeted these two genera in the environment of the Gayle Limestone, facilitated by the quiet stenohaline conditions and suitable water depths. There is weak evidence, from the occurrences of *Cavusgnathus* and *Mestognathus* on the north-west corner of the Askrigg Block, that these two genera were more common to the west of the Dent Fault, significantly in the area of the Howgill Fells Anticline, previously indicated as the source of the well-sorted calcarenite. Slight uplift of the Howgill Fells Anticline would have generated shallows as well as erosion, and provided a definitely agitated environment and possible euryhaline conditions. *Synclydognathus*, common in the Yoredale Group (Varker, 1967) but absent from the uppermost Brigantian Stage of basinal facies in the southern Pennines (Higgins, 1975), was confined to shelf environments of more stenohaline type than *Cavusgnathus*, its common associate in faunas from the South-West Province of the British Isles (Rhodes *et al.*, 1969), and the United States (Collinson *et al.*, 1971). Synclydognathid bearing animals seem to have been able to compete with the gnathodid-bearing animals in the environment of the Gayle Limestone. Thus *Synclydognathus* appears to occupy an ecological niche transitional between those of *Cavusgnathus* and *Gnathodus*, but overlapping the ecological tolerances of both.

The observed distribution of conodonts in the Gayle Limestone does not fit satisfactorily into commonly used models of conodont-ecology (Seddon & Sweet, 1971; Barnes & Fahraeus, 1975). The Gayle Limestone faunas show that lateral segregation of conodonts did occur, contrary to the pelagic model, but offered by Barnes & Fahraeus (1975) as the principal evidence for a nektobenthonic mode of life. However, the recognition in the Gayle Limestone of conodonts, which are abundant in basinal successions of near-equivalent age, suggests that some species display crude depth-segregation and were more common in the near-surface layers of the sea. This would appear to support the pelagic model rather than the nektobenthonic model. Klapper & Barrick (1978) also postulated that a more complex ecological model, characterised by interaction of several factors rather than controlled by a single factor, may be necessary to explain conodont distribution. The faunas of the Gayle Limestone suggest that this latter approach is more realistic. For example, the abundance of "basin-associated" conodonts in the Gayle Limestone, where "shelf-associated" genera are sparse, cannot be explained by any existing model of conodont ecology. Merrill & von Bitter's (1976) suggestion that wave-energy is a controlling factor of conodont distribution appears to be valid for the Gayle Limestone. Conodont-organisms, normally living at greater depths in the basin because of the thicker zone being subject to wave-agitation, could successfully enter the gentle shelf environment as a result of the shallowing of wave base, especially if a broad gap, associated with a deeper water zone, occurred at the shelf edge in addition to the tidal channels piercing the crinoid thickets. It is not suggested that this one factor alone is responsible for conodont distribution in the Gayle Limestone. The other suggestions of Merrill & von Bitter appear to have had no direct influence on the conodont faunas. The normal salinity of the shelf waters, by allowing more offshore conodont-bearing organisms to inhabit that environment, may have exerted an indirect influence in that these organisms outcompeted those normally living on the shelf. This is in keeping with Klapper & Barrick's (1978) statement that a limited number of species were confined to rigorous, fluctuating hydrodynamic regimes, whereas there were diverse associations of species in offshore, stable hydrographic regimes. The Gayle Limestone does not represent the former environment, and the sparsity of conodonts generally believed to be more successful in such conditions is an expected result.

5. CONCLUSIONS

The results obtained in this study show that detailed sedimentological analysis reveals deficiencies in models of conodont-ecology which focus on one dominant parameter. The conodont faunas of the Gayle Limestone were influenced by the proximity of shelf to basin, availability of nutrients, interaction of wave-energy and depth, and the shelf-topography, including the biogenically -produced shoal along the southern edge of the shelf. Other shelf environments need not be subject to the same influences. In consequence, different conodont faunas might be expected in other environments of Brigantian age. For example, a shelf-edge environment consisting of a reef complex might be expected to yield those species confined to rigorous, fluctuating hydrodynamic regimes (Klapper & Barrick, 1978). Brackish or hypersaline lagoon sediments might predictably yield euryhaline species such as *Cavusgnathus windsorensis* (von Bitter, 1976). Broad, shallow, very gentle carbonate ramps similarly would have been inhabited by restricted conodont faunas. Shelves of extreme shallowness might have been unattractive to even euryhaline, high-energy conodont animals. Modern carbonate environments are the results of interactions between numerous physical and chemical factors in widely different settings. It does not seem contentious to suggest that the Dinantian rocks of the British Isles represent a similar complexity of environments. If this is accepted, then it follows that different conodont faunas of equivalent age represent the responses of the conodont animals to this variety of environmental settings. Such responses will only be elucidated after recognition of separate environmental settings, by means of detailed sedimentological analysis such as that performed on the Gayle Limestone by Davies (1981).

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PLATE 1
Thin sections of the Gayle Limestone

A. Algal calcilutite (or wackestone). Oncolites (oncoids) with large intraclast nuclei (bottom right and top right) have thin encrustations of *Girvanella* (= algal coated intraclasts). There is extensive boring in the intraclast nuclei adjacent to the algal laminae. The enclosing sparse biomicrite contains abundant brachiopod (centre) and crinoid (lower centre) remains. Intraclasts include bryozoa with mud-infilled zooecia (upper left). Gayle Limestone, Lockey Beck (SD 855735), Pen-y-Ghent Gill. Sample GL14 was collected from this bed.

B. Bryozoa-bearing calcilutite (or bryozoan wackestone). Sparse biomicrite containing abundant fenestellid bryozoa and crinoid grains (top left and top right). Some of the micrite matrix has recrystallised to ferroan dolomite microspar (bottom right). Gayle Limestone, Lockey Beck (SD 855735, Pen-y-Ghent Gill. Sample GL15 was collected from this bed.

C. Coral-bearing calcilutite (or wackestone). *Lithostrotion junceum* in bioclastic micrite. Body cavities and voids (fenestral fabrics?) in micrite are filled with a non-ferroan calcite cement. Gayle Limestone, Hawkswick Moor (SD 941723), Littondale.

D. Pale calcilutite (or mudstone). Gastropod and other molluscan shell fragments in sparse biomicrite containing abundant sponge spicules. Non-ferroan calcite cements, of different ages, have replaced the molluscan shells and infilled the body chamber of the gastropod. The sponge spicules have been replaced by non-ferroan calcite and their axial canals are mostly micrite-filled. Gayle Limestone, Ray Gill Sike (SD 905894), Wensleydale. Sample GL40 was collected from this bed.

E. Crinoidal calcarenite (or packstone) from bedded Gayle Limestone. Packed bio-micrudite containing abundant disarticulated ossicles and columnals. Syntaxial overgrowths are confined to the central canals of ossicles and columnals because of the inhibiting effect of the micrite matrix. Gayle Limestone, Cray Gill (SD 943794), Wharfedale. Sample GL31 was collected from this bed.

F. Crinoidal calcarenite (or packstone) containing pyritised oncolites (oncoids). Packed biomicrite containing crinoid grains, bryozoa (upper left and lower left) and brachiopods (centre right). Gayle Limestone, Ray Gill Sike (SD 905894), Wensleydale. Sample GL42 was collected from this bed.

G. Stem calcirudite (or crinoidal rudstone) from bioherm. Packed biomicrudite in which lime mud has inhibited the development of overgrowths on crinoid debris. Sutured contacts between crinoid grains are the result of pressure solution during early compaction. Gayle Limestone, Bank Wood (SD 914849), Cragdale. Sample GL49 was collected from this bed.

H. Stem calcirudite (or crinoidal rudstone) from bedded Gayle Limestone. Packed biomicrudite containing lengths of stem and disarticulated ossicles. Large crinoid fragments have thin syntaxial overgrowths formed by neomorphic replacement of the micrite matrix. Gayle Limestone, Little Scoska Moor (SD 910724), Littondale. Sample GL12 was collected from this bed.

I. Well sorted calcarenite (or grainstone). Biosparite containing abundant brachiopod and crinoid remains with micrite envelopes (= cortoids) and minor amounts of foraminifera and green algae. Gayle Limestone, River Rawthey (SD 719974). Sample GL62 was collected from this bed.

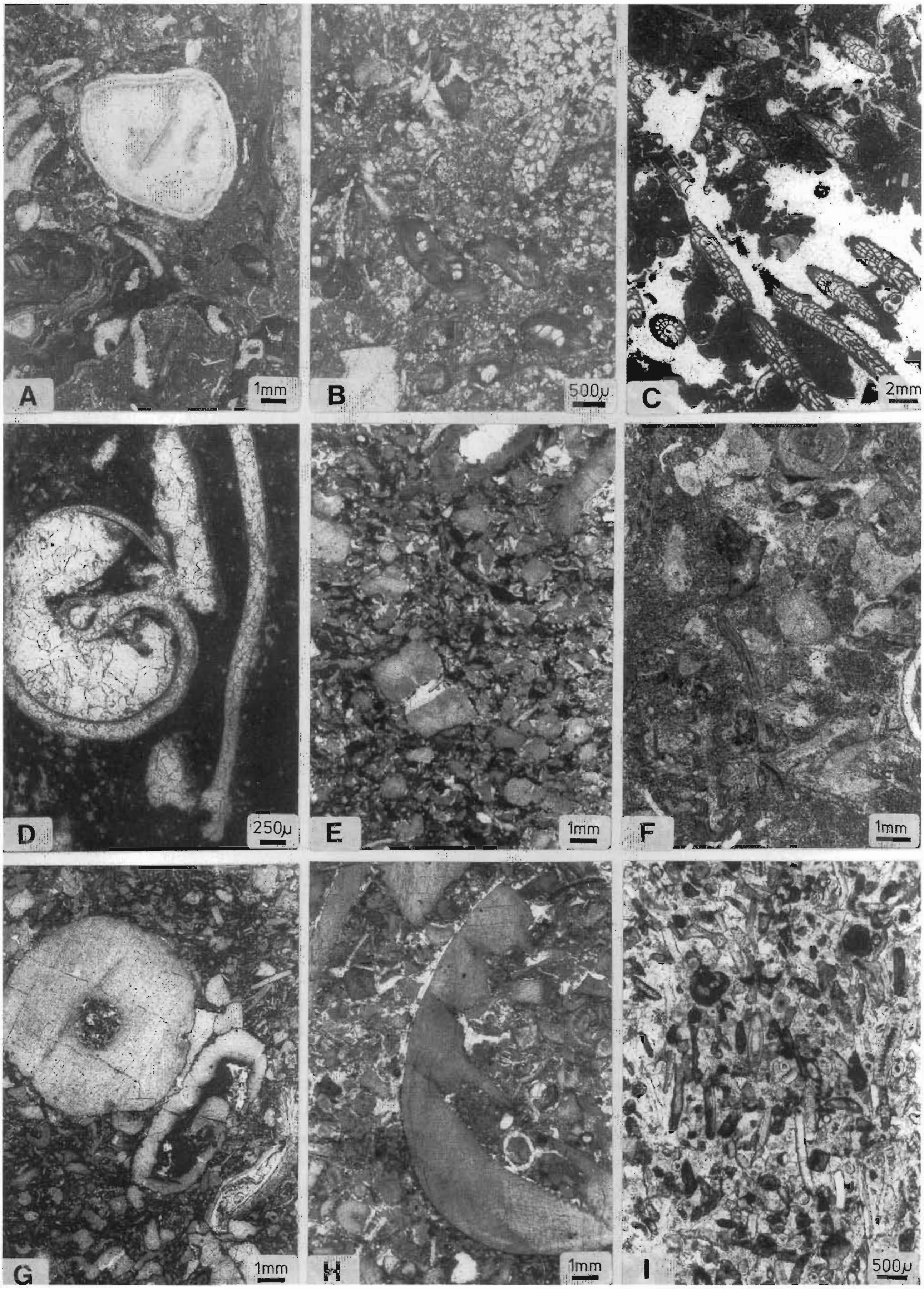
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PLATE 2
Gayle Limestone conodonts

All specimens coated with ammonium chloride and magnified x 45

1a,1b,1c *Gnathodus girtyi* Hass : Upper, lower and outer lateral views of Pa element specimen GyL 2 Sample GL20.

2a,2b *Gnathodus bilineatus bilineatus* (Roundy): Lower and upper views of Pa element specimen GyL 8 Sample GL16.

3a,3b,3c *Gnathodus homopunctatus* Ziegler: Upper, lower and lateral views of Pa element specimen GyL 3 Sample GL14.

4a,4b,4c *Lochriea mononodosa* (Rhodes, Austin Druce): Upper, lower and lateral views of Pa element specimen GyL 15 Sample GL56.

5a,5b,5c *Lochriea commutata* (Branson & Mehl): Upper, lower and lateral views of Pa element specimen GyL 13 Sample GL2.

6a,6b *Gnathodus symmutatus* Rhodes, Austin & Druce: Upper and lateral views of Pa element specimen GyL 4 Sample GL6.

7a,7b,7c *Lochriea nodosa* (Bischoff): Upper, lower and lateral views of Pa element specimen GyL 14 Sample GL34.

8a,8b,8c *Mestognathus* sp. indet.: Upper, lower and inner lateral views of Pa element specimen GyL 23 Sample GL52.

9a,9b,9c *Cavusgnathus unicornis* Youngquist & Miller: lower, upper and inner lateral views of Pa element specimen GyL 22 Sample GL52.

10 *Synclydognathus* Pa element *'Spathognathodus scitulus'*, (Hinde): Lateral view of specimen GyL 29 Sample GL41.

11 *Hindeodus cristula* (Youngquist & Miller) Pa element: Lateral view of speciment GyL 10 Sample GL20.

12 *Neoprioniodus peracutus* (Hinde): Lateral view of M element specimen GyL 17 Sample GL20.

13a,13b *Hibbardella acuta* Murray & Chronic: Lateral and posterior views of Sa element specimen GyL 5 Sample GL41.

14 *Neoprioniodus* cf. *N. parvus* Higgins: Lateral view of M element specimen GyL 18 Sample GL33.

15 *Synclydognathus* S element '*Apathognathus laeviposticus*' (Rexroad & Collinson): Inner lateral view of specimen GyL 25 Sample GL14.

16 *Roundya barnettana* Hass: Posterior view of Sa element specimen GyL 36 Sample GL23.

17 *Neoprioniodus scitulus* (Branson & Mehl): Lateral view of M element specimen GyL 16 Sample GL4.

18 *Neoprioniodus singularis* (Hass): Lateral view of M element specimen GyL 12 Sample GL14.

19 *Ozarkodina delicatula* (Stauffer & Plummer): Lateral view of Pb element specimen GyL 6 Sample GL23.

20 *Synprioniodina microdenta* Ellison: Lateral view of M element specimen GyL 9 Sample GL54.

21 *Synclydognathus* S element '*Apatognathus petilus*' Varker: Inner lateral view of specimen GyL 30 Sample GL19.

22 *Synclydognathus* S element '*Apatognathus chauliodus*' Varker: Inner lateral view of specimen GyL 28 Sample GL14.

23 *Synclydognathus libratus* (Varker): Inner lateral view of S element specimen GyL 24 Sample GL6.

24 *Synclydognathus geminus* (Hinde): Inner lateral view of S element specimen GyL 26 Sample GL33.

25 *Synclydognathus* S element '*Apatognathus scalenus*' Varker: Inner lateral view of specimen GyL 27 Sample GL14.

26 *Hindeodus cristula* (Youngquist & Miller) M element: Lateral view of specimen GyL 11 Sample GL19.

27 *Lonchodina furnishi* Rexroad: Inner lateral view of S element specimen GyL 31 Sample GL34.

28 *Ligonodina levis* Branson & Mehl: Inner lateral view of S element specimen GyL 32 Sample GL28.

29 *Hindeodella germana* Holmes: Lateral view of Sc element specimen GyL 42 Sample GL6.

30 *Hindeodella ibergenis* Bischoff: Lateral view of Sc element specimen GyL 7 Sample GL6.

31 *Hindeodella simplex* Higgins & Bouckaert: Lateral view of Sc element specimen GyL 20 Sample GL34.

32 *Hibbardella milleri* Rexroad: Posterior view of Sa element specimen GyL 41 Sample GL16.

33 *Magnilaterella complectens* (Clarke): Inner lateral view of S element specimen GyL 40 Sample GL16.

34 *Ligonodina tenuis* Branson & Mehl: Inner lateral view of S element specimen Gyl 35 Sample GL19.

35 *Hindeodella cawdorensis* Higgins: Lateral view of Sc element specimen GyL 19 Sample GL59.

36 *Ligonodina roundyi* Hass: Inner lateral view of S element specimen GyL 34 Sample GL23.

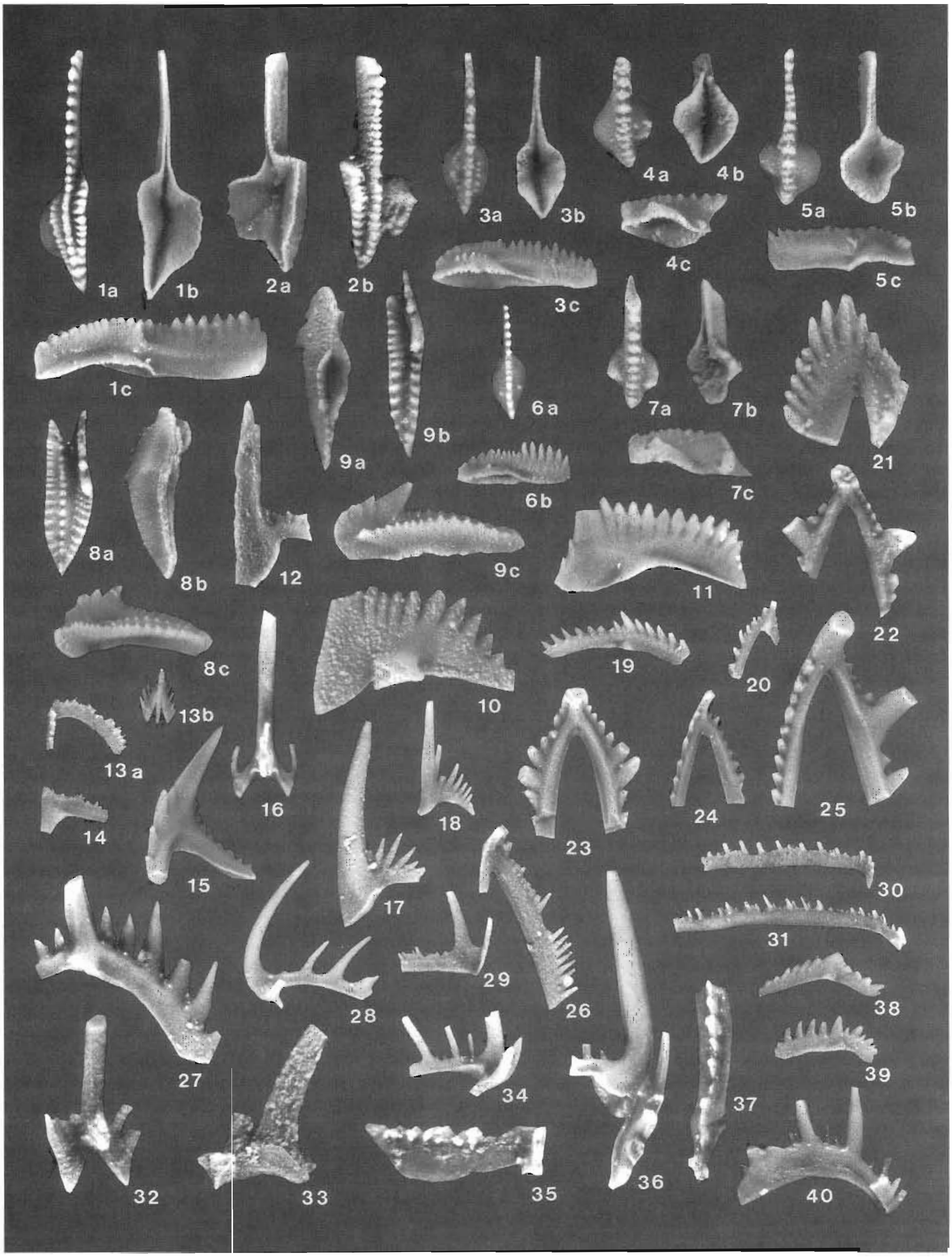
37 *Geniculatus* sp. indet.: Upper view of specimen GyL 39 Sample GL34.

38 *Ozarkodina collinsoni* Higgins: Lateral view of Pb element specimen GyL 37 Sample GL2.

39 *Subbryantodus subaequalis* Higgins: Lateral view of Pb element specimen GyL 38 Sample GL2.

40 *Kladognathus macrodentatus* (Higgins): Inner lateral view of S element specimen GyL 43 Sample GL20.

Specimens deposited in the collections of the Department of Geology, University of Southampton, England.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