CONODONTS OF THE GENUS *APATOGNATHUS* BRANSON AND MEHL FROM THE YOREDALE SERIES OF THE NORTH OF ENGLAND

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ABSTRACT. The paper describes six species of conodonts assigned to the genus *Apatognathus* Branson and Mehl 1934, from the Yoredale Series of the Askrigg and Alston Blocks in northern England. *A? chaulioda*, *A? cuspidata*, *A? librata*, *A? petila*, and *A? scalena* are new species, whilst *A? gemina* (Hinde) is redescribed. The previously recorded occurrences of the genus are listed along with a consideration of possible homeomorphy. The orientation of the genus is reorganized and the distribution of the Yoredale species through the series described. The possibility of facies control of the genus during Carboniferous times is also discussed.

THE Yoredale Series consists of repeated alternations of shallow-water sediments, which, in the type-area of Wensleydale, NW. Yorkshire, extend upwards from the Upper Viséan (D_1–D_2 junction) into the Namurian (E_1–E_2) and thus span the Lower/Upper Carboniferous boundary. According to Dunham (1948) each unit or cyclothem can be stated to consist in general terms of: (1) marine limestone; (2) marine shale; (3) unfossiliferous (?non-marine) ferruginous shale; (4) sandy shale, shaley sandstone or 'grey-beds' (interbedded shales, siltstones, and sandstones); (5) sandstone; (6) ganister or underclay; (7) coal; variations of the succession for individual cyclothems may be considerable. This type of sedimentary succession occurs over practically the whole of the stable Askrigg and Alston Block areas in the north of England and also extends northwards into the Northumberland Trough and Scottish Borderland.

Identification of beds, recognition of their age and subsequent correlation from one area to another within the distribution of the Yoredale Series is important, since the series occupies a critical stratigraphic horizon spanning the Viséan–Namurian junction. So far most palaeontologic evidence has concerned only the macrofossils and it is unfortunate that on this evidence accurate identification of age and stratigraphic correlation have proved difficult. Thus the coral/brachiopod zones are somewhat insensitive for such a relatively short period of time and under the prevailing environmental conditions. Goniatites, although extremely sensitive (Rayner 1953; Johnson, Hodge, and Fairbairn 1962) are of rare occurrence and thus of limited application. There has, therefore, existed a pressing need for a study of all aspects of the microfaunal and microfloral content of the Yoredale Series, in the hope of providing an effective means of identification and correlation. Of the microfauna, conodonts appear to offer considerable possibilities.

These fossils, which are of world-wide occurrence, show a large amount of variation in form and rapid evolutionary changes during their long stratigraphic history. In addition they have the added advantage over goniatites that their distribution often occurs over a wider lithologic range. Their remains have been obtained in fairly large numbers from all the major Yoredale limestones digested and from some of the associated shales. The present paper presents the first account of some aspects of these conodont faunas

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and their application in studies of the Yoredale Succession. The study is concerned with the succession within the limits of the Hawes Limestone (basal D_2) and the Mirk Fell Beds (E_2) (see text-fig. 1).

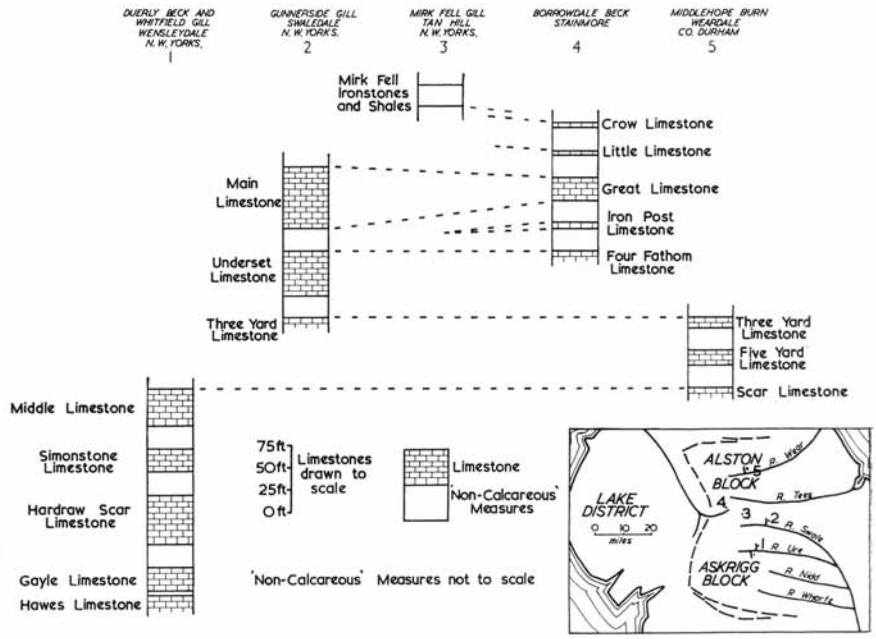
The complete conodont faunas of the Yoredale Series have been examined with a view to producing a zonal scheme for the succession. The present paper, however, is restricted to a single genus, assigned to *Apatognathus* Branson and Mehl 1934, since it is considered necessary to attempt an elucidation of the various problems concerning this genus before such a zonal scheme may be erected. *Apatognathus* represents over 10% of the total conodont fauna in many of the samples treated and its appearance in the Yoredale Series in relatively large numbers and displaying a wide degree of variation is of considerable interest. The genus is relatively uncommon and until recently (Lindström 1964, see also p. 126) was considered to range from Upper Devonian to Triassic or Cretaceous strata. The sporadic stratigraphic and geographic distribution of this genus have resulted in a number of problems, some of which are considered in the light of information resulting from the Yoredale occurrence. Another problem to be considered is the great amount of confusion concerning the orientation of the *Apatognathus* units. Six species are described, five of which are new.

History of Yoredale Studies. Although it is over 130 years since the classic work of Sedgwick (1835) and Phillips (1836), the amount of literature concerning the series in the type-area of Wensleydale, is small. The only accounts published between 1836 and 1958 were those of Hudson in 1924, when he discovered faunal rhythms within the larger scale sedimentary rhythms and 1933, when he revised his earlier work. The account by Moore (1958), 'The Yoredale Series of Upper Wensleydale and adjacent parts of north-west Yorkshire', dealt primarily with lateral variations in lithology and the palaeogeography governing deposition of the series. There are, however, numerous accounts of the Yoredale succession in regions outside the type-area and a detailed historical survey up to 1953 is given by Rayner (1953). Since 1958 interest in these sediments has intensified, particularly with reference to their conditions of deposition.

Methods of Study. Samples were collected of Yoredale limestones and some of the associated shales from various localities of the Askrigg and Alston Blocks (shown in text-fig. 1). There was an intentional degree of stratigraphic overlap or duplication in the collection of material from one collecting area to another. The sampling interval varied, the Gayle and Middle Limestones being sampled at 1-ft. intervals and in no case did the interval exceed 5 ft. Each sample weighed up to 3 kg. of which $1\frac{3}{4}$ kg. were chosen as a standard weight for digestion in 10–15% acetic acid. Shale samples, the most important of which were the Mirk Fell shales, were broken down by methods which variously included the use of sodium hypochlorite, hydrogen peroxide, and white spirit, the method chosen depending largely upon the characteristics of the shale. Some calcareous shales were treated with acetic acid in the normal manner. All residues were washed and sieved, the required size fraction passing a 20-mesh sieve and being retained by a 100-mesh sieve. These wet fractions were finally dried and the conodonts extracted by hand-picking.

PREVIOUSLY RECORDED OCCURRENCES OF THE GENUS *APATOGNATHUS*

For many years the genus *Apatognathus* was considered to be an index fossil of the Upper Devonian (Branson and Mehl 1934; Ellison 1946; Weller *et al.* 1948; Mehl 1960). Specimens referred to this genus were, however, found at higher horizons during recent



TEXT-FIG. 1. Chart illustrating the Yoredale Succession studied and the location of sampling areas.

years (see below) and the genus was thought to occur in Upper Devonian, Middle Tournaisian, Upper Viséan–Lower Namurian or Middle Mississippian, Permian, Middle Triassic, and possibly Upper Cretaceous strata. Both the stratigraphic and geographic distribution of these occurrences are important considerations in various sections of this report and a summary is therefore outlined below.

Three species of *Apatognathus* have been recorded from the Upper Devonian of Europe, the U.S.A., and Africa. The most restricted in range is the type-species, *A. varians* Branson and Mehl 1934, recorded in America from the Grassy Creek Formation and also from similar horizons by Klapper (1958) and Klapper and Furnish (1962). In Europe the species is recorded in zone toV from Germany by Bischoff and Ziegler (1956) and Freyer (1961).

The two remaining species, *A. lipperti* Bischoff 1956 and *A. inversus* Sannemann 1955, differ considerably from the type-species. Lindström (1964, p. 153) commented that:

'Several species with the same plan (as Ziegler's genus *Gnamptognathus*) but without the accessory process have been brought to *Apatognathus* e.g. *A. lipperti* Bischoff 1956. These species, which do not resemble the type-species of *Apatognathus* are herein brought to *Gnamptognathus*.' Lindström, in addition, considered that some species of *Falcodus* (Bischoff and Ziegler 1957; Ziegler 1958) seem to belong to *Apatognathus*. The Upper Devonian thus contains the type-species of *Apatognathus* plus possibly some representatives at present identified as *Falcodus*.

In spite of the very extensive study given to the Lower Carboniferous of Europe and the Mississippian of America by conodont workers, there is only one record, from Belgium, of *Apatognathus* occurring between the base of the system and the Upper Viséan (Europe) or the upper part of the Valmeyeran Series (U.S.A.). This anomalous situation has been noted by several authors. Scott and Collinson (1961) remarked that in spite of the occurrence of the genus in the St. Louis Formation, equivalent to the base of the *Goniatites* stage of Germany, they have not found it in the Hannibal, Chouteau, or any of the other Lower Mississippian Formations of Western Illinois. They therefore concluded that the Middle Mississippian occurrence might represent a case of homeomorphy similar to that discussed by Rexroad (1958) for the conodont genera *Taphrognathus* and *Streptognathodus*.

The first record of the genus in the Carboniferous System was that of Bischoff (1957), when he recorded *A. varians* in the *Goniatites striatus* zone (cu III β) of Germany. In view of the restricted range of this species in the Upper Devonian and the fact that this record was of a single unfigured specimen, little emphasis could be placed upon this Carboniferous occurrence. However, Conil (1959) has since recorded this species and a form which he compared with this species, both undescribed and unfigured, from the Tn_2 Zone of Belgium, which is at about the middle of the Belgian Tournaisian succession and is equivalent to the Z_2 zone in England.

Hinde (1900) described a conodont fauna from the Scottish Carboniferous Limestone Series of the Midland Valley. This included several new species of conodonts, including *Prioniodus geminus* and *Prioniodus porcatus* each of which have since been redescribed by Clarke (1960) and transferred to the genus *Apatognathus*. Specimens of this genus have also appeared, in large numbers in the St. Louis Formation (Valmeyeran Series) of America (Rexroad and Collinson 1963). This formation is equated with the *Goniatites crenistria* zone (cu III α) of Europe by Collinson, Scott, and Rexroad (1962). These authors record the lowest Mississippian occurrence of the genus in the Warsaw Formation (Valmeyean Series), which they equate with the cu II δ goniatite zone (Viséan) of Europe.

The genus *Apatognathus* is no longer considered to occur in strata younger than Carboniferous age, although three species referred to this genus have in the past been described from beds as young as Cretaceous in age.

Diebel (1956) described a conodont fauna, which included *A. ziegleri* sp. nov., from the Upper Chalk, Cretaceous, of the Cameroons but since there have been no reports of any conodonts from the whole of the Jurassic period, a certain amount of uncertainty is cast upon this Cretaceous fauna. Lindström (1964), however, considers this fauna to be too well preserved to have been derived by mechanical re-working of older sediments.

Clark and Ethington (1962) equated the middle Triassic species *A. longidentatus* Tatge 1956 with *A. ziegleri* and the latter species has since been transferred to the genus

Gnamptognathus, Ziegler, by Lindström (1964). *A. tribulosus* Clark and Ethington 1962 has been similarly transferred (Lindström 1964).

Thus, of the eight named species of *Apotognathus* previously described, only the type-species plus the two Carboniferous species, i.e. *A. gemina* (Hinde) and *A. porcata* (Hinde) remained before the present paper.

An examination of the genus *Apatognathus* illustrates the apparently disconnected nature of its various appearances and this resulted in many workers considering most of the forms of *Apatognathus* to be homeomorphic. Clark and Ethington (1962, p. 107), for instance, expressed an opinion common among recent workers that: '. . . of the various species which have been referred to *Apatognathus* only the type seems to be properly classified. All the others probably should be placed in a different genus.' The foregoing paragraphs indicate that a majority of the species have recently been transferred to *Gnamptognathus* but even the remaining Carboniferous representatives of *Apatognathus* present some problems. As already stated, Scott and Collinson (1961) considered that in view of the absence of this genus in Lower Mississippian formations the Middle Mississippian occurrence might represent a case of homeomorphy. Unfortunately, however, the sporadic occurrence of the genus also results in a lack of knowledge of the ancestry of any of these forms. Collinson, Scott, and Rexroad (1962, p. 3) presumed the 'homeomorphs' to have arisen from *Synprioniodina* but in view of the deficiency of definite evidence perhaps a more suitable term, with no ancestral implications, would be 'morphic equivalents' rather than 'homeomorphs'. The above authors expressed this doubt in the origin of the various species of *Apatognathus* by referring to them as *Apatognathus*? spp. and the practice is continued by the present author, until such times that the complete ranges and origins of the different species are known.

SYSTEMATIC PALAEONTOLOGY

The new material which is described in the following section represents over 10% of the whole conodont faunas from the Yoredale limestones. The faunas were well-preserved, easily extracted, and were abundant at certain horizons. All the type specimens and other figured specimens occurring in this paper are now deposited in the collection of the Micropalaeontology Laboratory, Department of Geology, University of Sheffield. The reference numbers of the type specimens are included in the descriptions.

Genus APATOGNATHUS Branson and Mehl 1934

Type Species. Apatognathus varians Branson and Mehl 1934.

Original Generic Description of Branson and Mehl. 'Units consisting of a sharply-arched base, the limbs of which are denticulate, bar-like, and parallel or slightly divergent. The limbs are joined at the apex on one side of the arch by a thin lamella of variable length. An apical denticle of large size is curved toward one limb of the arch and toward the face of the arch opposite the apical lamella. The limb-teeth are small, discrete and directed toward the face of the arch toward which the apical denticle bends. The symmetry of the arch is broken by the trend of the apical denticle and in some forms by the asymmetrical development of limb denticles.'

Orientation of Units. The variable and yet basically simple form of this genus has resulted in much confusion in orientation. Difficulties have arisen over the following factors:

1. The highly arched character of the unit. 2. The extreme asymmetry of some forms of the genus and the virtual symmetry of others. 3. The variable amount of thickening and twisting which may affect one or both bars. 4. The bars are invariably in different planes. 5. The very variable denticulation.

The result is that no two authors have adopted the same method of orientation in their descriptions. The original description and orientation by Branson and Mehl was based upon the assumption that the unit functioned as a sheath about the anterior end of the mandible of the conodontifer, with the limbs or bars roughly horizontal. They therefore suggested the following descriptive terms: the face of the arch without the connecting lamella was designated upper or oral, the side with the lamella aboral, and the limb towards which the apical denticle bends the outer limb or oral bar. However, the conodont is no longer considered to be a jaw-supporting mechanism and in addition the orientation suggested by Branson and Mehl causes confusion since it does not follow the accepted pattern for the orientation of conodonts in general.

The orientations used by all the authors who have previously described the genus, including those species recently transferred to *Gnamptognathus* are indicated on the hypothetical specimen in text-fig. 2*a*, *b*. The orientation and nomenclature used in this paper are indicated in text-fig. 2*c*, *d*, are outlined below, and can be seen to follow the conventional pattern of orientation for the majority of conodonts.

The convex side of the unit is the outer lateral side and the concave side of the inner lateral side. The denticles are borne on the oral surfaces of the bars irrespective of the inclination or twisting of the bars. The aboral surface is that which bears the aboral groove whilst the basal pit is at the apex of the unit beneath the base of the apical cusp. In asymmetric forms the apical cusp curves away from the anterior bar and towards the posterior bar, whether the specimen be sinistral or dextral. Directions along the bars are known as apical, towards the apical cusp and adapical, away from the apical cusp.

The posterior bar may be recognized by the use of several factors, including: (1) the apical cusp curves towards the posterior bar in asymmetric forms; (2) if the bars are unequally thickened the posterior bar always has the greatest amount of thickening; (3) the posterior bar is inwardly directed, in varying degrees, relative to the anterior bar.

Specimen index numbers are compiled as follows, e.g. 26(5)GG202. 26(5) is the film reference, GG the locality of the sample (Gunnerside Gill, Swaledale) and 202 the sample number. Each description includes a statement of the number of well-preserved specimens studied, together with (in brackets), the total for that species including identifiable fragments.

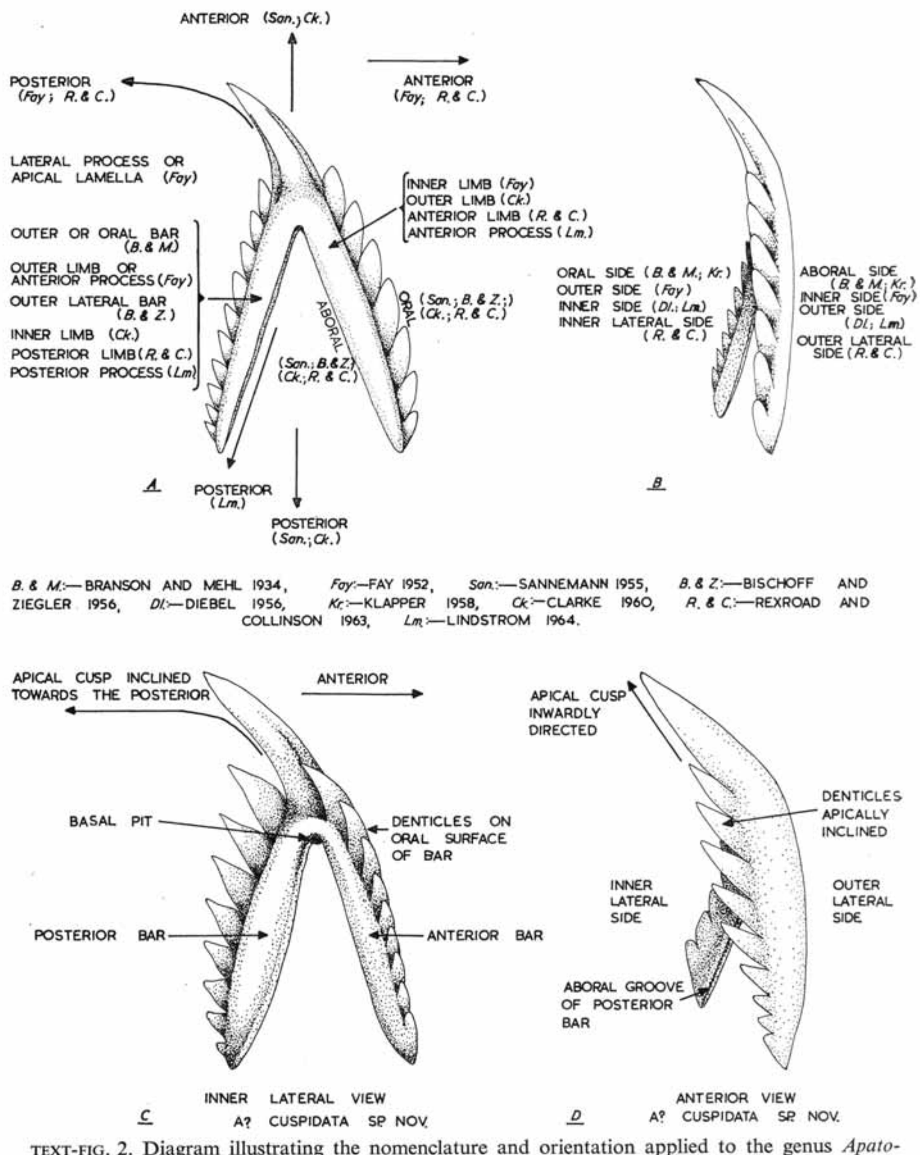
Apatognathus? chaulioda sp. nov.

Plate 17, figs. 1, 2, 3, 5

Diagnosis. An *Apatognathus?* on each bar of which is a bar cusp approximately the size of the apical cusp and separated from the latter by a few, small, compressed denticles.

Description. An asymmetric unit with two bars diverging at 26–35 degrees.

From the inner lateral view the two bars are of equal dimensions, with inner lateral sides



TEXT-FIG. 2. Diagram illustrating the nomenclature and orientation applied to the genus *Apatognathus?* by previous authors (2*a*, *b*) compared with that used by the present author (2*c*, *d*).

inclined to each other particularly at the apex. Each bar is divided into an apical and a longer adapical part by a prominent bar cusp. Thickening in mature specimens is concentrated at the apex of the unit and extends equally along each bar as a smooth, wide, and sometimes diminishing ridge.

The usually strong apical cusp is of variable length, as wide and thick as a bar at its base, sharply pointed, posteriorly curved and inclined, and may be laterally flanged. The bar cusps are similar in size and shape, may be even wider at their bases than the apical cusp, and are apically inclined.

The denticles between the apical and bar cusps are shorter than the height of the bar and although fused, may be discrete in juvenile forms. There is a maximum of about five denticles in this position on each bar but never more on the posterior bar than on the anterior bar. The remaining denticles are discrete, usually longer than the height of the bar, and similar in shape to the apical set.

From the outer lateral view, a prominent, wide ridge curves round the apex of the unit and is gradually reduced along the bars. The aboral margin of the bars is sharp and the apical lamella variable in size.

From the anterior view, the base of the bar is straight but the height of the bar increases apically and culminates in the inwardly directed apical cusp. Inward inclination of the denticles is slight.

From the aboral view, the aboral groove is prominent, deep, and wide and the basal pit is deep and circular.

Comparisons. This species is distinctive in its possession of a large bar cusp on each bar. *A? scalena* sp. nov. has a bar cusp only on the posterior bar.

Discussion. The major variations in this species concern the number of denticles between the apical and bar cusps and also the extent of the thickening of the bars. If thickening extends from the apex beyond the base of the bar cusps, the whole length of the bar is usually thickened.

Occurrence. The Yoredale Series of the north of England.

Range. Hawes Limestone to the Four Fathom or Underset Limestone. Absent from the Hardraw Scar and Simonstone Limestones.

Type Specimen. 26(5)GG202, Plate 17, Figs. 1, 2.

Number of specimens. 23(68).

Type Locality. Four Fathom Limestone of Gunnerside Gill, Swaledale. G.R. 937007.

Apatognathus? cuspidata sp. nov.

Plate 17, figs. 4, 6, 7, 8, 9, 10

Diagnosis. An *Apatognathus*? with small denticles on the anterior bar and larger denticles on the posterior bar, the latter being less steeply inclined than the anterior bar on the inner lateral side, and an apical cusp which is more than half the bar length.

Description. An asymmetric species with bars diverging at about 25 degrees.

From the inner lateral view the anterior bar is straight and high with a prominent narrow ridge, which in mature specimens extends the whole length of the bar on the inner side of the denticles. The inner lateral surface is steeply and uniformly inclined inwards. The denticles are triangular, sharply pointed, apically inclined, strongly inclined inwards, with a small decrease in size adapically and number from 8 to 10 but always one in excess of the posterior bar.

The apical cusp is at least half as long as the bars, sharply pointed, as stout as a bar at its base where it is laterally flanged, and inwardly and posterially directed.

The posterior bar is straight and highest two-thirds the distance from the apex. A prominent ridge extends along the bar on the inner side of the denticles. The inclination of the inner lateral side is less than that of the anterior bar and also decreases adapically. Apical and inward inclination of the denticles is also less than on the anterior bar, though they may be larger and more discrete.

From the outer lateral view, the base of the apical cusp is smooth, convex, and continuous with a strong ridge which extends along each bar. That of the anterior bar curves upwards to the oral margin and accentuates the steep inclination of the outer lateral side. That of the posterior bar is straight. The aboral margins of the bars are sharp. Apical lamella small.

From the anterior view, the prominent ridge on the outer lateral side forms the base of the bar in this view. Base slightly convex and the height of the bar decreases adapically. The denticles are fused for one-third of their length.

From the aboral view, the aboral groove is narrow, deep, and bounded by two prominent ridges. The basal pit is circular.

Comparisons. This species differs from the other species in its combination of a very large apical cusp, strong, regular denticulation, and the difference in inclination of the anterior and posterior bars. It does, however, bear some similarities to the juvenile forms of the species figured by Rexroad and Collinson (1963) as *A? porcata* (Hinde).

Occurrence. The Yoredale Series of the North of England.

Range. Simonstone Limestone to the Main Limestone.

Type Specimen. 28(6)BB205, Plate 17, fig. 7. *Number of specimens*. 20(85).

Type Locality. Great Limestone, Borrowdale Beck, Stainmore, Westmorland. G.R. 834160.

EXPLANATION OF PLATE 17

All figures ×41.

Figs. 1–3, 5. *Apatognathus? chaulioda* sp. nov. 1, Inner lateral view of type-specimen 26(5)GG202. 2, Outer lateral view of type-specimen. 3, Inner lateral view of specimen 23(1)MG285. 5, Outer lateral view of specimen 34(3)GB8A.

Figs. 4, 6–8, 10. *A? cuspidata* sp. nov. 4, Inner lateral view of specimen 25(4)SW182, with broken denticles and cusp but with bars complete. 6, Inner lateral view of specimen 31(3)BB159. 7, Inner lateral view of type-specimen 28(6)BB205. 8, Inner lateral view of specimen 29(2)BB205. 10, Outer lateral view of large specimen 31(2)BB159.

Figs. 9, 12, 13. *A? gemina* (Hinde). 9, Inner lateral view of specimen 81(1)GB110A. 12, Oral view of specimen 80(5)GB110J, posterior bar only, showing extensive lateral thickening. 13, Aboral view of same specimen showing position of aboral groove.

Fig. 11. *A? petila* sp. nov. Outer lateral view of type-specimen 16(6)MG39, with complete anterior bar.

Apatognathus? gemina (Hinde)

Plate 17, figs. 9, 12, 13

1900 *Prioniodus geminus* Hinde, pl. 10, fig. 25.
1928 *Prioniodina? gemina* (Hinde); Holmes, p. 19, pl. 5, fig. 10.
1960 *Apatognathus geminus* (Hinde); Clarke, p. 4, pl. 1, figs. 1, 2.

Description. An asymmetric unit with bars diverging at about 20 degrees.

From the inner lateral view, the unit is strong, highly thickened, and twisted at its apex. The bars are straight, with the thickening evident as a prominent ridge extending along each bar. The ridge of the posterior bar, where the thickening is most strongly developed, is higher and sharper than that of the anterior bar. The posterior bar is strongly inclined inwards adapically. The apical twisting of the unit results in the bars being in different planes and the aboral side of the anterior bar may be visible in this view. The apically inclined denticles of the anterior bar are irregular but at least equal in length to the height of the bar and with little inward inclination. Inward inclination of the cusp is strong. The latter is inclined slightly posteriorly and is often flanged asymmetrically, the posterior flange being the larger. The cusp is as broad and thick as a bar at its base. The posterior bar denticles are smaller and more numerous than those of the anterior bar, apically and inwardly inclined, roughly triangular in outline and may be fused at their bases.

The outer lateral side of the anterior bar is continuous with the base of the denticles and has a low ridge running near the base of the bar. The cusp is smooth, broad, flat, and continuous with the bars. The posterior bar has an exaggerated, sharp, narrow ridge extending its whole length. The apical lamella is very small and may not be visible.

From the posterior view, lateral thickening of the posterior bar is very strong with the result that its oral surface is wider than the height of the bar, convex and with slightly irregular lateral margins. The apical cusp is thick at its base and curves strongly inwards in a smooth curve.

From the aboral view, the aboral groove is wide, deep, and bounded by two prominent lips. The basal pit is deep and circular.

Comparisons: The above description of specimens from the Yoredale Series shows this species to differ from others in its large amount of lateral thickening, particularly of the posterior bar, and the apical twisting of the unit. It is distinguished from *A? cuspidata* also in its less regular denticulation, the presence of larger denticles adjacent to the apical cusp and a wider aboral groove.

Discussion. The denticulation of this species is variable but the number of denticles on the posterior bar exceeds those of the anterior bar. Those adjacent to the apical cusp may be somewhat larger than the remaining denticles.

Occurrence. Type locality: Upper Limestone Glencart, Dalry. Upper Limestone, Linn Spout, Dalry, Skateraw. Middle Limestone, Dunbar. Yoredale Series of the North of England.

Range in the Yoredale Series. Hawes Limestone to the Middle Limestone. *Number of specimens*. 22(68).

Apatognathus? librata sp. nov.

Plate 18, figs. 3, 6, 8, 9, 12, 13

Diagnosis. A robust, wide-angled, almost symmetric *Apatognathus?* with large, subequal denticles on both limbs.

Description. Mature specimens are large, strong, approximately symmetric in lateral view, and with bars diverging at 45–50 degrees.

From the inner lateral view, both bars are thick, strong, high at the apex, gradually decreasing in height adapically and with flat oral surfaces on which are borne strongly inwardly inclined denticles. The inner lateral surfaces of the bars are steeply inclined towards each other, particularly at the apex, and are almost flat.

Denticles of each bar are subequal, longer than the height of the bar, sharply pointed, in contact for over half their length, and with a slight regular decrease in size adapically. In mature specimens a large denticle may be developed on one or both bars and separated from the apical cusp by a denticle of normal size.

The apical cusp is central, little larger than the denticles and of similar shape, strongly inclined inwards, and with no posterior inclination.

From the outer lateral view, the outer lateral surface is convex and continuous with the outer surfaces of the denticles, the growth lamellae of which are seen to extend into the bars. The small apical lamella is continuous with a prominent ridge which passes down the outer side of each bar becoming more orally placed adapically.

From the anterior view, the aboral margin of the bar is slightly convex. The denticles are inclined very strongly inwards and decrease in length adapically. The apical cusp is inwardly inclined at 45–50 degrees and leaves the apex of the unit at an abrupt angle.

From the aboral view, the aboral groove is narrow, shallow, and borne on the sharp aboral margin. In mature specimens the basal pit is small and circular.

Comparisons. This species is probably the most distinctive of the six species described since no other has such uniform denticulation combined with so high a degree of symmetry.

Discussion. In young specimens the bars are delicate, blade-like, and equal in thickness

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EXPLANATION OF PLATE 18

All figures ×41.

Figs. 1, 2, 4, 5. *Apatognathus? scalena* sp. nov. 1 and 2, Outer and inner lateral views of type-specimen 32(4)BB213, showing the greater length of the anterior bar and pronounced posterior bar cusp. 4 and 5, Outer and inner lateral views of specimen 33(3)GG217, with short posterior bar and broken anterior bar.

Figs. 3, 6, 8, 9, 12, 13. *A? librata* sp. nov. 3, Inner lateral view of specimen 31(6)BB159, showing large denticle near apical cusp. 6 and 8, Inner and outer lateral views of immature specimen 30(2)BB212. 9, Inner lateral view of specimen 28(4)BB205. 12, Inner lateral view of an almost complete, small, immature specimen exhibiting a marked degree of symmetry 29(5)BB159. 13, Inner lateral view of the type-specimen 18(2)MG132.

Figs. 7, 10, 11. *A? petila* sp. nov. 7, Inner lateral view of large, thickened specimen 20(5)MG259, showing contortion of the apical denticles and a bulbous thickening of the posterior bar. 10, Inner lateral view of specimen 34(5)GB110. 11, Outer lateral view of an immature specimen 24(4)SW182.

to the denticles, whilst the basal pit is spindle-shaped and relatively larger. The onset of maturity is marked by an extensive thickening of the inner lateral sides of the bars, particularly at the apex. Thus the oral surfaces of the bars become flattened, the inner lateral sides steepened, and the basal pit constricted. Thickening also affects the apical cusp and denticles.

Occurrence. The Yoredale Series of the North of England.

Range. Gayle Limestone to the Little Limestone.

Type Specimen. 18(2)MG132, Plate 18, fig. 13. *Number of specimens*. 47(157).

Type Locality. Simonstone Limestone, Whitfield Gill, Askrigg, Wensleydale. G.R. 935918.

Apatognathus petila sp. nov.

Plate 17, fig. 11, Plate 18, figs. 7, 10, 11

Diagnosis. An *Apatognathus?* with a small apical cusp, a strongly inwardly inclined anterior bar on which the denticles increase in size apically, and a posterior bar with uniform denticulation and no inward inclination.

Description. An asymmetric unit with limbs diverging at 38–45 degrees.

From the inner lateral view, the anterior bar is blade-like and curved mainly at the adapical end. The inner lateral side is steeply inclined inwards particularly at the apex. Thickening is slight. The denticles near the apex of the unit are large, sharply pointed, sharp edged, apically directed, fused for two-thirds their length, and highly inclined inwards. In addition, those denticles adjacent to the cusp may be posteriorly curved and inclined. Adapically the denticles are shorter and develop an adapical inclination, with the last denticle terminating the bar.

The apical cusp is only slightly larger than the adjacent denticles of the anterior bar, is of similar shape, highly inclined inwards, and posteriorly inclined and curved.

The posterior bar is of uniform height, slightly thickened, and is in a plane almost at right angles to that of the anterior bar. It has no inward inclination on its inner lateral side or denticles. The latter are of uniform length, shorter than the height of the bar, fused for two-thirds their length, apically directed and narrower and more sharply pointed than those of the anterior bar.

From the outer lateral view, the outer lateral surface of the unit is smooth, convex, and continuous with the base of the denticles. A low ridge extends down the anterior bar a uniform short distance above the aboral margin and disappears at two-thirds the length of the bar. On the posterior bar, however, the ridge crosses the outer lateral surface from an aboral to an oral position and then runs along the base of the denticles. The denticles of both bars may be of irregular shape or contorted in the region of the apical cusp.

From the anterior view, the aboral margin of the bar is convex. The adapical decrease in the height of the bar and length of the denticles is pronounced. The apical cusp and adjacent denticles are directed very strongly inwards.

From the aboral view, the aboral groove is wide and deep and bounded by two sharp ridges. The basal pit is large and spindle-shaped.

Comparisons. This species differs from others of the genus in its combined lack of a distinct apical cusp and the contrast in inclination of the bars. The latter feature, which is more marked than in *A? scalena* sp. nov. increases towards the apex, where the denticles and anterior bar may be directed inwards at 90 degrees. The contortion of the denticles in the region of the apical cusp has not been seen in other species.

Discussion. Only a small amount of thickening takes place but denticles may become fused. Posterior bar denticles appear to be most prone to fusion, occasionally becoming completely fused in groups of three. This species bears some similarities with some of the specimens figured by Rexroad and Collinson (1963) as *A? porcata* (Hinde), particularly their large, mature forms, but the ontogeny of *A? petila* sp. nov. shows less variation in form as well as other differences and in view of the fact that the type specimen of *A? porcata* (Hinde) is a broken specimen consisting of a single bar, the Yoredale Specimens are described as a new species.

Occurrence. The Yoredale Series of the North of England.

Range. Gayle Limestone to the Main Limestone.

Type Specimen. 16(6)MG39, Plate 17, fig. 11. *Number of specimens*. 38(130).

Type Locality. Hardraw Scar Limestone, Whitfield Gill, Askrigg, Wensleydale, G.R. 939915.

Apatognathus? scalena sp. nov.

Plate 18, figs. 1, 2, 4, 5

1963 *Apatognathus? gemina* (Hinde); Rexroad and Collinson, p. 7, pl. 1, figs. 12–17.

Diagnosis. An *Apatognathus?* with subequal denticles on the anterior bar but variable denticles and a single large bar cusp on the posterior bar.

Description. A highly asymmetric species with bars diverging at about 20°.

From the inner lateral view, the anterior bar is straight, twisted on its own axis, its inner lateral side steeply inclined at the apex, and less steeply adapically. The apical part of the bar is thickened with its flat oral surface slightly wider than the denticles it bears. Adapically the bar is blade-like and of equal thickness to the denticles. The latter decrease in size adapically and are of uniform shape. The inward inclination of the denticles increases apically and the denticles adjacent to the apical cusp are, in addition, posteriorly inclined.

In young forms the apical cusp appears as a posteriorly directed extension of the anterior bar but in mature forms it is similar in shape and only slightly larger than the adjacent denticles of the anterior bar.

The posterior bar is slightly shorter than the anterior bar and straight, with its inner lateral surface uniformly and less steeply inclined. Occurring at its mid-length is a large, compressed bar cusp, which is wider than the height of the bar. Between the apical and bar cusps are a few denticles which in mature forms are small and regular. Also in mature forms the denticle on each side of the bar cusp is commonly larger than the others and may rival the bar cusp in size. Adapically from the latter the denticles decrease in size.

From the outer lateral view, a prominent, sharp ridge extends along each bar from the apex. That of the anterior bar maintains a uniform distance from the aboral margin but that of the posterior bar curves up to the base of the bar cusp. The anterior bar is of uniform height whereas the posterior bar increases in height from the apex to the bar cusp and then decreases adapically. Apical lamella small.

From the anterior view, the aboral margin of the bar is sharp and strongly convex. The anterior bar denticles, up to 16 in number, are of uniform width and shape and in contact for most of their length. The bar curves into the inwardly inclined apical cusp in a single smooth curve.

From the aboral view, the aboral groove is wide, deep, and bounded by strong ridges. Basal pit deep and spindle-shaped.

Comparisons. This species differs from other species of *Apatognathus?* in its large posterior bar cusp which is similar to that found on both bars of *A? chaulioda* sp. nov. The anterior bar, however, bears certain similarities with that of *A? petila* sp. nov. in its uniform denticulation, twisting, and high angle of inclination.

Discussion. The bar cusp of young forms is relatively larger than that of mature forms.

Occurrence. St. Louis Formation of the Valmeyeran Series, Mississippian, U.S.A. The Yoredale Series of the North of England.

Range in the Yoredale Series. Simonstone Limestone to the Main Limestone.

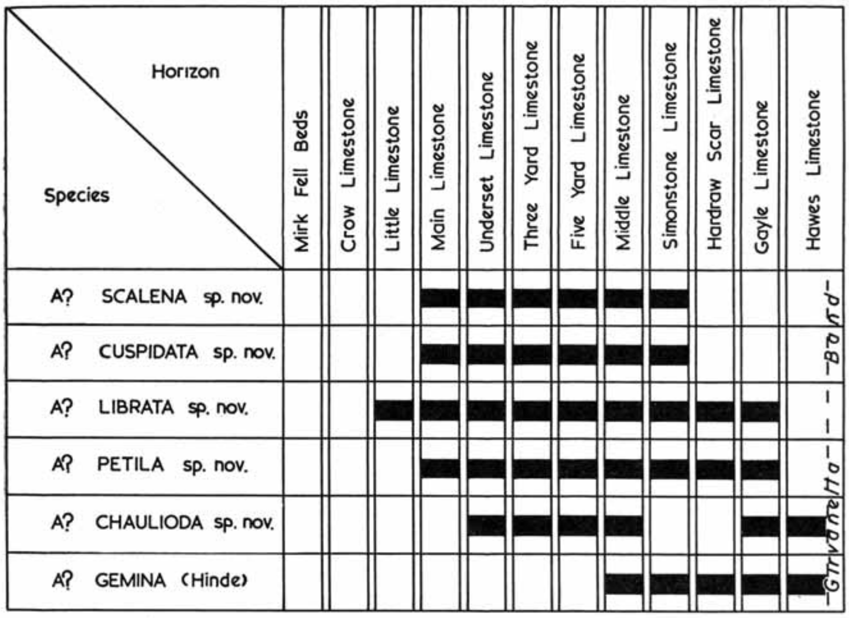
Type Specimen. 32(4)BB213. Plate 18, figs. 1, 2. *Number of specimens*. 13(51).

Type Locality. Great Limestone, Borrowdale Beck, Stainmore, Westmorland. G.R. 834160.

DISTRIBUTION OF THE GENUS *APATOGNATHUS?* IN THE YOREDALE SERIES

The distribution through the Yoredale Series of the six species of *Apatognathus?* described in the present paper is shown in text-fig. 3. This figure shows the genus to be present in every major limestone except the Crow, which was too siliceous to yield any conodonts.

The Hawes Limestone contained moderately small faunas of conodonts, up to thirty-five specimens per kilogram of rock, in which *A? chaulioda* sp. nov. and *A? gemina* (Hinde) were the only species of this genus to be present. The lowest occurrences in the Yoredale Series of *A? petila* sp. nov. and *A? librata* sp. nov. were in the Gayle Limestone, in which they were combined with the above species and occurred in complete faunas of over 100 specimens per kilogram. The Hardraw Scar Limestone, however, yielded only three specimens of *Apatognathus?*, i.e. single specimens of *A? gemina* (Hinde), *A? petila* sp. nov., and *A? librata* sp. nov. *A? chaulioda* sp. nov. was not found but this is not surprising in view of the small size of the faunas which appears to be characteristic of the Hardraw Scar Limestone in the Whitfield Gill locality. The Simonstone and Middle Limestones yielded large numbers of specimens of this genus. The Middle Limestone was in fact the only limestone to contain all six species but, as will be seen from text-fig. 3, *A? chaulioda* sp. nov. has a projected range through the Simonstone Limestone since it is found as far up the succession as the Underset Limestone. The Five Yard Limestone yielded relatively small numbers of conodonts but these included five species of *Apatognathus?*. *A? gemina* (Hinde), which was absent, did not occur in the Three Yard Limestone above, in spite of the fact that the latter yielded the largest faunas in the whole of the study, with concentrations exceeding 500 specimens per kilogram in the Gunnerside Gill locality and 350 per kilogram in Weardale. The Underset or Four Fathom Limestone contained *A? librata* sp. nov., *A? scalena* sp. nov., *A? cuspidata* sp. nov., and *A? petila* sp. nov., plus the highest occurrence of *A? chaulioda* sp. nov. The large faunas of the Main Limestone included the highest occurrences of *A? petila* sp. nov., *A? scalena* sp. nov., and *A? cuspidata* sp. nov., plus *A? librata* sp. nov., which was the only species to continue through into the Little Limestone. The Mirk Fell Beds



TEXT-FIG. 3. Range chart of *Apatognathus?* species occurring in the Yoredale Series.

yielded large conodont faunas but they included no species of *Apatognathus?*. The genus must therefore disappear between the Little Limestone and the Mirk Fell Beds after having first suffered a drastic decline in numbers above the Main Limestone.

POSSIBLE FACIES CONTROL OF THE GENUS *APATOGNATHUS?* IN VISÉAN–MIDDLE MISSISSIPPIAN TIMES

Some characteristics of conodont distribution. Conodonts are of world-wide distribution and one of their great advantages in use for zonation purposes is that they are essentially free of facies control. This is evident in both small-scale facies variations from lithology to lithology and also in large-scale variations from, for instance, a basin type of sedimentation to a shelf environment. An illustration of this was given by Rexroad (1958) who described the conodonts from the Glen Dean Formation (Chester Series), and who found that out of 27 species, 21 were common to both limestone and shale. Of the other species two, which were found only in the shale, were represented by only four specimens, and four found only in the limestone he considered to reflect the method of sampling rather than environmental factors.

Facies control of the Viséan–Middle Mississippian representatives of the genus Apatognathus? During the Viséan or Middle Mississippian times *Apatognathus?* appears to have favoured certain conditions to the exclusion of others. After a long period of absence the genus suddenly appeared in relative abundance in three separate regions and at approximately similar horizons. These three regions, the Illinois Basin of the U.S.A., the Midland Valley of Scotland, and the Askrigg and Alston Blocks of the North of England, although not identical lithologically, are each represented by shallow-water cyclic sediments in which goniatites are rare and the fauna is mainly benthonic. The contrast, rather than being from lithology to lithology, is therefore between a coral/brachiopod facies where *Apatognathus*? is present and a cephalopod facies, where the genus is absent. This is particularly well shown in Britain, where *Apatognathus?* is absent from the P and E_1 zones of the Midlands and Lancashire (Dr. A. C. Higgins—personal communication), but is present at equivalent horizons in the coral/brachiopod facies of the Askrigg and Alston Blocks. The facies control of the genus is further illustrated by the fact that even within the Yoredale Series there are no representatives of *Apatognathus?* in the Mirk Fell Beds, which consist of a shale and ironstone sequence containing goniatites of E_2 age but they do occur at this horizon in the Upper Limestone Group of the Midland Valley of Scotland (Clarke 1960).

CONCLUSIONS

A number of facts have therefore accumulated as a result of the present study of the Yoredale Series. Most important of these is that well-preserved conodonts are present in abundance, at least in the limestones, from which they are easily extracted. A common constituent of these faunas is the otherwise relatively uncommon genus *Apatognathus?* Branson and Mehl 1934 which exhibits what is apparently the greatest amount of variation in form which has so far been found in this genus in any one locality. Six species have been described, five of which are new and they have shown themselves to be of value in the stratigraphic succession of the Yoredale Series. When combined with the remainder of the fauna an accurate zonal scheme, based upon conodonts, is possible. All the forms described have been included in the genus *Apatognathus?* although it is inevitable that further reorganization will be necessary when the ranges and origins of the group are more fully known. At present the term 'morphic equivalent' is thus proposed as preferable to 'homeomorph' which implies a knowledge of the ancestry of the form under consideration. The present study has indicated the type of situation under which the genus might be found in the future, since it does appear to be at least to some extent controlled by the presence of a shallow-water coral/brachiopod facies in which goniatites are uncommon.

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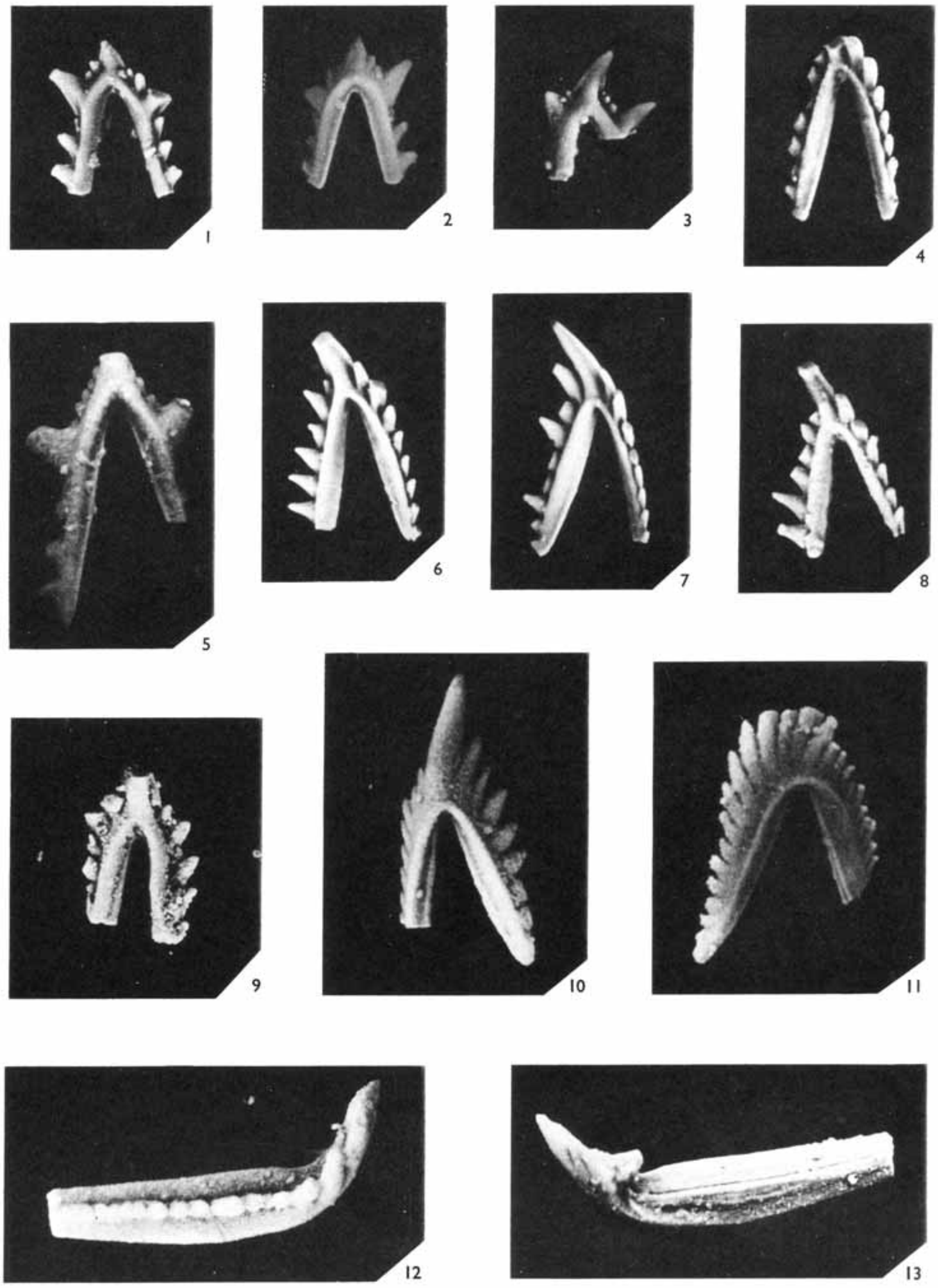
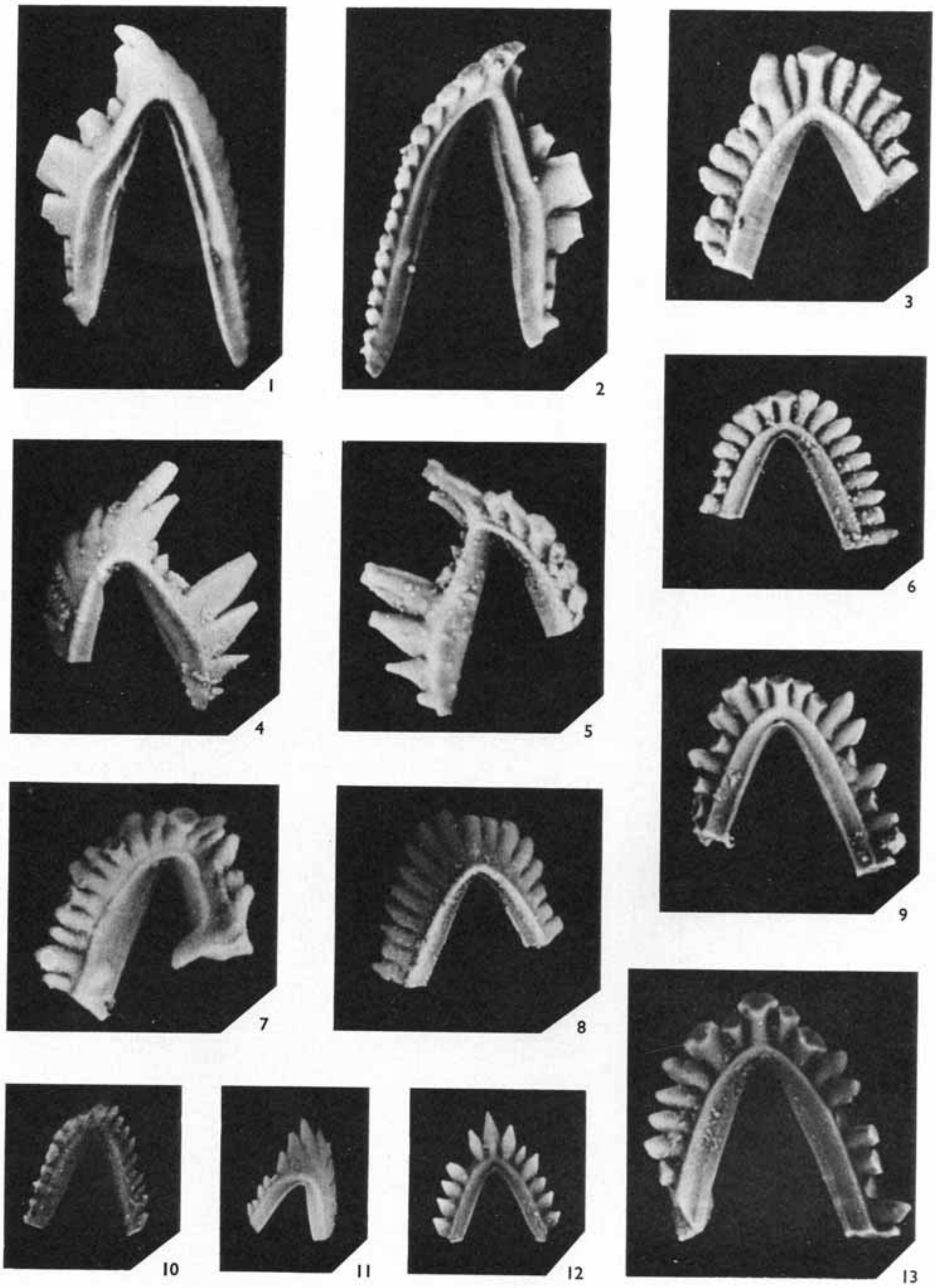


VARKER, Carboniferous *Apatognathus ?* from England



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