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First published in 1992 by the Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario M5S 2C6.

Publication date: 1 December 1992
ISBN: 0-88854-405-7
ISSN: 0384-8159

Canadian Cataloguing in Publication Data

Purnell, Mark A., 1964–
Conodonts of the Lower Border Group and equivalent strata (Lower Carboniferous) in Northern Cumbria and the Scottish Borders, U.K.

(Life Sciences Contribution ; no. 156)
Includes bibliographical references.
ISBN 0-88854-405-7

1. Conodonts - Cumbria (England). 2. Conodonts - England, Northern. 3. Paleontology - Carboniferous. 4. Paleontology - Cumbria. 5. Paleontology - England, Northern. I. Royal Ontario Museum. II. Title. III. Series.

QE899.2.C65P87 1992 562.2094278 C92-095152-X

ROYAL ONTARIO MUSEUM PUBLICATIONS IN LIFE SCIENCES
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Manuscript Editor: M. D. Engstrom
Production Editor: K. Mototsune

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The Royal Ontario Museum is an agency of the Ontario Ministry of Culture and Communications.
Printed and bound in Canada

CONTENTS

Conodonts of the Lower Border Group and Equivalent Strata (Lower Carboniferous) in Northern Cumbria and the Scottish Borders, U.K.

Abstract

The shallow-shelf carbonates of the Lower Border Group and equivalent strata of the Northumberland trough have yielded conodont elements belonging to 28 multielement species. Study of these cavusgnathid-dominated faunas highlights the need for major revision of the Cavusgnathidae. *Cloghergnathus globenskii* Austin is an ecophenotype of *Taphrognathus varians* Branson and Mehl; *Cloghergnathus* Austin is a junior synonym of *Taphrognathus* Branson and Mehl. *Capricornognathus* Austin appears to be a junior synonym of *Patrognathus* Rhodes, Austin, and Druce.

The apparatuses of *Cavusgnathus hudsoni* (Metcalfe), *Taphrognathus varians, Polygnathus mehli* Thompson, and *"Apatognathus" cuspidatus* Varker are described for the first time. *Patrognathus capricornis* (Druce), *Mestognathus beckmanni* Bischoff, *Polygnathus bischoffi* Rhodes, Austin, and Druce, and *"Apatognathus"* sp. a are partially reconstructed. The assignment of *C. hudsoni* to *Cavusgnathus* extends the range of the genus into the Tournaisian Series in Britain.

Introduction

GEOLOGICAL SETTING: THE NORTHUMBERLAND TROUGH

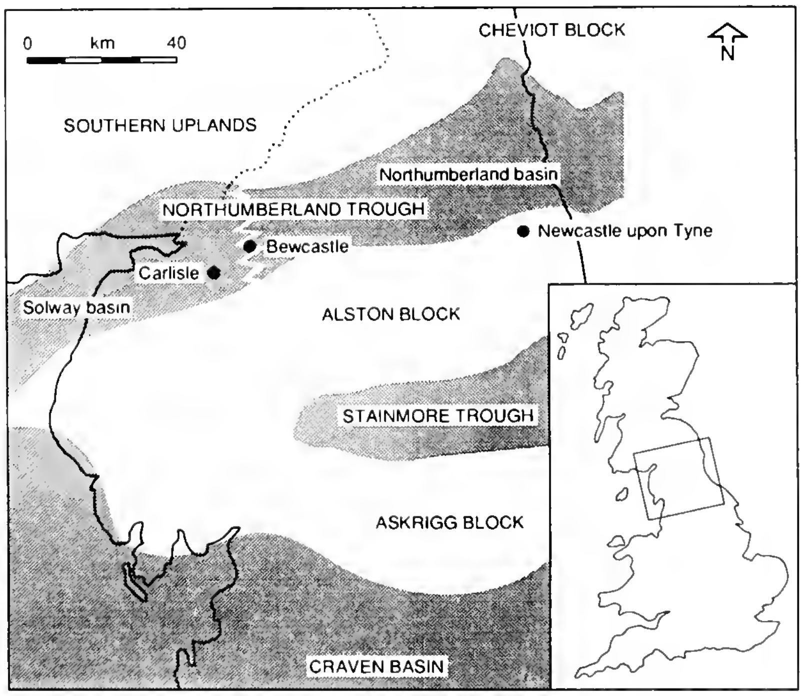
During the late Paleozoic, crustal extension associated with subduction-collision processes led to the formation of a number of sedimentary basins in what is now northern Britain (Johnson, 1981; Bott, 1987; Leeder, 1988; cf. Haszeldine, 1984, 1988). The Northumberland trough, comprising the Northumberland and Solway basins (Leeder, 1971, 1974a), developed during the Carboniferous as a half-graben structure between the Southern Uplands to the north and the Alston block to the south (Text-Fig. 1). Rapid, fault-controlled subsidence of the Northumberland trough took place during the early Dinantian (Johnson, 1984; Kimbell et al., 1989). At that time, the emergent margins of the trough were sources of clastic sediment (Leeder, 1974b). Marginal clastic deposition persisted in the Solway basin (Ord, Clemmey, and Leeder, 1988), but in the Northumberland basin axial drainage systems were dominant for most of the Dinantian. These drainage systems were sourced in the north and east (Robson, 1956; Frost, 1969; Leeder, 1974b) and flowed towards the shallow, gulflike sea in the west. Marine influence in the trough, therefore, decreased eastwards (Garwood, 1931; Day, 1970; Johnson, 1984) and marine strata have not been recorded east or north of the Rothbury area (Text-Fig. 2).

The character of Dinantian sediments in the trough reflects the interplay of fluviodeltaic and shallow marine depositional systems (Leeder, 1974a, b, 1975a, b; Johnson, 1984). Sedimentation kept pace with subsidence (Johnson, 1984), and water depth in the trough probably never exceeded 50 m (Leeder and McMahon, 1988).

STRATIGRAPHIC FRAMEWORK

The outcrop of the Cementstone Group and Lower Border Group in the Northumberland basin, and the equivalent strata in the Solway basin is shown in Text-Fig. 2. With the exception of coastal sections on the Solway Firth, exposure is limited to isolated stream sections and rare quarries. There is considerable variation in the sediment characteristics and in the lithostratigraphic terminology applied to these strata in different areas of the Northumberland trough. Throughout this work the following stratigraphic schemes are followed: Fowler (1936, 1966) for sections located in the Rothbury and North Tyne areas; Leeder (1974b) for the Newcastleton-Langholm area; Day (1970) for the Bewcastle area; Craig (1956) for the Kirkbean outlier; Deegan (1973) and Ord, Clemmey, and Leeder (1988) for the Rerrick outlier (see Text-Fig. 2 for locations). Where appropriate, lithostratigraphic terms are modified according to Holland et al. (1978), although the term "band" is replaced by "Member." Biostratigraphic terminology also follows Holland et al. (1978). Locality details are included as Appendix I. Stratigraphic relationships between Lower Border Group sections and equivalent strata within the Northumberland trough are shown in Text-Fig. 3.

The Cementstone Group in the Rothbury area comprises a generally thinly-bedded sequence of alternating sandstones, shales, and lime mudstones (Fowler, 1936). The lime mudstones are commonly sandy or dolomitic (Fowler, 1936), and the limestone members towards the top of the group are dominated by calcareous algae, chiefly in the form of oncoids. Deposition of these sediments took place in a shallow, restricted intertidal setting or a coastal plain environment with periodic marine influence (Belt, Freshney, and Read, 1967). The algal members were deposited in a shallow, restricted shelf/lagoon environment.



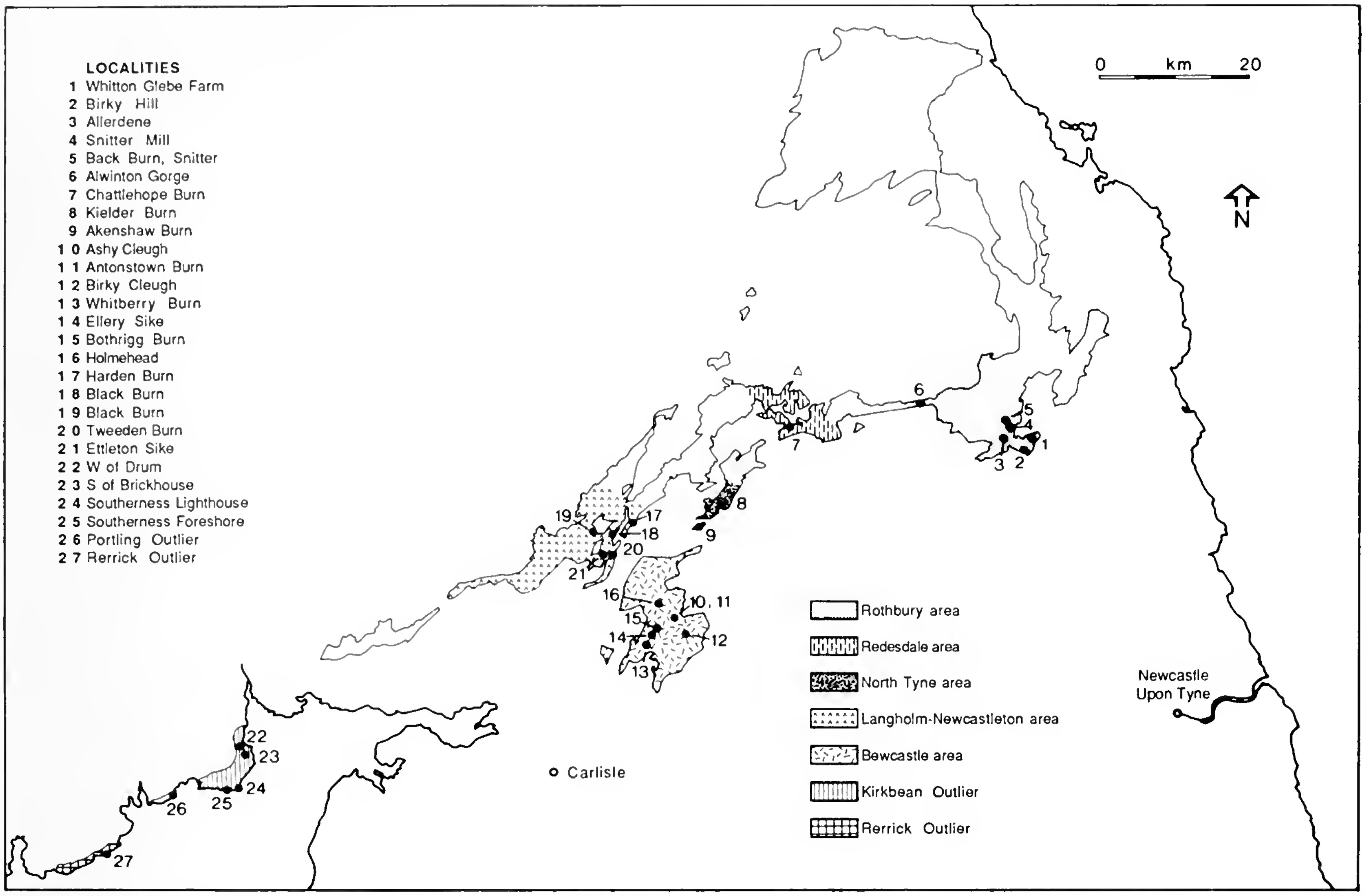
TEXT-FIG. 1. Location and palaeogeographic setting of the Northumberland trough.

In the "North Tyne basin" (Fowler, 1966), the Cementstone Group is probably not more than 180 m thick (Fowler, 1966) and consists of sandstones, shales, and limestones. Some of the limestones contain marine faunal components such as crinoid ossicles and brachiopods (Fowler, 1966; pers. obs.). The character of the sequence reflects the interaction of fluviodeltaic and marine depositional systems (cf. Fowler, 1966).

The sediments of the Lower Border Group in the Bewcastle area were deposited in a variety of environments reflecting periodic delta progradation into a shallow marine gulf (Leeder, 1974b, 1975a, b). Leeder (1974b) discussed the detailed sedimentology of the clastic deltaic facies. Carbonate depositional environments ranged from intertidal to shallow subtidal marine (see Leeder, 1975a, b).

In the Newcastleton-Langholm area, the Whita Formation is more than 500 m thick near Langholm and is composed mainly of sandstones deposited in a fluvial environment (Leeder, 1974b). The Black Burn Formation comprises more than 150 m of sandstones, shales, and limestones deposited in coastal plain, marginal marine, and deltaic environments (Leeder, 1974b). The Arnton Fell Formation is more than 200 m thick and is made up of sandstones and shales with rare thin beds of limestone. The sequence reflects deposition in a fluvial setting with ephemeral lake development (Leeder, 1974b). A section exposed in Black Burn (G.R. NY 47878880 to 48768869; section 11 of Leeder, 1972, 1974b; locality 18 on Text-Fig. 2) was considered to be part of the Arnton Fell Formation by Leeder (1972). This section was included in the formation in figure 1 of Leeder (1974b) but not in the details of sections (1974b:175); its stratigraphic position is uncertain. More than 250 m of alternating beds of sandstone, shale, and limestone make up the Liddel Formation. Clastic strata were deposited in deltaic environments (Leeder, 1974b); carbonate beds in a range of shallow subtidal and probable intertidal marine environments (Leeder, 1975a, b). The Harden Member is distinguished by its distinctive fauna, which includes abundant *Syringothyris* cf. *cuspidata* (J. Sowerby) (Lumsden et al., 1967). It was deposited in a shallow subtidal marine environment.

The Basal Cementstone Formation of the Cementstone Group in the Kirkbean outlier is composed of shales and lime mudstones. Some of the latter are dolomitic and occasionally contain ostracodes, bivalves, or vermiform gastropods (Craig, 1956; Leeder, 1974b; pers. obs.). Deposition probably took place in a shallow, very restricted marine or coastal plain environment, similar to that discussed by Belt et al. (1967). The Southerness Formation comprises approximately 140 m of alternating shales and fossiliferous limestones, containing a fauna dominated by brachiopods and molluscs (Craig, 1956;



TEXT-FIG. 2. Outcrop of the Lower Border and Cementstone groups in the Northumberland basin, and equivalent strata in the Solway basin, showing localities and geographic subdivisions used in the text. For locality details see Appendix I.

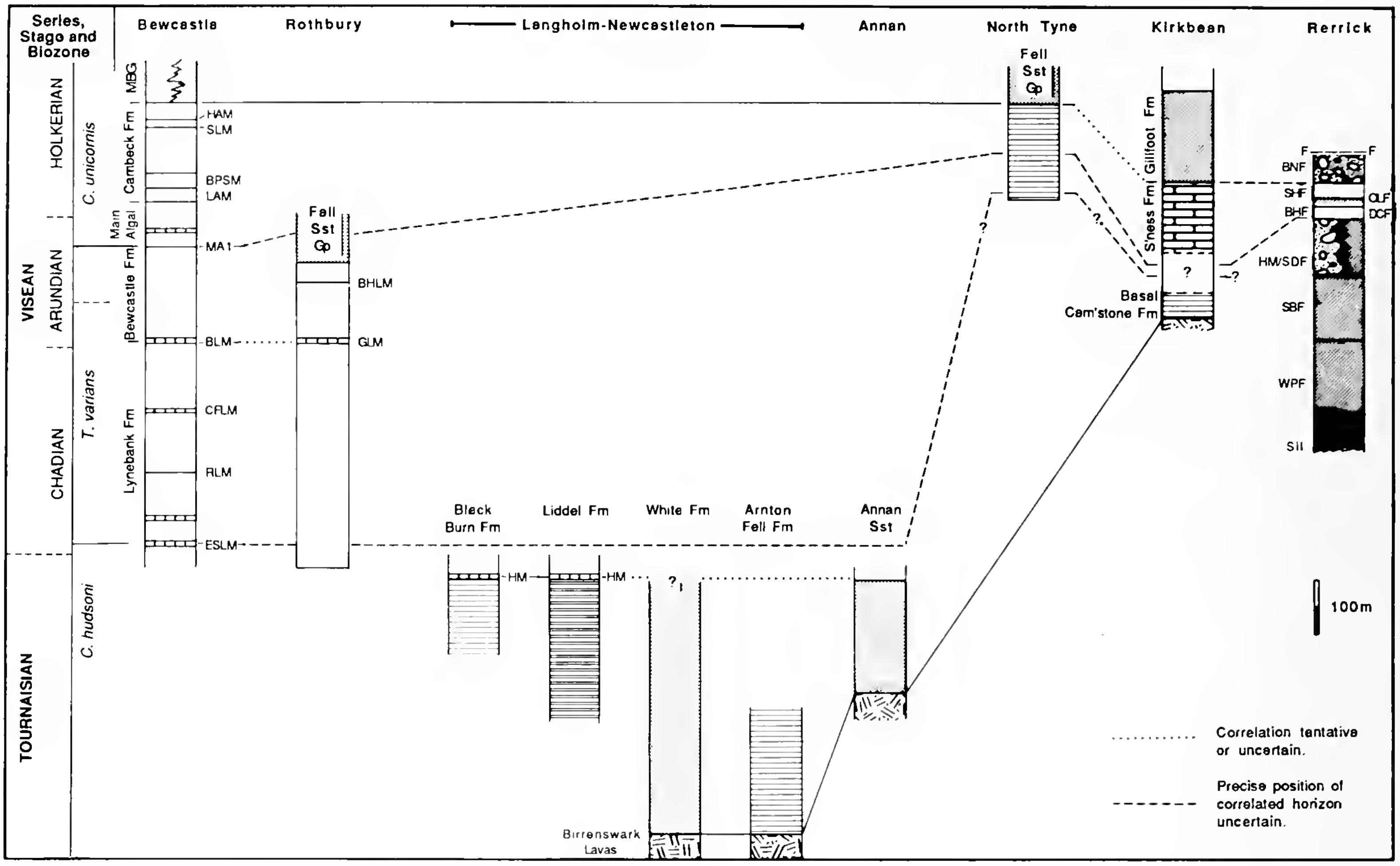
pers. obs.). These strata were probably deposited in a shallow open marine or slightly restricted subtidal environment. The Gillfoot Formation is dominantly composed of reddish-brown conglomerates and sandstones (Craig, 1956). Occasional thin limestones and some of the sandstone beds contain a fauna that includes brachiopods and corals (Craig, 1956; pers. obs.). The depositional environment was, therefore, at least periodically marine.

In the Rerrick outlier, the Wall Hill Sandstone and Orroland groups together represent the approximate lateral equivalents of the Lower Border Group (Deegan, 1973). The Wall Hill Sandstone Group is 360 m thick and comprises the White Port, Sheep Bught, and Abbey Head formations, each composed of different proportions of conglomerates, sandstones, siltstones, and shales (Deegan, 1973). These strata were deposited in a variety of fluvial environments (Deegan, 1973) and have not been sampled for conodonts. Strata of the Orroland Group reflect deposition under a range of dominantly fluvial and alluvial conditions. Of the seven formations of the group (see Deegan, 1973), only the Barlacco Heugh and Orroland Lodge formations contain marginal marine strata.

CONODONT FAUNA

Previous work on British Dinantian conodonts was reviewed by Varker and Sevastopulo (1985). Few studies have dealt with shallow-shelf conodont faunas of Dinantian age; Rhodes, Austin, and Druce (1969) is the most recent major systematic work to do so. Since that publication, there has been a major shift away from traditional "form taxonomy" towards a more biologically sound, multielement concept of conodont species. The systematic palaeontology of shallow-shelf faunas is, therefore, in need of thorough revision.

Conodont faunas from shallow restricted environments are usually limited in their diversity (e.g., von Bitter and Plint-Geberl, 1982; Higgins and Varker, 1982; Austin and Davies, 1984). This may limit their biostratigraphic utility, but such faunas provide good evidence for the multielement composition of conodont species (von Bitter, 1976; Kozur, 1976). Study of the low-diversity faunas recovered from restricted facies of the Northumberland trough sequence has enabled reconstruction of the apparatuses of several species of conodonts.



TEXT-FIG. 3. Stratigraphic framework of the Lower Border and Cementstone groups and equivalent strata in the Northumberland trough. Conodont biozonation and correlation from Purnell (1989); local correlation in the Langholm-Newcastleton area follows Leeder (1974b). Sections are not arranged geographically. MBG = Middle Border Group; ESLM = Ellery Sike Limestone Member; RLM = Rawney Limestone Member; CFLM = Common Flat Limestone Member; BLM = Bogside Limestone Member; MA 1 = Main Algal Member One; LAM = Lower Antiquatonia Member; BPSM = Barron's Pike Sandstone Member; SLM = Syringothyris Limestone Member; HAM = Hillend Algal Member; GLM = Glebe Limestone Member; BHLM = Birky Hill Limestone Member; HM = Harden Member; WPF = White Port Formation; SBF = Sheep Bught Formation; HM/SDF = Hanged Man and Spouty Dennans formations; DCF = Dropping Craig Formation; BHF = Barlacco Heugh Formation; OLF = Orroland Lodge Formation; SHF = Scar Heugh Formation; BNF = Black Neuk Formation.

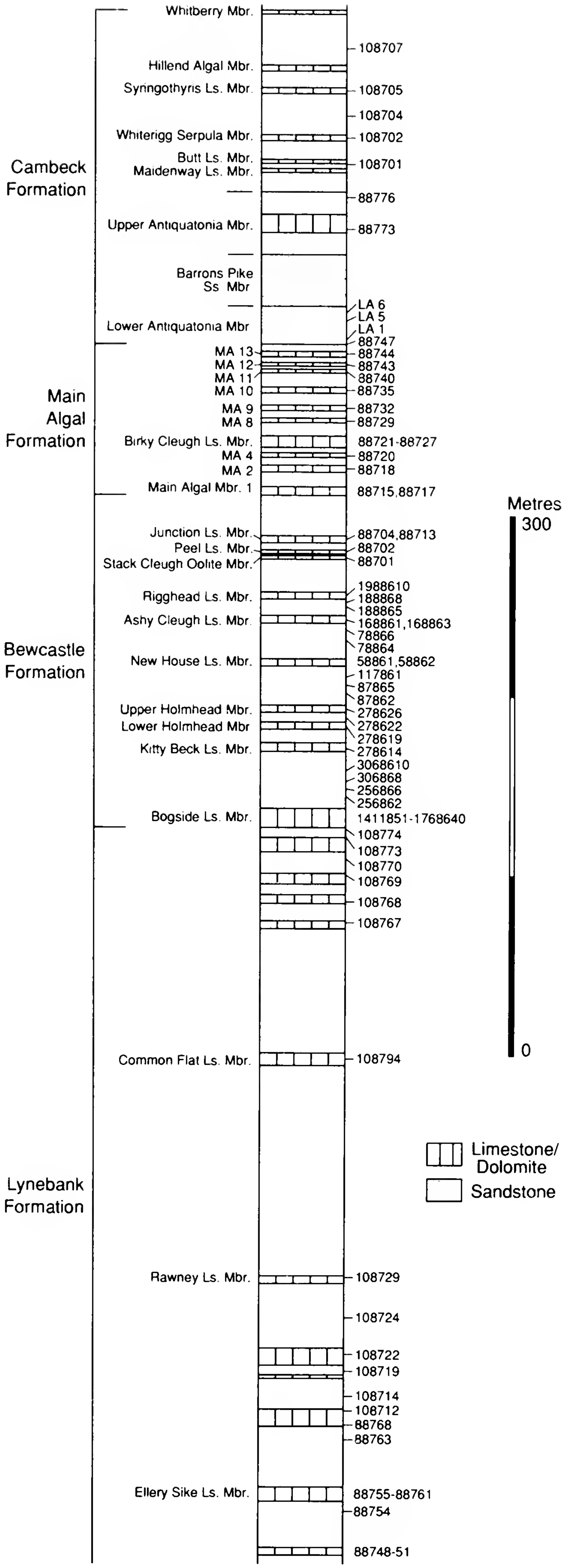
Materials and Methods

One hundred and ninety-five samples from the Lower Border Group and equivalent strata were processed for conodonts using standard recovery techniques (Austin, 1987). Most samples were taken from the Lower Border Group in its type area (Text-Fig. 4). Samples were selected to maximize yield and stratigraphic coverage, but also to represent the broad range of carbonate facies encountered. Almost 5000 conodont elements were recovered, most of which were assigned to one of 28 species of 12 genera.

With a few exceptions, the suprageneric classification of Sweet (1988) is followed herein. The Conodonta, however, are referred to the phylum Chordata (Aldridge et al., 1986; see Smith, 1990, for discussion).

Wherever possible, synonymy lists are abbreviated to give the original species designation, important taxonomic changes, and the most recent reference containing a more complete list. All synonymy lists are annotated using the symbols recommended by Matthews (1973, after Richter, 1948; Rabien, 1954). To avoid confusion, these symbols are enclosed in square brackets and appear to the left of taxonomic names.

Element notation and, except where indicated otherwise, morphological terminology follows Sweet (1981a, b); symmetry classification follows Lane (1968); and heterochronic terminology follows Alberch et al. (1979). Open nomenclature and the signs for taxonomic uncertainty follow Bengtson (1988). The use of quotation marks to indicate invalid or obsolete taxonomic names follows Jeppsson and Merrill (1982). The terms dextral and sinistral are used to describe curvature of elements (contra Sweet, 1981b:W63, W67). In upper view, dextral elements are convex towards the right, sinistral elements are convex towards the left. Under "Material Studied" (and in Appendix II), numbers in parentheses refer to additional, poorly preserved, usually fragmentary specimens and to questionably assigned specimens. All figured material is deposited in the Department of Invertebrate Palaeontology, Royal Ontario Museum.



TEXT-FIG. 4. Generalized vertical section through the Lower Border Group in the Bewcastle area showing sample distribution and lithostratigraphic terminology (based on Day, 1970; and measured sections of the author). For locality details see Appendix I.

Systematic Palaeontology

Phylum Chordata Bateson, 1886
Class Conodonta Pander, 1856
Subclass Conodonti Branson, 1938
Order Ozarkodinida Dzik, 1976
Family Anchignathodontidae Clark, 1972

Genus *Hindeodus* Rexroad and Furnish, 1964

Hindeodus Rexroad and Furnish, 1964:671.
Anchignathodus Sweet, 1970:7.

DIAGNOSIS
See Sweet (*in* Ziegler, 1977:203–4).

TYPE SPECIES
Trichonodella imperfecta Rexroad, 1957, by original designation (= Sa element of *Hindeodus cristula* (Youngquist and Miller, 1949)).

Hindeodus crassidentatus (Branson and Mehl, 1934b)?

Plate 1, Figs. 1a, b

Bispathodus stabilis (Branson and Mehl)—Armstrong and Purnell, 1987, pl. 1, fig. 5.

MATERIAL STUDIED
Pa elements, 3(4) from the Cambeck and Bewcastle formations, Lower Border Group, and the Southerness Formation, Cementstone Group.

DESCRIPTION
Apparatus unknown. See Branson and Mehl (1934b:276) under *Spathodus crassidentatus* for a description of Pa elements.

DISCUSSION
These specimens are indistinguishable from *"Spathognathodus crassidentatus" sensu* Klapper (1966), assigned by Sweet (1988) to *Hindeodus*. Their occurrence in rocks of Chadian and Arundian age is considerably above the range indicated for the species by Klapper (1966) and by Rexroad and Thompson (1979). This apparent anomaly suggests that the range of the species is greater than previously thought, or that these specimens are reworked. Alternatively, they may represent a younger homeomorph of *H. crassidentatus*. Considering their simple carminate morphology, the latter possibility is the most likely. Without additional information, such as ontogeny or apparatus structure, the assignment of these and similar specimens remains problematical (see Rexroad and Thompson, 1979; discussion of Gen. a sp. a).

Family Cavusgnathidae Austin and Rhodes, *in* Robison, 1981

DISCUSSION
The family Cavusgnathidae as defined by Austin and Rhodes (*in* Robison, 1981) contains seven genera. Of these, *Capricornognathus* Austin (*in* Austin and Mitchell, 1975) and *Cloghergnathus* Austin (*in* Austin and Mitchell, 1975) are herein considered junior synonyms of *Patrognathus* Rhodes, Austin, and Druce, 1969, and of *Taphrognathus* Branson and Mehl, 1941, respectively.

The apparatuses of the remaining five genera are, as far as they are known, similar, and the genera are differentiated on Pa element morphology (Table 1). Considering the similarities between these genera and the rather minor differences that divide them, compared with their intra- and interspecific variability, the separate generic status of each is perhaps unjustified (cf. Sweet, 1988). A major revision of the systematics of the Cavusgnathidae based on apparatus structure and phylogenetic information is required but is beyond the scope of this study.

TABLE 1. Pa element characteristics important in differentiating genera of Cavusgnathidae.

Cavusgnathus Harris and Hollingsworth 1933	*Taphrognathus* Branson and Mehl 1941c	*Adetognathus* Lane 1967	*Clydagnathus* Rhodes, Austin, and Druce 1969	*Patrognathus* Rhodes, Austin, and Druce 1969
Right lateral anterior blade	Right, left, or medial anterior blade	Right or left lateral anterior blade	Right lateral anterior blade	Medial anterior blade
Ridged platform ornament	Nodose, ridged, or smooth platform ornament	Ridged platform ornament	Discrete nodose platform ornament	Nodose and/or ridged platform ornament
Class IIIa symmetry	Class II or III symmetry	Class II or IIIb symmetry	Class IIIa symmetry	Class IIIa symmetry
Blade profile variable	Blade profile variable	Blade profile variable	Blade usually highest posteriorly	Blade highest posteriorly

Genus *Cavusgnathus* Harris and Hollingsworth, 1933

Cavusgnathus Harris and Hollingsworth, 1933:200.
Lewistownella Scott, 1942:299.
Windsorgnathus Austin, *in* Austin and Mitchell, 1975:53.

REVISED DIAGNOSIS

Apparatus seximembrate when fully developed: Pa elements carminiscaphate to anguliscaphate with conspicuous central trough; anterior blade attached to right side of platform; parapets transversely ridged; basal cavity bilaterally subsymmetrical to asymmetrically flared. Pb elements angulate; M elements dolabrate; Sa element alate; Sb and Sc elements bipennate. Pa elements paired with Class IIIa symmetry; all other elements, apart from the Sa, symmetrically paired.

TYPE SPECIES

Cavusgnathus alta Harris and Hollingsworth, 1933, by original designation.

DISCUSSION

This concept of *Cavusgnathus* is essentially the same as that of Norby (1976) and Rexroad (1981). Nonplatform elements of various *Cavusgnathus* species are similar, and generally they can be specifically assigned only in samples that contain Pa elements of just one *Cavusgnathus* species.

Cavusgnathus hudsoni (Metcalfe, 1981)

Plate 1, Figs. 2–14

[v.] *Cavusgnathus charactus* Rexroad—Rhodes, Austin, and Druce, 1969:79–80, pl. 13, figs. 6, 7, 13 [Pa elements].

[v.] *Taphrognathus varians* Branson and Mehl—Rhodes, Austin, and Druce, 1969:241, 242, pl. 13, figs. 4, 5 [Pa elements].

Cavusgnathus unicornis? Youngquist and Miller—Druce, 1969:48, 49, pl. 3, figs. 1, 2 [Pa elements].

[v.] *Taphrognathus varians*—Austin, 1973, figs. 1.20, 1.21 [cop. Rhodes, Austin, and Druce, 1969, pl. 13, figs. 4a, 6a] [Pa elements].

[v.] *Windsorgnathus windsorensis* (Globensky)—Austin *in* Austin and Mitchell, 1975:53, pl. 1, figs. 20, 23, 25 [Pa elements].

[v.] *Hibbardella parva* Rhodes, Austin, and Druce—Austin *in* Austin and Mitchell, 1975:45, table 2 [Sa element] [not figured].

[non] *Clydagnathus*? *hudsoni* Metcalfe, 1980:176, pl. 13, figs. 8, 9.

[v*] *Clydagnathus*? *hudsoni* Metcalfe, 1981:19, pl. 1, fig. 5 [Pa element].

[v.] *Taphrognathus varians*—Austin and Rhodes *in* Robison, 1981, fig. 108,1 [cop. Rhodes, Austin, and Druce, 1969, pl. 13, figs. 5a–c] [Pa element].

Taphrognathus sp. Austin and Davies, 1984, pl. 2, figs. 2, 3, 9 [Pa elements].

Cloghergnathus sp. Austin and Davies, 1984, pl. 2, figs. 4, 6, 27 [Pa elements].

Cavusgnathus sp. Austin and Davies, 1984, pl. 2, figs. 5, 7, 8 [Pa elements].

[(?)] *Cavusgnathus unicornis*—Austin and Davies, 1984, pl. 2, figs. 25, 26 [Pa elements].

[v.] *Cavusgnathus charactus*—Varker and Sevastopulo, 1985, pl. 5.6, figs. 14, 15 [cop. Rhodes, Austin, and Druce, 1969, pl. 13, figs. 7c, 7a] [Pa element].

REVISED DIAGNOSIS

Pa element diagnostic: anterior blade higher than long, fixed for up to approximately half its length, higher than parapets; central trough may be closed by the anterior end of the left parapet; parapets convex upwards; basal cavity bears a medial groove for its entire length.

HOLOTYPE

British Geological Survey, MPK 1907 (Metcalfe, 1981, pl. 1, fig. 5).

TYPE HORIZON AND LOCALITY

Haw Bank Limestone sample 272 of Metcalfe (1981), Haw Bank Quarry, North Yorkshire, U.K. (G.R. SE 015532).

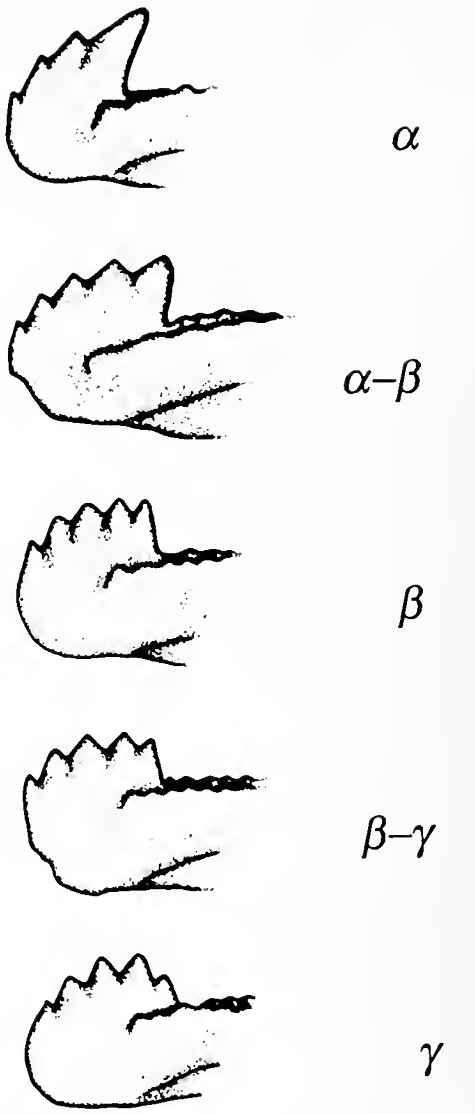
MATERIAL STUDIED

Pa elements, 259(65) [α blade, 47(1); β blade 65; γ blade 12; intermediate blade 107; indeterminable blade morphology 28(64). 192 Pa elements complete enough for curvature determination: 104 sinistral, 68 dextral, and 20 straight]. Pb elements, 47(15); M elements, 23(1); Sa elements, 6(2); Sb elements, 3; Sc elements, 5(1). All material from the Liddel and Lynebank Formations, Lower Border Group.

DESCRIPTION

Pa elements. The anterior blade is between one-quarter and two-fifths of total element length. It is composed of three to five, rarely six, laterally compressed denticles, fused apart from their tips, and is always developed on the right side of the element. A notch is commonly developed between the blade and the right parapet, occasionally with some medial displacement of the blade. The shape of the blade in lateral view is comparable to that of *C. unicornis sensu* Rexroad (1981) and may be of α, β , γ, or intermediate form (see Text-Fig. 5). α–β intermediate blades are particularly common, denticles increasing in size and height posteriorly, but lacking a conspicuously larger posterior denticle. The posteriormost blade denticle is often reclined and is always higher than the anterior end of the right parapet. Blade height is greater than or equal to length; the fixed blade is usually between one-fifth and one-half of total blade length but may be slightly more or less.

The platform height is greater than or, less commonly, equal to width, decreasing slightly in the posterior half. The platform may be straight but usually exhibits some lateral curvature with the outer margin convex and the inner margin convex, straight, or concave. In some specimens, the interplay of arching and lateral curvature give a twisted appearance to the posterior end of the platform. The length of the platform, measured from the anterior end of the left parapet to the posterior tip, is generally between four and six times the width, occasionally as much as seven times or as little as three times. Maximum platform width is attained either around midlength, gradually tapering to the posterior, or in the posterior third, tapering more rapidly. The parapets are ornamented by weak transverse ridges which may be more strongly developed in larger specimens. The ridges extend up to the parapet crests and create a serrated profile, the strength of which depends on the development of the ridges. The medial trough becomes shallower anteriorly and posteriorly according to the downward curvature of the parapets. In most specimens, the trough remains open at the anterior end but the left parapet may converge with the blade to more or less close the gap. Two or three nodes may be present in the posterior part of the trough forming a short carina of variable strength. The posterior tip of the platform is generally sharply pointed and the carina, if present, may extend posteriorly as a short blade. The lower profile of the platform in lateral view is concave, generally not strongly so, but this is more evident when viewed from the right. In some specimens, the lower margin of the blade is slightly upturned relative to the platform.



TEXT-FIG. 5. Blade form in *Cavusgnathus hudsoni*. Blade type indicated by Greek letters.

The basal cavity is lanceolate, tapering anteriorly and posteriorly. It is widest and deepest just anterior of element midlength and comes to a point at, or very close to, the posterior tip of the element. A medial groove is present along the entire length of the cavity; on either side of this groove, both sides of the cavity extend an approximately equal distance anteriorly. The generally slight asymmetry of the cavity increases in some larger specimens with greater lateral flaring.

Pb elements. See Rexroad (1957:36) under *Ozarkodina compressa*. These elements are variable; some specimens (e.g., Pl. 1, Fig. 10) have a relatively large basal cavity, widest beneath the cusp, and a strongly reclined cusp and denticles. Such specimens approach the morphology of *"Subbryantodus stipans" sensu* Rexroad (1957). Norby (1976) noted the similarity between *"S. stipans"* and the Pb elements of *Cavusgnathus*. Stratigraphically younger specimens are like *"O. compressa"* but tend to have more discrete, elongate denticles and cusp.

M elements. See Rexroad (1957:34) under *Neoprioniodus loxus*. Some M elements of *C. hudsoni* (e.g., Pl. 1, Fig. 14) show less downward deflection of the posterior process than *"N. loxus"* and approach "*Neoprioniodus varians* (Branson and Mehl)" in form. The discreteness of major denticles and the development of minor denticles also vary.

Sa elements. See Rexroad (1958a:18) under *Hibbardella ortha*.

Sb elements. The anterior process is incomplete in all specimens but is at least as long as the posterior process. It is laterally compressed and bears five discrete thin denticles, subcircular in cross-section, with one or two minor denticles occasionally developed between them. The denticles are erect at the anterior end but are increasingly reclined towards the cusp. The cusp itself is reclined; it is slightly larger than the anterior process denticles but is otherwise similar. The posterior process is slightly higher and thicker and is deflected slightly downwards relative to the anterior. The denticulation is similar to that of the anterior process but the five major denticles increase in size, height, and reclination, posteriorly. The figured specimen (Pl. 1, Fig. 13) has two minor denticles on the posterobasal edge of the last major denticle. The lower edge has a sharp downward deflection at the posterior end of some specimens. The basal cavity is developed obliquely beneath the cusp, aligned with its long axis. It is narrow, shallow and elongate, rather conical in one small specimen, and tapers anteriorly and posteriorly. The cavity does not appear to continue as a groove along the process, but a thin zone of recessive basal margin is developed along the lower edge of the posterior process.

Sc elements. See Hass (1953:81) under *Hindeodella ensis* and Clarke (1960:8) under *H. tenuis*.

DISCUSSION

The Pa elements of *C. hudsoni* exhibit considerable variation in many aspects of their morphology. Individual characters vary continuously and in discord with other characters; no consistently recognizable relationship between different characters has been observed. The arbitrary choice of a single character to subdivide this plexus into a number of more convenient "species" would be a backward step taxonomically. Rather, these variable elements are interpreted as members of a single species with considerable plasticity in Pa element development.

Clydagnathus? *hudsoni* Metcalfe, 1981, falls comfortably within the range of variation described above. The original concept of the species (Metcalfe, 1981) was more restricted, almost certainly due to the small sample size of 10 Pa elements. The assignment to *Clydagnathus*? based on anterior closure of the trough has been emended: firstly because of the variability of the character, and secondly because anterior trough closure is no longer considered diagnostic of *Clydagnathus* (Nicoll and Druce, 1979; contra Rhodes, Austin, and Druce, 1969). The posterior blade denticle is broken in the holotype of *Cavusgnathus hudsoni*; originally the blade probably had an a α–β intermediate form.

The specimens from the Main Algal "series" (= Liddel Formation) of Harden Burn, Roxburghshire, figured by Rhodes, Austin, and Druce (1969) as *Cavusgnathus charactus* Rexroad and *Taphrognathus varians* Branson and Mehl, are referred to *C. hudsoni*. One of these specimens was subsequently figured as *T. varians* in the *Treatise on Invertebrate Paleontology* (Austin and Rhodes *in* Robison, 1981).

Nicoll and Druce (1979) included within their concept of *Clydagnathus cavusformis* specimens figured by Druce (1969) as *Cavusgnathus*? *unicornis*. These specimens appear to have ridged platform ornament rather than the nodose ornament characteristic of *Clydagnathus* and are herein considered to belong to *C. hudsoni*. Austin (*in* Austin and Mitchell, 1975) distinguished his new genus *Windsorgnathus* from *Cavusgnathus* on stratigraphic evidence alone. Austin and Rhodes (*in* Robison, 1981) placed *Cavusgnathus* and *Windsorgnathus* in synonymy. *Windsorgnathus windsorensis sensu* Austin (*in* Austin and Mitchell, 1975) is distinct from *Clydagnathus windsorensis* (Globensky) (von Bitter and Austin, 1984) and is identical to *Cavusgnathus hudsoni* from the Lynebank Formation of the Northumberland trough. *C. hudsoni* also occurs in Tournaisian strata of the Irish Republic, variously reported as species of *Cavusgnathus*, *Clydagnathus*, and *Taphrognathus* (Johnston, 1976; Marchant, 1978; Rees, 1987).

Variation in *C. hudsoni* Pa elements appears to have decreased through time. Specimens of upper Tournaisian age from Ireland, from the Craven basin (Metcalfe, 1981),

TABLE 2. Distinguishing characteristics of *Cavusgnathus charactus* Rexroad, *C. hudsoni* (Metcalfe), and *C. unicornis* Youngquist and Miller. Characteristics of *C. charactus* based on Rexroad (1957); those of *C. hudsoni* on personal observation; those of *C. unicornis* on Youngquist and Miller (1949), Rexroad (1957), Rexroad (1981), and various published plates.

Cavusgnathus charactus	*Cavusgnathus hudsoni*	*Cavusgnathus unicornis*
"Attachment scar" anterior of basal cavity	No "attachment scar"	No "attachment scar"
6–8 blade denticles	3–5 blade denticles	5–8 blade denticles
Blade < 1/3 free	Blade > 1/2 free	Blade < 1/2 free
Blade slightly > 1/3 of element length	Blade usually < 1/3 of element length	Blade commonly > 1/3 of element length
Inner parapet nearly straight, convex at tip	Inner parapet convex, straight, or concave	Both parapets convex outwards
Trough always open at anterior end	Trough may be closed at anterior end	Trough always open at anterior end
Parapet notch diagnostic	Parapet notch common	Parapet notch rare
Blade slightly convex	α, β, γ, and intermediate blade morphologies	α, β, γ, and intermediate blade morphologies
	Blade height > length	Blade height < length
	Platform widest at midlength or in posterior 1/3	Platform widest near apical denticle

and from the Liddel Formation (Rhodes, Austin, and Druce, 1969; Austin and Davies, 1984; this study) exhibit greater morphological plasticity than specimens of Chadian age from Northern Ireland (Austin *in* Austin and Mitchell, 1975), and from the Lynebank Formation (this study). This apparent trend may prove spurious given that, at present, many more specimens are known from Tournaisian strata.

In the Cavusgnathidae, genera and species within a genus are mainly distinguished on Pa element morphology. Although certain Pa element specimens within the range of variation of *Cavusgnathus hudsoni* approach the morphology of *C. charactus* and *C. unicornis*, they can be differentiated on the basis of the characters in Table 2. *Cavusgnathus altus* differs in the shape and proportions of the irregular cockscomblike blade and in the termination of the basal cavity one-quarter to one-fifth of the platform length from the posterior end. The platform ornament, blade shape and proportions, and the strong downward deflection of the lower edge of the blade, only rarely developed in *C. hudsoni*, serve to distinguish *C. naviculus*.

An Sa element occurring with *C. hudsoni* in the Lower Carboniferous Shale of Northern Ireland was identified by Austin (*in* Austin and Mitchell, 1975) as *Hibbardella parva*. This element is very similar to the Sa element figured here (Pl. 1, Fig. 11) and probably belongs to *C. hudsoni*. Sc elements of *C. hudsoni* show considerable variation, especially in the degree of inward and upward or downward curvature of the anterior process. One of the figured specimens (Pl. 1, Fig. 12) has very little inward curvature of the process and may be transitional to an Sb element. The other figured specimen (Pl. 1, Fig. 9) shows the abrupt downward curvature of the lower edge developed at the posterior end of some specimens.

Cavusgnathus unicornis Youngquist and Miller, 1949

Plate 2, Figs. 1–5, 7

Cavusgnathus unicornis Youngquist and Miller, 1949:619, pl. 101, figs. 18–23 [Pa element, α morphotype].

Cavusgnathus regularis Youngquist and Miller, 1949:619, pl. 101, figs. 24, 25 [Pa element, β morphotype].

[v*] *Cavusgnathus convexa* Rexroad, 1957:17, pl. 1, figs. 3–6 [Pa element, γ morphotype].

Neoprioniodus loxus Rexroad, 1957:34, pl. 2, figs. 8, 9, 14 [M element].

Ozarkodina compressa Rexroad, 1957:36, pl. 2, figs. 1, 2 [Pb element].

Hibbardella ortha Rexroad, 1958a:18, pl. 2, figs. 9–12 [Sa element].

Cavusgnathus unicornis—Rexroad, 1981:8, 9, pl. 1, figs. 17, 22, 26, 27 [Pa element, α morphotype], fig. 21 [Pa element, β morphotype], figs. 18–20, 23 [Pa element, γ morphotype], figs. 7, 8 [M element].

Cavusgnathus unicornis—Rexroad and Horowitz, 1990: 499, pl. 1, figs. 12, 13, 16, 17 [Pa element, α morphotype], figs. 11, 14, 15 [Pa element, β morphotype], fig. 10 [Pa element, γ morphotype], fig. 18 [Pa element, α morphotype?], fig. 19 [Pa element, α – β intermediate morphotype] [includes synonymy].

DIAGNOSIS

See Rexroad (1981:8).

HOLOTYPE

State University of Iowa, 4174 (Youngquist and Miller, 1949, pl. 101, figs. 18, 19).

TYPE HORIZON AND LOCALITY

Pella beds, Chesterian age; Pella South West, Marrion County, Iowa, U.S.A.

MATERIAL STUDIED

Pa elements, α morphotype, 19(1); β morphotype, 14(5); γ morphotype, 8(1); intermediate morphotype, 14(2); indeterminate morphotype, 6(26). Pb elements, 10(7); M elements, 24(7); Sa elements, 2(7); Sb elements, (1); Sc elements, 1(1). Material from the Main Algal and Cambeck formations, Lower Border Group, the Cementstone Group, and the Orroland group.

DESCRIPTION

Pa elements. α morphotype, see Youngquist and Miller (1949:619) and Rhodes, Austin, and Druce (1969:82) under *Cavusgnathus unicornis*; β morphotype, see Youngquist and Miller (1949:619) under *C. regularis*; γ morphotype, see Rexroad (1957:17) under *C. convexa*.

Pb elements. See Rexroad (1957:36) under *Ozarkodina compressa*.

M elements. See Branson and Mehl (1941a:174) under *Prioniodus varians* and Rexroad (1957:34) under *Neoprioniodus loxus*. These forms represent end members of the range of variation in *C. unicornis* M elements.

Sa elements. See Rexroad (1958a:18) under *Hibbardella ortha*.

Sc elements. See Hass (1953:81) under *Hindeodella ensis*, and Clarke (1960:8) under *H. tenuis*.

DISCUSSION

The concept of *C. unicornis* followed herein is essentially the same as that of Rexroad (1981). Pa elements with a low blade, which in some specimens approaches the morphology of *Cavusgnathus* sp. *sensu* Rexroad (1981), are not uncommon in the Northumberland trough and are herein considered as variants of *C. unicornis*. Slight lateral offset of the anterior blade, encountered only rarely in the present study, is also considered to represent intraspecific variation (cf. Rexroad and Nicoll, 1965:18, pl. 1, figs. 21–23). M elements of *"N. loxus"* and *"N. varians"* forms differ in little other than the angle of downward deflection of the posterior process (Rexroad, 1958a; Norby, 1976), although *"N. varians"* may be more robust (Norby, 1976). Both forms were considered by Rexroad and Horowitz (1990) to be morphotypes of M elements shared by *C. unicornis* and *C. charactus* (contra Rexroad, 1981). Both are included in *C. unicornis* herein. Some specimens develop an inclined basal cavity, which forms an anticusplike anterobasal termination. Similar anticusps are seen in *Cavusgnathus* M elements from the Bear Gulch Limestone, Montana (Conway Morris, 1990, fig. 7; pers. obs.).

A single Sb element in sample 1768701 has been tentatively assigned to *C. unicornis*. The presence of other cavusgnathid Pa elements with *C. unicornis* in this sample precludes more certain assignment.

Cavusgnathus cf. *hudsoni* (Metcalfe, 1981)

MATERIAL STUDIED

A single Pa element from the Bewcastle Formation, Lower Border Group.

DESCRIPTION

Apparatus unknown. The single sinistral specimen of *C.* cf. *hudsoni* (γ morphotype) differs from *C. hudsoni* in having a higher blade than γ morphotypes of the species. It has very weak platform ornament and a lateral ridge along the left side of the blade as an anterior extension of the platform. The basal cavity does not reach the posterior end of the element; it bears thickened lips, the outer of which dips downwards.

DISCUSSION

This element may represent an extreme variant of *C. hudsoni*.

Cavusgnathus cf. *unicornis* Youngquist and Miller, 1949

Plate 2, Figs. 6a, b

MATERIAL STUDIED

A single Pa element from the Lower Antiquatonia Member of the Cambeck Formation, Lower Border Group.

DESCRIPTION

The single Pa element specimen differs from *C. unicornis* only in the break up of the transverse ridges into nodes in the posterior half of the platform (a character usually seen only in *C. naviculus*), and in the suppression of parapet development in the posterior third of the element, to form a low flat broad posterior platform.

DISCUSSION

Some depression of the posterior part of the platform has been recorded in *C. unicornis* Pa elements (e.g., Rexroad, 1981, pl. 1, figs. 17, 22) although not to the extent to which it is developed in *C.* cf. *unicornis*. This specimen may, however, be an aberrant *C. unicornis* Pa γ element.

***Cavusgnathus*? sp. a**

Plate 2, Fig. 8

MATERIAL STUDIED

2(1) Pa elements from the Cambeck Formation, Lower Border Group.

DESCRIPTION

Apparatus unknown. Pa elements bear a short anterior blade, free for almost all its length. The blade is composed of a large cusp with a smaller "piggy back" denticle to the anterior. Blade height is approximately twice its length. One specimen has a small denticle posterior of the cusp. The platform is higher than it is wide and is ornamented with low indistinct nodes, which become more discrete posteriorly. The medial trough is shallow and narrow, shallowing posteriorly and more or less closed anteriorly by convergence of the left parapet with the blade. In lateral view, the lower surface of these elements is straight or concave, and the upper surface of the platform is convex. The two most complete specimens recovered are sinistrally curved. The lanceolate basal cavity is subsymmetrical and would almost certainly extend to the posterior tip of complete specimens. It is deepest and widest just anterior of midlength and, although constricted anteriorly, it extends under the blade. Posteriorly the cavity tapers gradually.

DISCUSSION

These specimens resemble some Pa elements of *Clydagnathus windsorensis* (Globensky) but lack the discrete nodose ornament diagnostic of the genus.

Genus *Clydagnathus* Rhodes, Austin, and Druce, 1969

Clydagnathus Rhodes, Austin, and Druce, 1969:84.

DIAGNOSIS

See Rhodes, Austin, and Druce (1969:84).

TYPE SPECIES

Clydagnathus cavusformis Rhodes, Austin, and Druce, 1969, by original designation.

DISCUSSION

Rhodes, Austin, and Druce (1969:85) distinguished *Clydagnathus* from *Cavusgnathus* "by the general anterior closure of the oral trough, by the merging of the marginal ornament with the blade and by the lateral, rather than longitudinal expansion of the basal cavity." After examination of large numbers of *Clydagnathus* from Australia, however, Nicoll and Druce (1979) concluded that the genera could not be differentiated using these characters. Sandberg and Ziegler (1979) considered *Clydagnathus* and *Cavusgnathus* to be distinguishable solely in terms of their respective stratigraphic positions. With the reassignment of *Cavusgnathus windsorensis* Globensky to *Clydagnathus* (von Bitter and Plint, 1987) and the recognition of *Cavusgnathus* of Tournaisian age (see *Cavusgnathus hudsoni* above), this stratigraphic distinction can no longer be made.

The possession of nodose rather than ridged platform-element ornament has been used to differentiate *Clydagnathus* from *Cavusgnathus* herein. This appears to be in accord with the generic concept used by other workers (e.g., Nicoll and Druce, 1979; von Bitter and Plint, 1987) but a distinction at the generic level based on this character is probably unjustified (see discussion of the family Cavusgnathidae). In addition, *Clydagnathus* may be polyphyletic. A phylogenetic sequence from *"Spathognathodus" plumulus* (Rhodes, Austin, and Druce) through *Clydagnathus gilwernensis* Rhodes, Austin, and Druce to *Clydagnathus cavusformis* has been proposed (Rhodes, Austin, and Druce, 1969; Austin and Hill, 1973; Sandberg and Ziegler, 1979). However, Sandberg and Ziegler (1979) suggest that *Clydagnathus ormistoni* (Beinert, Klapper, Sandberg, and Ziegler) evolved from *Pandorinellina* cf. *insita* (Stauffer) or *Scaphignathus ziegleri* Druce. Preliminary evidence suggests that *Clydagnathus windsorensis* (Globensky) may be a progenetic offshoot of *Cavusgnathus* (see discussion of *Cl. windsorensis*). Generic revision of *Clydagnathus* is clearly required but must await description of the apparatus of the type species, *Cl. cavusformis*.

***Clydagnathus windsorensis* (Globensky, 1967)**
Plate 2, Figs. 9–15

[v*] *Cavusgnathus windsorensis* Globensky, 1967:439, pl. 57, figs. 3, 4, 7, 9, 11, 19, pl. 58, fig. 1 [Pa elements] [N.B. The specimen shown in pl. 57, fig. 7 is not the holotype].

[v.] *Cavusgnathus* cf. *windsorensis* Globensky, 1967:439, pl. 57, figs. 2, 6, 10 (specimen lost); 12, pl. 58, fig. 8 [Pa elements].

[vp] *Cavusgnathus* spp. Globensky, 1967:440, pl. 57, fig. 17 only [Pa element].

[v?] *Ozarkodina* sp. A Globensky, 1967:446, pl. 55, figs. 1, 5, 12 only [Pb elements].

[p?] *Taphrognathus varians* Branson and Mehl—Pierce and Langenheim, 1974:168, 169, pl. 1, figs. 3, 4, 6, 7 only [Pa elements].

[vp] *Cavusgnathus windsorensis*—von Bitter and Plint-Geberl, 1982:194, pl. 2, figs. 1–3, 16–18 [Pa elements]; pl. 6, fig. 18 [M element] only.

[vp?] *Cavusgnathus windsorensis*—von Bitter and Plint-Geberl, 1982:194, pl. 1, figs. 1–16; pl. 2, figs. 4–15 [Pa elements]; pl. 7, figs. 1, 5–7 [Pb elements]; pl. 3, figs. 15, 16 [Sa elements]; pl. 7, fig. 12 [Sb element]; figs. 15–18 [Sc elements].

[vp] *Cavusgnathus regularis* type—von Bitter and Plint-Geberl, 1982:197, pl. 3, fig. 18 only [Pa element].

[vnonp] *Cavusgnathus windsorensis*—von Bitter and Plint-Geberl, 1982, pl. 7, fig. 2 only [= *Vogelgnathus pesaquidi*, Pa element].

[(?)] *Clydagnathus*? cf. *cavusformis* Rhodes, Austin, and Druce—Briggs, Clarkson, and Aldridge, 1983:3–8, figs. 1, 2, 3 [whole animal].

Cavusgnathus windsorensis—von Bitter and Austin, 1984, pl. 19, figs. 1–10 [Pa elements].

[v.] *Clydagnathus windsorensis*—von Bitter and Plint, 1987:350, 351, figs. 2.1–2.6, 2.7(specimen lost), 2.10, 2.11, 2.14–2.17 [Pa elements], fig. 2.12, [Pb element], fig. 2.13 [M element], fig. 2.8 [Sa element], fig. 2.19 [Sb element], fig. 2.18 [Sc element].

[(?)] *Clydagnathus*? cf. *cavusformis*—Aldridge, 1987, fig. 1.9 [whole animal] [cop. Briggs, Clarkson, and Aldridge, 1983, figs. 1A, 3B].

DIAGNOSIS

See von Bitter and Plint (1987:351).

HOLOTYPE

University of New Brunswick 64-F-235 (Globensky, 1967, pl. 57, figs. 3, 4, 7).

TYPE HORIZON AND LOCALITY

Windsor Limestone, sample KD10 of Globensky (1967). On the Atlantic coast between the village of Skir Dhu and north shore about 330 m SW of Skir Dhu fisherman's wharf, Skir Dhu, Cape Breton Island, Nova Scotia, Canada.

MATERIAL STUDIED

Pa elements, 63(14); Pb elements, 15(8); M elements, 8(1); Sa elements, 4; Sb elements, 7(1); Sc elements, 12(6); mostly from the lower Lynebank Formation, Lower Border Group, but also from the Cambeck Formation, Lower Border Group, the Southerness and Basal Cementstone formations, Cementstone Group, and the Cementstone Group of Kielder Burn, Barrow Scar, and Black Burn.

DESCRIPTION

Pa elements. See Globensky (1967:439) under *Cavusgnathus windsorensis,* and the remarks of von Bitter and Plint (1987:351).

Pb elements. The anterior process is laterally compressed. It is straight or downcurved, generally only slightly, and occasionally incurved slightly. It becomes thicker towards the cusp and bears up to seven, commonly five, laterally compressed, elongate pointed denticles which are free for most of their length. The denticles are erect and slightly recurved, often becoming slightly reclined towards the cusp, and are highest around the middle of the process. The cusp is higher wider and thicker than the anterior denticles. It is reclined and recurved although usually not greatly so. The posterior process is lower than, but approximately equal in length to, the anterior, and may be less laterally compressed. It is straight or slightly downcurved, thins posteriorly, and bears five or six laterally compressed denticles. These denticles are subequal in size, generally smaller than those of the anterior process, and become increasingly reclined posteriorly. The basal cavity is relatively large. It is widest and deepest beneath the posterior edge of the cusp, and tapers posteriorly to a point at least half-way along the process. Anteriorly the cavity tapers a variable distance, but generally reaches a point approximately half-way along the process. The lips of the cavity often extend downwards, creating an undulating lower profile to the element.

M elements. The cusp is strongly proclined, its long axis forming an angle of approximately 130° with the axis of the posterior process. It is slightly incurved and laterally compressed, with sharp anterior and posterior edges and convex lateral surfaces. The posterior process is usually straight but may be curved at the anterior end where it joins the cusp. The thickness of the process decreases towards the posterior tip; its length may be greater than or less than that of the cusp. Depending on length, the process bears up to 10 small discrete pointed subequal denticles, that generally become more erect with respect to the process posteriorly. The small asymmetrical basal cavity is widest beneath the posterior part of the cusp, and has a small, occasionally thickened lip on the inner side. The cavity tapers posteriorly to a narrow groove extending down the sharp lower edge of the process. In a few specimens, one or two small fused denticles are developed anterior of the cusp.

Sa elements. See Rexroad (1958a:18) under *Hibbardella ortha.*

Sb elements. The anterior process is laterally compressed and straight or slightly incurved. It bears six or more laterally compressed denticles, free for most of their length, which curve inwards and become increasingly reclined posteriorly. The sharply pointed cusp is laterally compressed, reclined and incurved, and is larger than the anterior denticles. The posterior process is laterally compressed, straight, and larger than the anterior process. It bears up to approximately 10 laterally compressed denticles; these increase in size and reclination towards the posteriormost denticles, which may be larger than the cusp. The posterobasal termination beneath these denticles may be downturned. The basal cavity is small and is located to the anterior of the cusp, aligned with its long axis. It continues as a narrow groove along the sharp lower edge of the posterior process and part way along the anterior. In larger specimens, the groove is flanked by recessive basal margin.

Sc elements. See Clarke (1960:8) under *Hindeodella tenuis*.

DISCUSSION

The apparatus of *Clydagnathus windsorensis* from the Northumberland trough was reconstructed from essentially monospecific faunas recovered from three samples of the Ellery Sike Limestone Member of the Lynebank Formation, Lower Border Group. Certain morphological similarities, especially the elongate narrow cusps of the nonplatform elements, provide additional evidence of affinity.

Although similar to the type material (Globensky, 1967) and some of the material figured by von Bitter and Plint-Geberl (1982), *Cl. windsorensis* Pa elements from the Northumberland trough are different from specimens from the *Diplognathodus* Zone in southwest Newfoundland (von Bitter and Plint-Geberl, 1982, pl. 1, figs. 1–16, pl. 2, figs. 4–15). The latter elements belong to an apparatus that appears to lack M elements, has abbreviated Pb elements, and has an Sa element that may have lacked a posterior process (von Bitter and Plint-Geberl, 1982). Although these differences were considered to be intraspecific ecophenotypic variation (von Bitter and Plint-Geberl, 1982), *Diplognathodus* Zone specimens may prove to represent a different species.

In the Northumberland trough, stratigraphically younger specimens from the Cambeck Formation have blunter nodes, relatively longer, more arched platforms, and very short high blades, compared with specimens from the Lynebank Formation.

von Bitter and Plint (1987) included "*Ozarkodina acadiensis* Globensky" in synonymy with *Cl. windsorensis* as the Pb element. The figured specimens of Globensky (1967) have an incurved posterior process, a character not observed in other *Cl. windsorensis* Pb elements. They are probably the Pb elements of *Lochriea scotiaensis* (Globensky). Five Pb elements from the Lynebank Formation are questionably assigned to *Cl. windsorensis* herein, as they have a larger number of denticles and a smaller cusp than is usually seen in this species.

The M, Sa, and Sc elements of *Cl. windsorensis* are similar to the homologous elements of species of *Cavusgnathus* and *Taphrognathus varians*.

The preference of *Cl. windsorensis* for shallow restricted probably euryhaline environments is well documented (e.g., Plint and von Bitter, 1986; Purnell, 1989). Gould (1977:324–325) argued that progenesis represents an effective adaptive strategy in such environments. The close morphological similarity between *Cl. windsorensis* elements, which are generally rather small, and juvenile *Cavusgnathus* elements suggests that *Cl. windsorensis* evolved as a progenetic offshoot of *Cavusgnathus*. The species is now known from strata of Chadian (this study) and Holkerian age (von Bitter and Austin, 1984; this study) and a progenetic response to environmental stress may, therefore, have occurred more than once.

Genus *Patrognathus* Rhodes, Austin, and Druce, 1969

Patrognathus Rhodes, Austin, and Druce, 1969:178.
Capricornognathus Austin *in* Austin and Mitchell, 1975:47.

DIAGNOSIS

See Rhodes, Austin, and Druce (1969:178).

TYPE SPECIES

Patrognathus variabilis Rhodes, Austin, and Druce, 1969, by original designation.

DISCUSSION

The diagnosis of *Capricornognathus* Austin (*in* Austin and Mitchell, 1975) corresponds closely to the description of *Taphrognathus capricornis* Druce of Druce (1970). Klapper (1971) noted the similarity between *T. capricornis* and *Patrognathus* and suggested that *T. capricornis* may be a younger representative of the genus. Indeed, *Capricornognathus*, according to the diagnosis of Austin (*in* Austin and Mitchell, 1975) differs from *Patrognathus sensu* Klapper (1971) only in that the former taxon may have ridged or nodose platform ornament and may possess a short posterior free blade and carina. In view of the overwhelming similarities between *T. capricornis* and *Patrognathus, T.*

capricornis, the type and only species of *Capricornognathus*, is herein placed in *Patrognathus* as it was by Metcalfe (1980, 1981) and Varker and Sevastopulo (1985).

Although *P. capricornis* is partially reconstructed herein, there is little evidence for the nature of the apparatus in other species of the genus, the type species included. Consequently, expansion of the generic diagnosis to include nonplatform elements would be premature. If the apparatus of *P. variabilis* Rhodes, Austin, and Druce proves significantly different from *P. capricornis*, another generic assignment must be sought for the latter species.

Patrognathus Pa elements are distinguished from those of other cavusgnathid genera by the presence of a medial anterior blade, free for all its length, with the highest denticle at the posterior end of the blade (Klapper, 1971). Some Pa elements of *Taphrognathus*? *transatlanticus* (von Bitter and Austin) have a similar blade profile, but the blade is a continuation of the outer parapet (von Bitter and Austin, 1984).

Patrognathus capricornis (Druce, 1970)

Plate 3, Figs. 1–9

[(?)] *Taphrognathus* sp. Druce, 1969:139, pl. 41, fig. 1 [Pa element].

Taphrognathus capricornis Druce, 1970:102, pl. 15, figs. 3–5 [Pa elements].

[?] *Patrognathus*? cf. *capricornis*—Jenkins, 1974:916 [Pa element] [not figured].

[v.] *Taphrognathus capricornis*—Austin, 1974, pl. 1, figs. 6, 19 [Pa elements].

[v(?)] *Patrognathus andersoni*—Austin, 1974, pl. 1, fig. 5 [?juvenile Pa element].

[v.] *Capricornognathus capricornis*—Austin *in* Austin and Mitchell, 1975:48, pl. 2, figs. 5–12, 14–19, 21, 23, 28, 30–33 [Pa elements; N.B. magnification of specimens between x50 and x60, not x40] [figs. 9, 12 cop. Austin, 1974, pl. 1, figs. 19, 6].

[v.] *Patrognathus andersoni* Klapper—Austin *in* Austin and Mitchell, 1975:52, pl. 2, figs. 3, 4, 13, 20, 22, 25 [Pa elements], figs. 1, 2, 24, 27 [?juvenile Pa elements; N.B. magnification of specimens between x50 and x60, not x40] [fig. 2 cop. Austin, 1974, pl. 1, fig. 5].

[v.] *Neoprioniodus* cf. *confluens* (Branson and Mehl)—Austin *in* Austin and Mitchell, 1975:45, table 2 [M element; not figured].

Patrognathus capricornis—Metcalfe, 1980, pl. 13, figs. 1, 2 [Pa element], fig. 3 [?juvenile Pa element].

[v.] *Patrognathus capricornis*—Metcalfe, 1981:39, pl. 9, figs. 1, 2 [Pa elements].

[v.] *Capricornognathus capricornis*—Austin and Rhodes *in* Robison, 1981:159, text-fig. 108,5 [Pa element] [cop. Austin *in* Austin and Mitchell, 1975, pl. 2, figs. 10, 33].

Patrognathus variabilis Rhodes, Austin, and Druce—Austin and Davies, 1984:207, text-fig. 15, pl. 1, figs. 10, 11 [Pa elements], fig. 8 [?juvenile Pa element].

[v.] *Patrognathus capricornis*—Varker and Sevastopulo, 1985, pl. 5.6, fig. 17 [Pa element] [cop. Metcalfe, 1981, pl. 9, fig. 1a].

[v.p] *Mestognathus beckmanni* Bischoff—Armstrong and Purnell, 1987, pl. 3, fig. 5 [Pb element], fig. 7 [M element] only.

[v.p] *Patrognathus variabilis*—Armstrong and Purnell, 1987, pl. 3, figs. 8, 9 [?juvenile Pa elements], fig. 10 [Sc element], fig. 11 [M element] only.

REVISED DIAGNOSIS

Apparatus at least quinquemembrate. Pa elements carminiscaphate, straight or slightly curved, with shallow central trough; left parapet bears one or two rows of rounded nodes; right parapet bears a single row of transverse ridges or tetrahedral nodes. Pb elements angulate; M elements dolabrate; Sa element alate; Sc elements bipennate. Pa elements paired with class IIIa symmetry; all others, apart from the Sa element, symmetrically paired.

HOLOTYPE

Bureau of Mineral Resources, Canberra, CPC 7796 (Druce, 1970, pl. 15, fig. 5).

TYPE HORIZON AND LOCALITY

Gargoogie Oolite Member, Rockhampton Group, Queensland, Australia (G.R. 322093, Rockhampton Sheet).

MATERIAL STUDIED

Pa elements, 16(1), juvenile Pa elements (*Patrognathus* sp. in Appendix II), 18(3); Pb elements, 5(1); M elements, 10(6); Sb elements, (1); Sc elements, 5(24). Mostly from the Bogside Limestone Member of the Bewcastle Formation but also from the Lynebank and Cambeck formations, Lower Border Group, the Southerness Formation, Cementstone Group, and the Orroland Group. In addition, the material of Austin (*in* Austin and Mitchell, 1975) and unpublished material collected by Dr. N. J. Riley from the Craven basin has been examined.

DESCRIPTION

Pa elements. See Metcalfe (1981:39).

Pb elements. See Rexroad (1957:36) under *Ozarkodina compressa. Patrognathus capricornis* Pb elements have a longer straighter anterior process than typical *"O. compressa"*-form Pb elements. This process bears between eight and ten subequal denticles and has a square anterobasal termination. The cusp and denticle shape resemble those of the anterior blade of Pa elements of the species.

M elements. See Rhodes, Austin, and Druce (1969:158, 159) under *Neoprioniodus confluens.*

Sa elements. See Rexroad (1958a:18) under *Hibbardella ortha.*

Sc elements. See Hass (1953:81, 82) under *Hindeodella ensis,* and Clarke (1960:8) under *H. tenuis.* The size of denticles on the posterior process of these elements alternates more regularly than in other cavusgnathids.

DISCUSSION

The apparatus of *Patrognathus capricornis* was reconstructed on the evidence of nonplatform elements associated with *Patrognathus* Pa elements in the low diversity faunas of the Northumberland trough. It is also assumed that *P. capricornis* had a typical ozarkodinid Bauplan similar to other cavusgnathids. Unfortunately, Pa elements of *Taphrognathus varians* and *Mestognathus* often occur with *Patrognathus,* and reduce the level of confidence that can be placed in the assignment of some of the elements. For example, although distributional and morphological evidence suggests that the Pb elements described above belong to *P. capricornis,* there is a possibility that they represent juvenile *Mestognathus* Pb elements. Similarly, some of the M elements assigned to *P. capricornis* may belong to *Mestognathus.*

One of the specimens figured as *P. capricornis* (Pl. 3, Fig. 6) resembles some *Adetognathus unicornis* Pa elements (e.g., Varker and Austin, 1974, pl. 6, fig. 18) and illustrates the problems of homeomorphy in the Cavusgnathidae.

M elements do not have the long anticusp of the lectotype of "*Neoprioniodus confluens* (Branson and Mehl)" also developed in one of the figured specimens of Rhodes, Austin, and Druce (1969, pl. 21, fig. 8). They are similar to the other figured specimen of Rhodes, Austin, and Druce (1969, pl. 21, fig. 2), and otherwise conform to their description. M elements of *"Neoprioniodus confluens"* form are consistently associated with *P. capricornis* Pa elements in the Northumberland trough, and also occur with *P. capricornis* in Northern Ireland (identified as *N.* cf. *confluens* by Austin *in* Austin and Mitchell, 1975, but not figured). M elements of this form also occur with *P. variabilis* Pa elements (Austin and Hill, 1973).

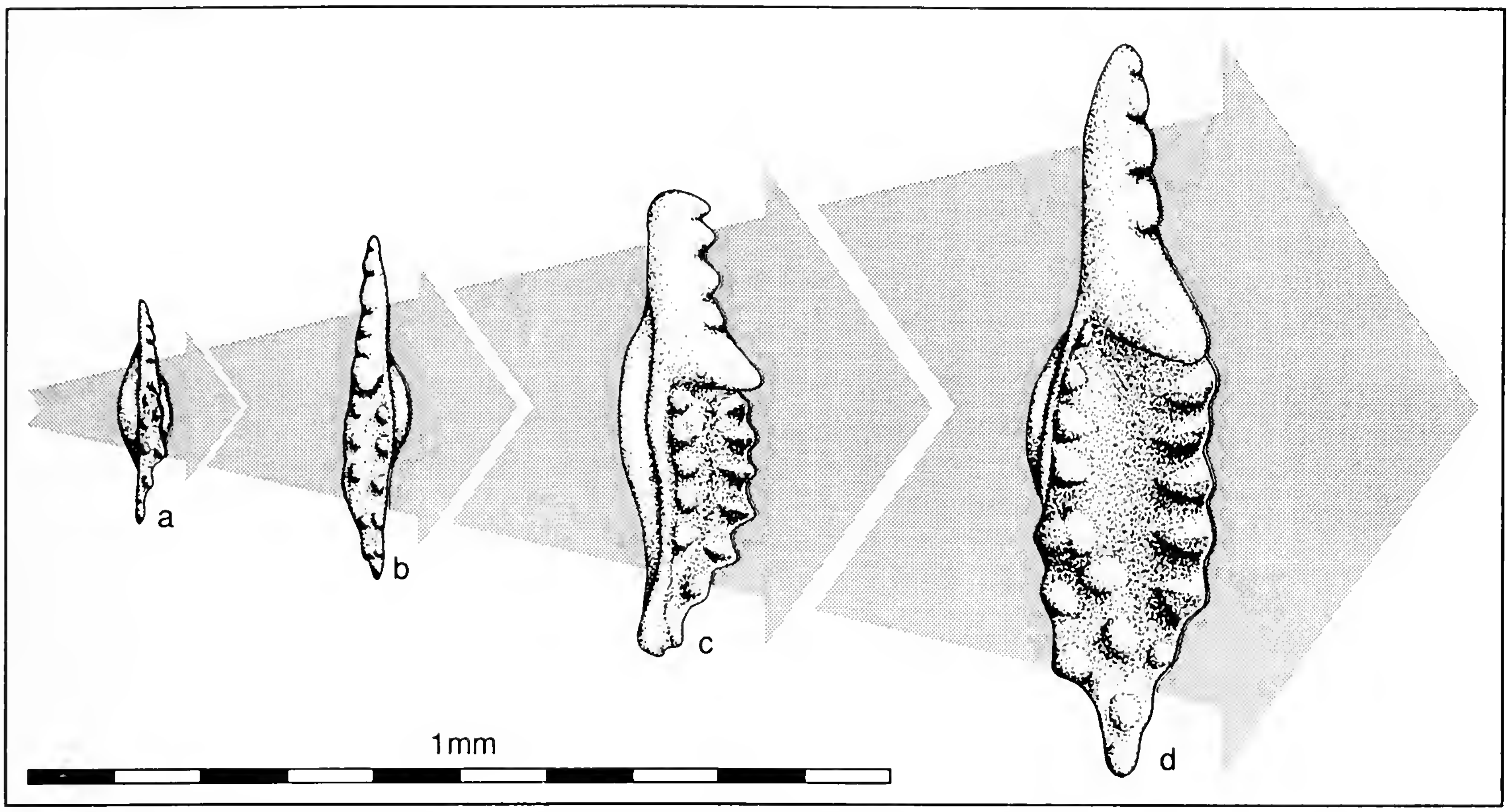
Sa elements of "*Hibbardella ortha* Rexroad"-form occur with *Patrognathus* Pa elements in the Bogside Limestone Member and are tentatively included within the apparatus. *Taphrognathus varians* Branson and Mehl also bore *"H. ortha"* Sa elements and the specimens occurring with *Patrognathus* may belong to *T. varians.* Alternatively, this element may be vicariously shared by the two species—vicarious, as used herein, refers to the presence of morphologically indistinguishable elements in two or more species of conodont (Klapper and Philip, 1971). Because of these uncertainties the possible Sa elements of *Patrognathus* are included in *T. varians* in Appendix II.

A single poorly preserved Sb element fragment, similar to a *T. varians* Sb element, was recovered in association with *Patrognathus* in this study. This element may belong to the apparatus. Sc elements assigned to *P. capricornis* resemble Sc elements of *T. varians.* Given the association of these Sc elements with *Patrognathus* Pa elements and the regular alternation of denticle size, similar to that of *P. capricornis* M elements, they probably belong to the latter species.

ONTOGENY

Pa elements of *P. capricornis* can be distinguished from other members of the genus primarily by the presence of ridges or tetrahedral nodes on the right parapet. However, the material studied and published plates clearly show that platform ornament changed through ontogeny. In very small specimens (Text-Fig. 6a; Pl. 3, Fig. 4), the right parapet is poorly developed compared to the left. As size increases, both parapets are equally developed and bear rounded nodes (Text-Fig. 6b; Pl. 3, Fig. 3). At an element length of approximately 0.5 mm to 0.6 mm, the nodes of the right parapet develop a sharp angular inner surface and become tetrahedral in shape (Text-Fig. 6c; Pl. 3, Fig. 7). These tetrahedral nodes then become more transversely elongate and develop into the ridges of mature elements (Pl. 3, Fig. 6). Finally, in most specimens approaching 0.85 mm to 0.9 mm in length, a second row of small nodes develops in the posterior part of the left parapet (Text-Fig. 6d).

Austin (*in* Austin and Mitchell, 1975) noted the similarity of small Pa elements of *P. capricornis* and *P. variabilis* Rhodes, Austin, and Druce to *P. andersoni* Klapper, and suggested that "*P. andersoni* could be a growth stage of both *C. capricornis* and *P. variabilis*" (Austin *in* Austin and Mitchell, 1975:52). However, neither *P. capricornis* nor *P. variabilis* was associated with *P. andersoni* in the study of Klapper (1971). Furthermore, all the specimens figured by Klapper (1971), except one, exceed 0.7 mm in length (calculated from plate) but do not appear to have tetrahedral nodes. Thus, small Pa elements of the three Carboniferous species of *Patrognathus* cannot be distinguished until adult characters start to develop (cf. Austin *in* Austin and Mitchell, 1975). Specimens of less than approximately 0.5 mm to 0.6 mm in length that lack the large flaring basal cavity of *P. variabilis* and the tetrahedral nodes of *P. capricornis,* and do not occur with specimens exhibiting adult characters of these species,



TEXT-FIG. 6. Ontogeny of Pa elements of *Patrognathus capricornis*. Figures based on actual specimens, broken parts restored: a) ROM 48814; b) ROM 48813; c) ROM 48810; d) Mil(c)565/17 (Austin and Mitchell, 1975, pl. 2, figs. 5, 19, 21).

should be assigned to *Patrognathus* sp. (e.g., Matthews and Naylor, 1973:356, pl. 35, figs. 12, 13; Lipnjagov, 1979, pl. 2, fig. 11; Kononova *in* Wagner, Higgins, and Meyen, 1979, pl. 1, fig. 17; Nicoll and Druce, 1979:28, pl. 15, figs. 3, 4). The similarity between different Pa element growth stages of these three species of *Patrognathus* suggests peramorphic evolution of *P. capricornis*.

Genus *Taphrognathus* Branson and Mehl, 1941

Taphrognathus Branson and Mehl, 1941b:181.
[non] *Taphrognathus* Welles, 1947.
Cloghergnathus Austin *in* Austin and Mitchell, 1975:48.

REVISED DIAGNOSIS

Apparatus seximembrate when fully developed. Pa elements carminiscaphate to anguliscaphate with conspicuous central trough; anterior free blade medial or lateral; parapets nodose, transversely ridged or smooth; basal cavity bilaterally symmetrical to moderately asymmetrical. Pb elements angulate; M elements dolabrate; Sa element alate; Sb elements bipennate; Sc elements bipennate. Pa elements paired with Class III, rarely Class II, symmetry; all other elements, apart from the Sa, symmetrically paired.

TYPE SPECIES

Taphrognathus varians Branson and Mehl, 1941b, by original designation.

DISCUSSION

The diagnosis of *Taphrognathus* is expanded to include nonplatform elements. The reconstruction is based on the nonplatform elements associated with *Taphrognathus* Pa elements in the low diversity faunas recovered from the Northumberland trough. *Taphrognathus carinatus* (Higgins and Varker) as reconstructed by Higgins and Varker (1982) is in broad agreement with this. It is assumed that *Taphrognathus* had a typical ozarkodinid Bauplan similar to previously reconstructed cavusgnathids.

Taphrognathus Pa elements exhibit considerable variation in many aspects of their morphology (Branson and Mehl, 1941b; Thompson and Goebel, 1969; Thompson and Fellows, 1970; Nicoll and Rexroad, 1975). In the U.S.A. this variation follows no stratigraphic or geographic pattern (Thompson and Goebel, 1969; Nicoll and Rexroad, 1975). In erecting *Taphrognathus* as a monospecific genus, Branson and Mehl (1941b) considered medial anterior blade position to be diagnostic. Consequently, the variation in blade position recorded in every documented occurrence of *Taphrognathus* has caused some taxonomic confusion. The majority of authors have either included forms showing lateral migration of the blade within *Taphrognathus* or considered them to be intermediate with *Cavusgnathus* (see Table 3). Austin (*in* Austin and Mitchell, 1975) erected the genus *Cloghergnathus* to accommodate lateral blade forms.

Study of the type material and generic diagnoses of *Taphrognathus* and *Cloghergnathus* reveals that they are differentiated only by blade position. Sound taxonomic characters should be recognizable throughout the ontogeny of an organism, show a minimum of variation within populations, and not be readily modified by the environment (Blackwelder, 1967; Raup and Stanley, 1978). Blade position in *Taphrognathus* and *Cloghergnathus* fulfils none of these criteria (see discussion of *T. varians*). The value of blade position as a taxonomic character is further undermined by the discordant nature of variation in the character. Taxonomic subdivisions defined on blade position, both within and between *Cloghergnathus* and *Taphrognathus*, do not correlate with the variation exhibited by other characters. Also, shifts in blade position are known to occur iteratively in the Cavusgnathidae (Druce, 1970; Austin, 1973; Mapes and Rexroad, 1986), making blade position a poor character on which to differentiate genera. Detailed palaeoecological analysis also indicates that the type species of *Cloghergnathus*, *C. globenskii* Austin, is an ecophenotype of *T. varians* (see discussion of *T. varians*). Therefore, the concept of *Taphrognathus* is expanded to include Pa elements with lateral blades, previously assigned to *Cloghergnathus*.

Platform-element symmetry may be of importance in both phylogeny (Lane, 1968) and functional morphology of conodonts (Aldridge et al., 1987; Nicoll, 1987). The symmetry of the Pa element pair has therefore been included in the revised diagnoses of *T. varians* and *T. carinatus*. Of the other species of *Taphrognathus*, *T. cravenus* (Metcalfe) Pa elements have medial to right blade development and a flared right parapet, probably pairing with Class IIIa symmetry. *Taphrognathus rhodesi* is known only from two specimens (Austin *in* Austin and Mitchell, 1975), and its symmetry cannot be determined. Although the close spacing of platform ribs diagnostic of *T. rhodesi* is rarely approached in other species of the genus, the status of a species of *Taphrognathus* based on only two specimens is questionable.

The concept of *Taphrognathus* discussed above confirms the homeomorphic relationship with *Adetognathus* Lane noted by previous authors (Rexroad, 1958b; Austin *in* Austin and Mitchell, 1975; Higgins and Varker, 1982) (see discussion of the Cavusgnathidae).

TABLE 3. Variation in blade position of *Taphrognathus varians* recorded by previous authors.

Author	Location	Number of *T. varians*	Number of Taphrognathids with Lateral Blades
Branson and Mehl, 1941	Iowa, Missouri	> 74	1 *T. varians* ?
Rexroad and Collinson, 1963	Illinois, Indiana, Kentucky	16	11 *Taphrognathus–Cavusgnathus* transitions
Rexroad and Collinson, 1965	Illinois	297	0 ?
Thompson and Goebel, 1968	Kansas	> 300	9 *Taphrognathus* sp.
Thompson and Fellows, 1970	Missouri, Arkansas, Oklahoma	12	1 New genus new species
Nicoll and Rexroad, 1975	Indiana	678	< 10 *T. varians* transitional to *Cavusgnathus*
Austin and Mitchell, 1975	Northern Ireland	2	15 *Cloghergnathus*
Higgins and Varker, 1982	Ravenstonedale	unknown	unknown *Cloghernathus carinatus*
Armstrong and Purnell, 1987	North Cumbria	12	194 *Cloghernathus* 21 *Cloghergnathus–Taphrognathus* intermediates
This study	Northumberland, North Cumbria	15 (morphotype I)	292 *Taphrognathus varians* (morphotypes II and III)

Taphrognathus carinatus (Higgins and Varker, 1982)

Plate 3, Figs. 10–15; Plate 4, Fig. 1

[v*p] *Cloghergnathus carinatus* Higgins and Varker, 1982:160, 161, pl. 18, figs. 1–3, 7–9, 11 only [Pa elements].

[v.p] *Cloghergnathus* non-platform elements Higgins and Varker, 1982:161, pl. 18, fig. 18 [Pb element], fig. 19 [Sc_1 element]; pl. 19, figs. 5, 6, 8 [Sa elements], fig. 20 [Sc_2 element] only [all referred to as *Cloghergnathus carinatus* in plate caption].

[vnonp] *Cloghergnathus carinatus* Higgins and Varker, 1982:160, 161, pl. 18, figs. 4–6, 10 only.

[vnonp] *Cloghergnathus* non-platform elements Higgins and Varker, 1982:161, pl. 19, figs. 4, 18 only [referred to as *Cloghergnathus carinatus* in plate captions].

[v.] *Lonchodina* sp. Higgins and Varker, 1982:164, pl. 18, fig. 17; pl. 19, figs. 1–3 [Sb elements].

[v.] *Neoprioniodus* sp. Higgins and Varker, 1982:164, pl. 19, fig. 17 [M element].

[v.] *Cloghergnathus carinatus*—Varker and Sevastopulo, 1985:200, pl. 5.5, figs. 6, 8, 10 [Pa elements] [cop. Higgins and Varker, 1982, pl. 18, figs. 1, 2, 7].

REVISED DIAGNOSIS

Platform elements arched with short inner lateral or medial anterior blade one-quarter to one-fifth of element length; blade convex and crestlike, extending above height of parapets but equal in height at its posterior end to the inner parapet; parapets nodose or transversely ridged; medial carina developed in posterior quarter of central trough; symmetry Class IIIb dominant.

HOLOTYPE

British Museum, R30 (Higgins and Varker, 1982, pl. 18, figs. 2, 7).

TYPE HORIZON AND LOCALITY

Scandal Beck Limestone, sample SB2 of Higgins and Varker (1982), Ravenstonedale, Cumbria, U.K. (G.R. NY 722044).

MATERIAL STUDIED

Pa elements, 16(4); Pb elements, 11; M elements, 3; Sa elements, 23(1); Sb elements, 5(1); Sc_1 elements, 5(6); Sc_2 elements, 11(2); all, apart from 2 Pa elements, from the Cementstone Group of the Rothbury area.

DESCRIPTION

Pa elements. See Higgins and Varker (1982:160).

Pb elements. The anterior process bears up to five laterally compressed denticles which may be long and discrete or rather short. The reclined cusp is also laterally compressed and is taller and broader than the anterior denticles. The posterior process is about half the length and height of the anterior and bears three short denticles. Both processes and the base of the cusp are laterally thickened, with distinct shoulders developed alongside the denticles nearest the cusp. The processes taper distally and have a slight inward flexure. The basal cavity is deep and surrounded by thickened lips that pass laterally into thin zones of recessive basal margin along the narrow lower edge of the processes. The cavity tapers anteriorly and posteriorly, extending as a groove along the processes.

M elements. See Higgins and Varker (1982:161) under *Neoprioniodus* sp.

Sa elements. See Higgins and Varker (1982:161, 162) under *Cloghergnathus* A_3 element. The elements figured by Higgins and Varker (1982) are missing the end of the posterior process. Examination of the specimens, however, suggests that the process was almost certainly short. The same is true of specimens from the Northumberland trough, with the process reduced to a small swelling at the base of the cusp in some specimens (e.g., Pl. 3, Fig. 13).

Sb elements. See Higgins and Varker (1982:161) under *Lonchodina* sp.

Sc_1 elements. These elements are indistinguishable from *T. varians* Sc elements.

Sc_2 elements. See Higgins and Varker (1982:161). The anterior process of these elements may have marked inward curvature.

DISCUSSION

The diagnosis given above is modified only slightly from that of Higgins and Varker (1982). With the recognition of *T. varians* morphotype III Pa elements (see below), inner lateral blade development and possession of a posterior carina can no longer be considered diagnostic of *T. carinatus* alone. However, the crestlike blade profile, larger blade denticles, the development of more nodose or bloated parapets, and the arching of the Pa element distinguish *T. carinatus* from other members of the genus. All elements of this species also tend to be robust but this may be an ecophenotypic character as *T. varians* elements occurring with *T. carinatus* exhibit the same tendency. Pa elements are sinistral or dextral but always with an inner or, less commonly, a more medial blade. Mirror-image pairing of elements (Class II symmetry) seems unlikely; Class IIIb symmetry must have been dominant.

Pb elements of *T. carinatus* differ from those of *T. varians* mainly in the thickening of the processes and the shortness of the posterior process. Some *T. carinatus* Pb elements approach the morphology of *T. varians* and vice versa, making specific assignment of some Pb elements difficult.

Higgins and Varker (1982) suggest that the M element of *T. carinatus* is of *"Neoprioniodus varians"* form. However, the specimen they figure as the M element (pl. 19, fig. 18) has a broad, laterally compressed cusp and a short posterior process. It is of *"N. scitulus"* form and does not belong in *Taphrognathus*. "*Neoprioniodus* sp." of

Higgins and Varker (1982) has several characters in common with other elements of *T. carinatus*; in particular, the posterior process denticulation, the cusp, and the basal cavity are very similar to their figured Pb element. M elements identical to "*Neoprioniodus* sp." occur with other *T. carinatus* elements in the Northumberland trough. The specimen figured herein (Pl. 3, Fig. 15) differs only in the shape of the anticusp and the amount of lateral thickening of the process. This specimen is only half the size of that figured by Higgins and Varker (1982) and this variation is probably ontogenetic. M elements of *"N. loxus"* and *"N. varians"* forms, similar to those of *T. varians*, also occur with *T. carinatus* elements. These M elements may have been borne by some *T. carinatus* in place of the more robust M elements discussed above.

The Sb element figured herein (Pl. 3, Fig. 12) is thinner and bears less laterally compressed denticles than the elements described by Higgins and Varker (1982). It is also smaller, and these differences are probably ontogenetic.

Taphrognathus carinatus and *T. varians* are found together in all but one sample from this study. This sample (186861; Appendix IIe) contains no Sc_1 elements. Although Higgins and Varker (1982) included these elements in the apparatus of *T. carinatus*, their concept of the species also included some Pa elements herein considered to be *T. varians*. Their Sc_1 elements may therefore have been associated with *T. varians*, and these elements may not belong in *T. carinatus*.

***Taphrognathus varians* Branson and Mehl, 1941**
Plate 4, Figs. 2–15; Plate 5, Figs. 1–3

[v*] *Taphrognathus varians* Branson and Mehl, 1941b:182, pl. 6, figs. 27–33, 35–40 [Pa elements, morphotype I], fig. 34 [Pa element, morphotype II].

[non] *Taphrognathus varians*—Cooper, 1947:92, pl. 20, figs. 14–16.

[v.] *Taphrognathus varians*—Rexroad and Collinson, 1963:21, pl. 1, figs. 18–20 [Pa elements, morphotype I], fig. 22 [Pa element, morphotype III].

[v.] *Taphrognathus–Cavusgnathus* transitions Rexroad and Collinson, 1963:20, pl. 1, figs. 21, 23, 24, 25 [Pa elements, morphotype III].

[v.] *Taphrognathus varians*—Rexroad and Collinson, 1965:24, pl. 1, figs. 30, 32 [Pa elements, morphotype I], fig. 31 [Pa element, morphotype I–III intermediate].

[v.] *Ozarkodina* sp. Rexroad and Collinson, 1965:13, pl. 1, fig. 6 [Pb element].

[v.] *Hibbardella ortha* Rexroad—Rexroad and Collinson, 1965:10, pl. 1, fig. 10 [Sa element].

[v.] *Neoprioniodus loxus* Rexroad—Rexroad and Collinson, 1965:12, pl. 1, figs. 11, 19 [M elements].

[v.] *Neoprioniodus insolatus* Hass—Rexroad and Collinson, 1965:11, 12, pl. 1, fig. 18.

Taphrognathus varians—Thompson and Goebel, 1969:44, 45, pl. 5, figs. 1, 3, 5, 9, 13, 14 [Pa elements, morphotype I], figs. 2, 4, 6–8, 12, 15 [Pa elements, morphotype II].

Taphrognathus sp. Thompson and Goebel, 1969:45, pl. 5, figs. 10, 11 [Pa element, morphotype II].

[vnon] *Taphrognathus varians*—Rhodes, Austin, and Druce, 1969:241, 242, pl. 13, figs. 4, 5.

Taphrognathus varians—Thompson and Fellows, 1970:114, 115, pl. 4, figs. 10, 15 [Pa element, morphotype I].

New genus and new species Thompson and Fellows, 1970:115, pl. 4, figs. 11, 14 [Pa element, morphotype III].

Taphrognathus–Cavusgnathus transitions Austin, 1973, fig. 1.17 [Pa element, morphotype I], figs. 1.12, 1.13, 1.14, 1.15 [Pa elements, morphotype III] [cop. Rexroad and Collinson, 1963, pl. 1, figs. 18b, 24, 25, 21b, 23].

[non] *Taphrognathus varians*—Austin, 1973, figs. 1.20, 1.21 [cop. Rhodes, Austin, and Druce, 1969, pl. 13, figs. 4a, 6a].

[(?)] *Taphrognathus varians*—Jenkins, 1974, pl. 119, fig. 5 [Pa element, morphotype I?].

[v.] *Taphrognathus varians*—Austin, 1974, pl. 1, fig. 18 [Pa element, morphotype I].

[v.] Gen. nov. sp. nov. A Austin, 1974, pl. 1, figs. 11, 12 [Pa element, morphotype II].

[p] *Taphrognathus varians*—Pierce and Langenheim, 1974:168, 169, pl. 1, figs. 1, 5 [Pa element, morphotype III?], fig. 2 [Pa element, morphotype II] only.

[v*.] *Cloghergnathus globenskii* Austin *in* Austin and Mitchell, 1975:48, 50, pl. 1, figs. 1–4, 8–15, 22, 27, 33 [Pa elements, morphotype II], figs. 7, 17, 26 [Pa element, morphotype I] [figs. 3, 8 cop. Austin, 1974, pl. 1, figs. 11, 12].

[v.] *Taphrognathus varians*—Austin *in* Austin and Mitchell, 1975:53, pl. 1, figs. 5, 6, 16, 18, 19, 30 [Pa elements, morphotype I] [fig. 5 cop. Austin, 1974, pl. 1, fig. 18].

Taphrognathus varians—Nicoll and Rexroad, 1975:27, pl. 4, figs. 7–16 [Pa elements, morphotype I].

Ozarkodina sp. Nicoll and Rexroad, 1975:26, pl. 5, figs. 4–6 [Pb elements].

Hibbardella ortha—Nicoll and Rexroad, 1975, pl. 5, figs. 7, 8 [Sa elements].

Neoprioniodus loxus—Nicoll and Rexroad, 1975, pl. 5, figs. 12–14 [M elements].

Taphrognathus varians—Ruppel, 1979, pl. 2, figs. 1–3, 10 [Pa elements, morphotype I].

Taphrognathus–Cavusgnathus transition Ruppel, 1979, pl. 2, figs. 4, 5 [Pa element, morphotype III].

Clydagnathus? *hudsoni* Metcalfe, 1980:176, pl. 13, figs. 8, 9 [Pa element, morphotype III].

[vp(?)] *Cloghergnathus cravenus* Metcalfe, 1981:17, pl. 11, fig. 2 only [Pa element, morphotype I].

[v.] *Cloghergnathus globenskii*—Metcalfe, 1981, pl. 12, figs. 1, 2 [Pa elements, morphotype II].

[v.] *Taphrognathus*? sp. Metcalfe, 1981:45, pl. 10, fig. 3 [Pa element, morphotype III].

[v.] *Cloghergnathus rhodesi* Austin— Metcalfe, 1981, pl. 10, fig. 4 [Pa element, morphotype III].

[v.] *Cloghergnathus globenskii*—Austin and Rhodes *in* Robison, 1981, text-fig. 108,3 [Pa element, morphotype I] [cop. Austin and Mitchell, 1975, pl. 1, figs. 7, 17].

[vnon] *Taphrognathus varians*—Austin and Rhodes *in* Robison, 1981, text-fig. 108,1 [cop. Rhodes, Austin, and Druce, 1969, pl. 13, figs. 5a–c].

[v] *Taphrognathus varians*—Higgins and Varker, 1982:165, pl. 18, fig. 15 [Pa element, morphotype III], fig. 16 [Pa element, morphotype I?, specimen lost].

[v.p] *Cloghergnathus carinatus* Higgins and Varker, 1982:160, 161, pl. 18, figs. 4–6, 10 only [Pa elements, morphotype III].

[vp(?)] *Cloghergnathus* non-platform elements Higgins and Varker, 1982:161, pl. 19, fig. 4 only [Pb element] [referred to as *Cloghergnathus carinatus* in plate caption].

[v?] *Neoprioniodus* cf. *acampylus* Rexroad and Collinson— Higgins and Varker, 1982:164, pl. 19, fig. 16 [Sb element].

Cloghergnathus sp. A Austin and Davies, 1984, pl. 1, figs. 4, 19 [Pa elements, morphotype III].

[(?)] *Taphrognathus* sp. A Austin and Davies, 1984, pl. 1, fig. 3 [Pa element, morphotype III?].

[v] *Taphrognathus varians*—Varker and Sevastopulo, 1985, pl. 5.5, fig. 2 [Pa element, morphotype III], fig. 4 [Pa element, morphotype I?, specimen lost] [cop. Higgins and Varker, 1982, pl. 18, figs. 15, 16].

Taphrognathus varians—Ruppel and Lemmer, 1986:34, pl. 1, figs. 1–3 [Pa elements, morphotype I], figs. 4, 5 [Pa element, morphotype III?].

Taphrognathus–Cavusgnathus transition Ruppel and Lemmer, 1986:34, pl. 1, fig. 6 [Pa element, morphotype III].

[v.] *Cloghergnathus* cf. *globenskii*—Armstrong and Purnell, 1987, pl. 2, fig. 1 [Pa element, morphotype II].

[v.] *Cloghergnathus–Taphrognathus* intermediate Armstrong and Purnell, 1987, pl. 2, figs. 2, 3 [Pa element, morphotype II].

[v.] *Cloghergnathus* sp. nov. Armstrong and Purnell, 1987, pl. 2, figs. 4, 5 [Pa elements, morphotype III].

[v?] *Cloghergnathus carinatus*—Armstrong and Purnell, 1987, pl. 1, fig. 17 [Pa element, morphotype III?].

[v.] *Cloghergnathus* sp. indet. Armstrong and Purnell, 1987, pl. 2, fig. 6 [M element], fig. 7 [Pb element], fig. 8 [?Sa element], fig. 9 [Sc element].

[v.p] *Patrognathus variabilis* Rhodes, Austin, and Druce— Armstrong and Purnell, 1987, pl. 3, fig. 12 [Sa element].

[v.] *Taphrognathus varians*—Armstrong and Purnell, 1987, pl. 3, fig. 14 [Pa element, morphotype I], fig. 15 [Pa element, juvenile].

REVISED DIAGNOSIS

Platform elements bear an anterior blade that is free for most of its length; blade denticles subequal or increasing in size anteriorly; height of posterior end of free blade and anterior end of parapets subequal; parapets transversely ridged. Class IIIb symmetry dominant, Class II rarely developed.

HOLOTYPE

University of Missouri, C578-5 (Branson and Mehl, 1941b, pl. 6, fig. 28).

TYPE HORIZON AND LOCALITY

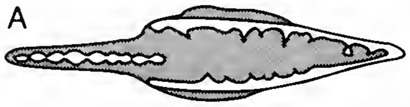
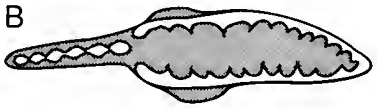
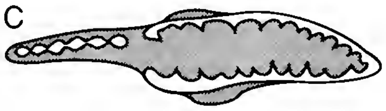
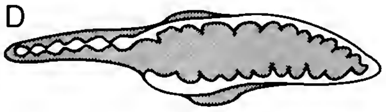
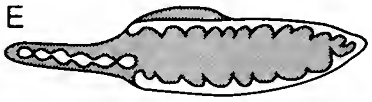
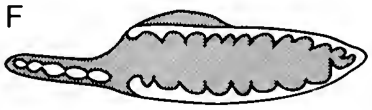
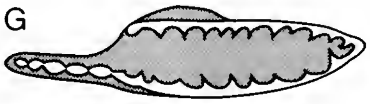
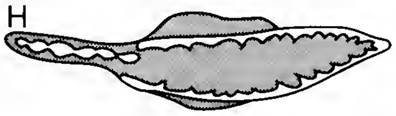
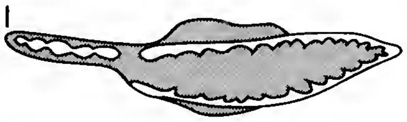
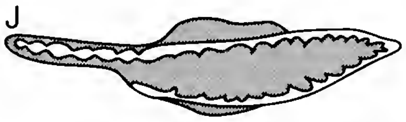
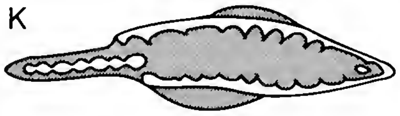
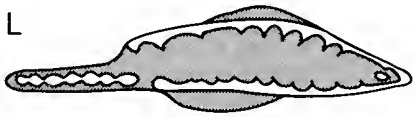
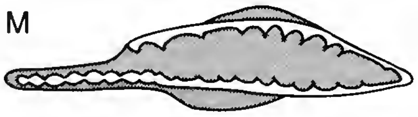
Keokuk shales and limestones (considered to be Salem by Rexroad and Collinson, 1963). The Troy locality about two miles east of Troy, on the Cuivre River in Lincoln County, State Highway 47, Missouri, U.S.A. (N.B. Not the Sylvan Beach locality.)

MATERIAL STUDIED

Pa elements, 372(225) [morphotype I, 13(2); morphotype II, 40(6); morphotype III, 253(32); morphotype indet., 66(185)]; Pb elements, 46(36); M elements, 52(18); Sa elements, 11(11); Sb elements, 15(5); Sc elements, 26(116); from the Lynebank and Bewcastle formations, Lower Border Group, and from the Cementstone Group. In addition, the type and figured material of Branson and Mehl (1941a) and 60 unfigured specimens collected by them from the Sylvan Beach locality were studied. The collections of Rexroad and Collinson (1963, 1965) and Austin (*in* Austin and Mitchell, 1975) were also examined.

DESCRIPTION

Pa elements. Three intergrading Pa element morphotypes are recognized on the basis of anterior blade position: in morphotype I (Pl. 4, Fig. 5) the blade is developed in a medial position terminating between the parapets of the platform; in morphotype II (Pl. 4, Figs. 2, 9) it is developed on the outer side of the element, with or without offset from the parapet; in morphotype III (Pl. 4, Figs. 3, 4) it is developed on the inner side with or without offset from the parapet (see Text-Fig. 7). Morphotypes II and III tend

Category		Curvature	Blade Position	Morpho-type
A		Straight, less commonly sinistral or dextral.	Medial.	I
B		Dextral.	Outer, detached, offset from right parapet.	II
C		Dextral.	Outer, detached, aligned with right parapet.	II
D		Dextral.	Outer, continuous with right parapet.	II
E		Sinistral.	Outer, detached, offset from left parapet.	II
F		Sinistral.	Outer, detached, aligned with left parapet.	II
G		Sinistral.	Outer, continuous with left parapet.	II
H		Sinistral.	Inner, detached, offset from right parapet.	III
I		Sinistral.	Inner, detached, aligned with right parapet.	III
J		Sinistral.	Inner, continuous with right parapet.	III
K		Dextral.	Inner, detached, offset from left parapet.	III
L		Dextral.	Inner, detached, aligned with left parapet.	III
M		Dextral.	Inner, continuous with left parapet.	III

TEXT-FIG. 7. Explanation of Pa element morphotype and blade position categories of *Taphrognathus varians*.

to develop greater lateral curvature than morphotype I. In all other respects they are similar.

At its posterior end, the anterior blade often overlaps with one or both parapets for a short distance but remains free for the greater part of its length. It bears between four and eleven denticles. These are fused apart from their tips and are generally subequal or increasing in size anteriorly apart from two or three smaller denticles often developed at the anterior end. The height of the posteriormost denticles of the free part of the blade is approximately equal to or slightly less than that of the anterior end of the nearest parapet. The blade is usually between one-quarter and two-fifths the length of the element.

The platform may be straight or sinuous but often exhibits some degree of sinistral or dextral curvature, the outer parapet being convex, the inner concave, straight, or slightly convex. The upper parts of the inner surfaces of the parapets are ornamented by weak ridges, usually becoming slightly stronger towards the posterior, often more strongly developed in larger specimens. The ridges extend part-way down the parapet surfaces, dying out towards the median trough which is generally unornamented; occasionally a weak posterior carina of a few nodes is developed. The trough may be constricted slightly at its anterior end, but is never closed, by inward curvature of one of the parapets. Irrespective of element curvature, the right parapet is often higher than the left in the anterior half of the platform. The posterior end of the platform is sharply pointed and usually terminates as a short bladelike structure, often formed as an extension of the weak carina or one of the parapets. In lateral view, the upper surface of the platform is gently convex. It has a serrated or crenulated profile, the strength of which depends on the strength of the parapet ornament. The lower surface is generally slightly concave or flat, and the overall height of the element slightly decreases posteriorly. The platform width is between one-quarter and one-fifth of its length, usually widest around the midlength of the element.

The basal cavity is lanceolate, occupying most of the lower surface. It is widest and deepest around element midlength, tapering more rapidly anteriorly than posteriorly. It continues as a groove under part of the anterior blade, and extends to a point at, or just short of, the posteriormost tip of the element. The cavity possesses a weak medial groove for its entire length and may be subsymmetrical to moderately asymmetrical.

Pb elements. See Rexroad (1957:36) under *Ozarkodina compressa*. *T. varians* Pb elements of this study differ from *"O. compressa" sensu* Rexroad (1957) in having slightly fewer denticles. Also, they have basal grooves that extend from the basal cavity but do not usually reach the distal ends of the processes.

M elements. See Branson and Mehl (1941b:174) under *Prioniodus varians*, and Rexroad (1957:34) under *Neoprioniodus loxus*. M elements occur as *"N. loxus"* and *"N. varians"* morphotypes. In *T. varians*, as may be the case in *Cavusgnathus* (Rexroad, 1958a; Norby, 1976), these morphotypes differ in little other than the angle of downward deflection of the posterior process and represent extremes in the range of variation in M elements. Occasionally a small denticle is present on the lower anterior edge of the cusp.

Sa elements. See Rexroad (1958a:18) under *Hibbardella ortha*. These elements vary in the angle of divergence of the lateral processes.

Sb elements. The anterior process is straight and bears as many as 12 denticles that alternate irregularly in size. These denticles are usually subcircular in cross-section. They are suberect at the anterior end of the process and become increasingly reclined posteriorly. The process is laterally compressed, and deflected slightly inwards and either upwards or downwards relative to the posterior process. The cusp is only slightly larger than the process denticles and is reclined.

Although incomplete in all specimens, the posterior process is slightly longer than the anterior and is also slightly higher and less laterally compressed. It bears at least three laterally compressed major denticles with up to three minor denticles between each one. The denticles are discrete for most of their length and are inclined posteriorly. The small basal cavity is developed obliquely beneath the cusp. It has a small lip on the inner side and tapers to the anterior and posterior, continuing along the processes as a groove. Sb elements resemble Sc elements in general character but have a longer anterior process.

Sc elements. See Hass (1953:81, 82) under *Hindeodella ensis*, and Clarke (1960:8) under *H. tenuis*. The posterior process of *T. varians* Sc elements is shorter than described by Hass (1953). The elements are variable, especially in the regularity of alternation in size of denticles on the posterior process and the degree of inward curvature of the anterior process. The posterobasal termination of some elements is abruptly downcurved beneath the steeply inclined posterior denticles.

DISCUSSION

Expansion of the generic concept of *Taphrognathus* to include Pa elements with a range of blade positions reduces taxonomic confusion at the genus level. Blade position, however, has also been used as a taxonomic character at the species level in *Taphrognathus*. *Taphrognathus varians sensu* Branson and Mehl (1941b), *T. globenskii* (Austin) (*in* Austin and Mitchell, 1975), and *Taphrognathus* sp. nov. *sensu* Armstrong and Purnell (1987) are differentiated primarily using blade position. In the present study, blade position was found to vary continuously and in discord with other characters such as curvature and carina development. Nicoll and Rexroad (1975) also noted the nonsystematic variation of these and other characters in their large collections of *T. varians*. In fact, all published work on *T. varians* documents variation in blade position (see Table 3).

Blade position is not a sound character on which to differentiate species in *Taphrognathus*. In addition to its continuous variation, it varies through ontogeny (see discussion below), and is subject to environmental modification. To examine its relationship with environment, the continuum of blade position was arbitrarily divided into 13 categories (Text-Fig. 7) and the environmental distribution of these categories in the Bogside Limestone Member in Ashy Cleugh (locality 10; Appendix IIb) was analyzed (Text-Fig. 8). The Bogside Limestone Member was deposited below normal wave base in a restricted microtidal shallow-shelf setting subject to fluctuations in salinity and periodic agitation by storms (Purnell, 1989). The environmental gradient used in Text-Fig. 8 is the result of unconstrained seriation of sedimentological data for all samples of the Bogside Limestone Member from locality 10 (see Brower and Burroughs, 1982; Brower and Kile, 1988, for discussion of seriation). The resultant arrangement of samples, which reflects an environmental gradient of increasing restriction (Purnell, 1989), was then used in direct gradient analysis of *T. varians* morphotypes (see Cisne and Rabe, 1978; Springer and Bambach, 1985, for discussion of gradient analysis). Morphotype I elements (approximately equivalent to *T. varians sensu* Branson and Mehl; A in Text-Fig. 8) and morphotype II elements (approximately equivalent to *Cloghergnathus globenskii*; B–G in Text-Fig. 8) are present only in the most restricted environments. Morphotype III elements have a much broader environmental range. This distribution of morphotypes reflects increasing variability of blade position with increasing environmental restriction and supports the hypothesis that blade position is an ecophenotypic character. This trend might be a sampling artifact, the increase in observed variation reflecting the larger number of specimens recovered from the more restricted environments. However, the variation exhibited by specimens of some samples that are not high in abundance (e.g., samples 1768632 and 1411851) suggests that the trend is real.

In conclusion, blade position in *T. varians* is of highly dubious taxonomic significance. In the Bogside Limestone Member, specimens that would previously have been assigned to *C. globenskii* (the type species of *Cloghergnathus*) are ecophenotypic variants of *T. varians sensu* Branson and Mehl. The holotype of *C. globenskii* also comes from a sample that includes *T. varians sensu* Branson and Mehl, and intermediate forms.

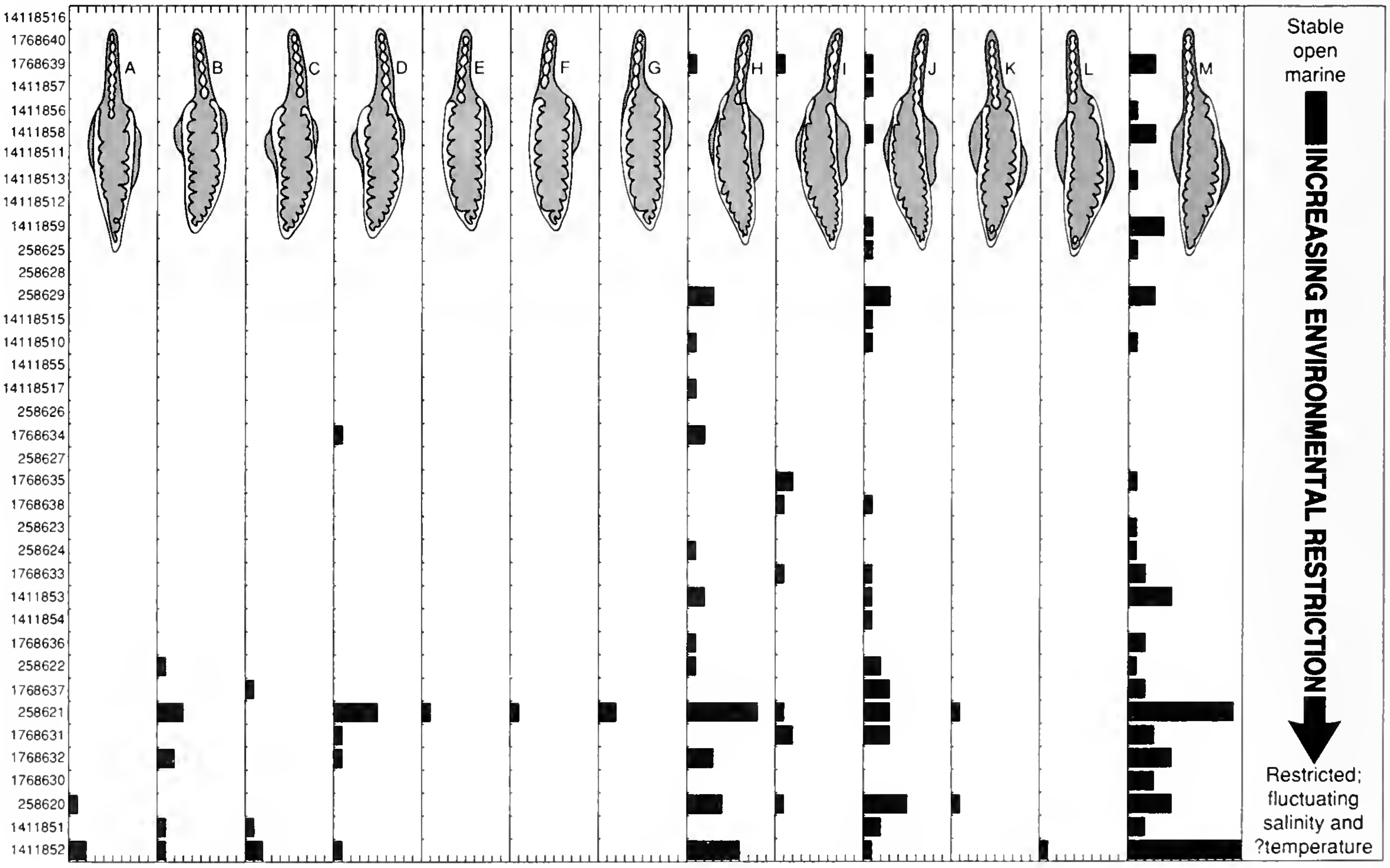
The three morphotypes of *T. varians* described herein differ only in blade position and serve as aids to discussion of intraspecific variation. These morphotypes are not randomly distributed. Most American *T. varians* faunas are dominated by morphotype I (e.g., Branson and Mehl, 1941b; Thompson and Goebel, 1969; Nicoll and Rexroad, 1975); the limited Irish fauna of Austin and Mitchell (1975) is dominated by morphotype II; Northumberland trough faunas are dominated by morphotype III (Armstrong and Purnell, 1987; this study). This geographical distribution might suggest that morphotypes I, II, and III represent three subspecies (*sensu* Mayr, 1969:41); however, the morphotypes are not geographically mutually exclusive. The separate populations show considerable overlap in their ranges of variation, and the distribution of morphotypes probably reflects different bias within the same range of variation in separate geographical areas. The holotype of *T. varians*, for example, although part of an American morphotype I-dominated fauna, is intermediate between morphotypes I and II.

Taphrognathus cravenus (Metcalfe) is distinguished from *T. varians* primarily by the lateral flare or "winged" appearance of the anterior end of the right parapet. From the available material, it is unclear whether or not this character is consistently developed and of sufficient importance to maintain *T. cravenus* as a separate species. One of the specimens figured by Metcalfe (1981, pl. 11, fig. 2) lacks this character and is included in synonymy with *T. varians*. Metcalfe (1981) also reported a single specimen of *T. rhodesi* Austin (*in* Austin and Mitchell, 1975). This specimen is overgrown, but appears to lack the diagnostic platform ornament of *T. rhodesi* and is probably *T. varians*.

The apparatus of *T. varians* is very similar to species of *Cavusgnathus*. Indeed, the nonplatform elements of *T. varians*, *C. unicornis* Youngquist and Miller, and *C. altus* Harris and Hollingsworth would previously have been referred to the same discrete element species. It is only because *Cavusgnathus* Pa elements do not occur with *T. varians* Pa elements in the Northumberland trough that the nonplatform elements of *T. varians* can be positively assigned.

Although they did not reconstruct the apparatus, Nicoll (1971) and Nicoll and Rexroad (1975) suggested that *"O. compressa"* type elements were associated with *T. varians* Pa elements. This is borne out by the present study. Higgins and Varker (1982) figured two Pb elements that they considered to belong to *T. carinatus*. One of these is probably a *T. varians* Pb element, but it is possible that Pb elements of *T. carinatus* and *T. varians* intergrade.

The M elements of *T. varians* vary in the angle of downward deflection of the posterior process between *"N. loxus" and "N. varians"* type elements. American authors



TEXT-FIG. 8. Distribution of *Taphrognathus varians* Pa element morphotypes along a gradient of increasing environmental restriction in the Bogside Limestone Member. Each increment of horizontal scale equals one Pa element; sample numbers at left.

have in the past assigned their *T. varians* M elements to *"N. loxus,"* the form with greater downward process deflection (e.g., Thompson and Goebel, 1969; Nicoll and Rexroad, 1975). The more common form of element in the Northumberland trough is of *"N. varians"* form. This geographic distribution corresponds to that of the Pa element morphotypes. Morphological intergradation and co-occurrence of the different forms of M element suggest that they vary intraspecifically. M elements of this type may also have been present in some *T. carinatus* (see discussion of *T. carinatus*).

Sa elements of *Patrognathus capricornis* (Druce) are indistinguishable from those of *T. varians* (see discussion of *P. capricornis*). The specimen figured as "*Clogher-gnathus*? sp. indet. Sa element" by Armstrong and Purnell (1987, pl. 2, fig. 18) does not have the characteristic triangular cusp cross-section but is tentatively retained within *T. varians*.

The single specimen of *Neoprioniodus* cf. *acampylus* recovered by Higgins and Varker (1982) has a small indistinct basal cavity halfway along its length, and closely resembles *T. varians* Sb elements. The state of preservation of the specimen precludes a definite assignment.

ONTOGENY

During ontogeny the relative proportions of different parts of *T. varians* Pa elements change markedly (see Text-Fig. 9). The smallest specimen recovered (0.2 mm in length; Text-Fig. 9a) is essentially bladelike with discrete pointed denticles and a short low platform developed as a slight expansion of the upper part of the posterior third of the element. The basal cavity is developed beneath the blade rather than the incipient platform. With increasing maturity (Text-Fig. 9b, c), the platform becomes better developed but is only weakly ornamented. At this stage, the blade is medial in position, about half the length of the element, and still bears more discrete denticles than at adult stage. The element is straight and the basal cavity extends under both the platform and the blade. Variation in blade position develops only after this stage, enabling differentiation of morphotypes I, II, and III (Text-Fig. 9d, e, f). Some immature Pa elements of *T. varians* resemble *T.*? *transatlanticus* in their small size and weak platform ornament. One figured specimen (Pl. 4, Fig. 7) illustrates this resemblance. Only close examination of the platform under SEM reveals that the right parapet bears incipient ornament consisting of slight pinching and swelling rather than the unornamented surface characteristic of *T.*? *transatlanticus* (see discussion of *T.*? *transatlanticus*). In addition to variation in blade position, increase in size and maturity is accompanied by relative shortening of the free blade to one-quarter to one-fifth of element length, development of stronger and more numerous transverse ribs on the parapets, and constriction of the anterior end of the basal cavity restricting it to the lower surface of the platform.

Published plates and the collection of Branson and Mehl (1941b) suggest that most *T. varians* Pa elements from the U.S.A. have an upper surface that is flat or slightly concave in its posterior half, whereas *T. varians* Pa elements of this study generally have convex upper platform surfaces. These differences are probably ontogenetic. Most figured *T. varians* from the U.S.A. and the specimens of Branson and Mehl (1941b) are over 1 mm in length; comparatively few specimens of this size have been found in the Northumberland trough. The few smaller specimens of *T. varians* that have been figured by American authors generally have convex upper platform surfaces (e.g., Rexroad and Collinson, 1963, pl. 1, figs. 18, 21). A few large specimens encountered in this study do, however, retain a convex platform surface as a consequence of being arched.

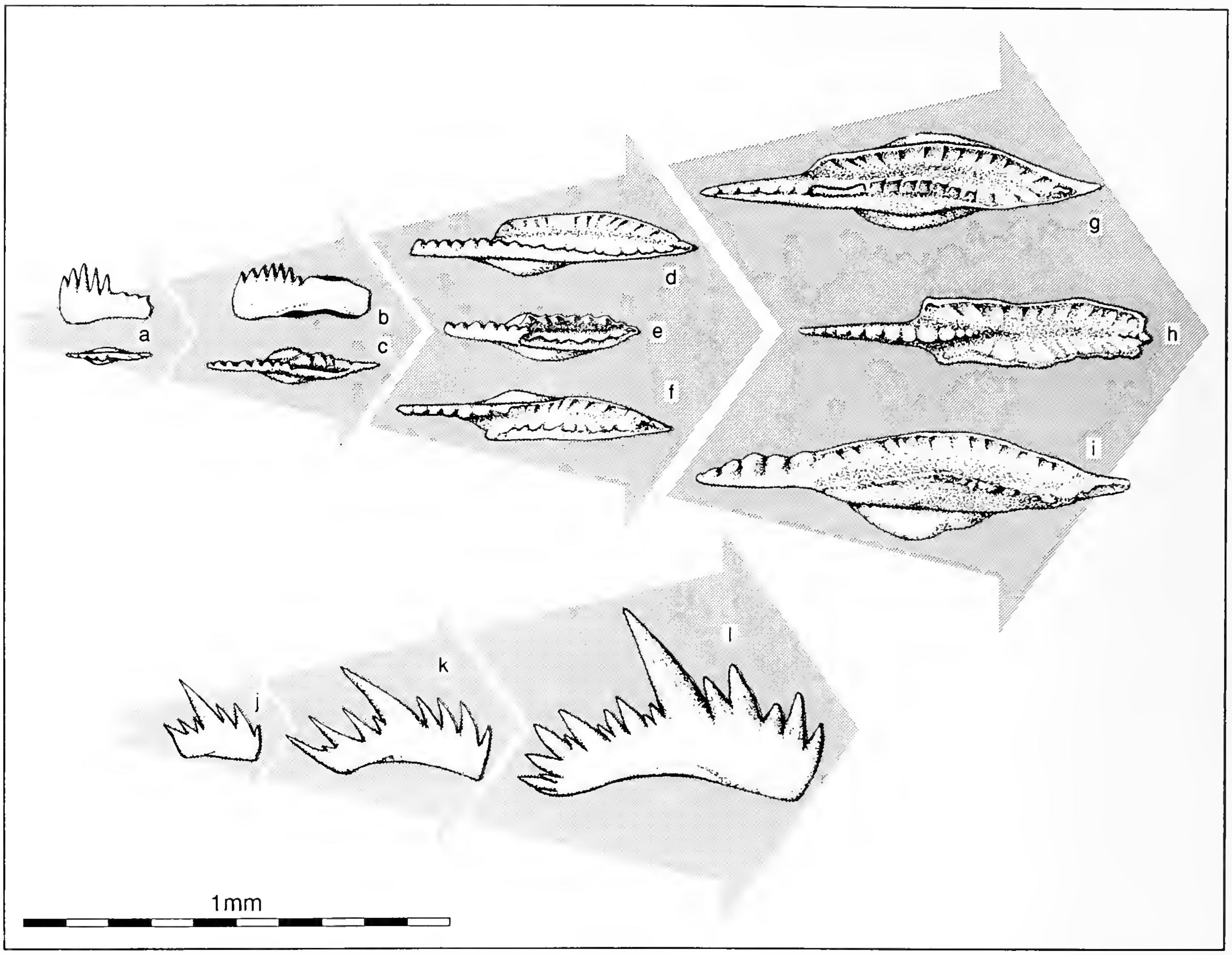
Text-Fig. 9 also illustrates the ontogeny of Pb elements. The smallest specimens (j) are short and straight; the processes have only two or three sharply pointed denticles; the basal cavity is relatively large and elongate, tapering to the ends of the processes. With increasing maturity the number of process denticles increases and the basal cavity becomes relatively smaller and more constricted.

The ontogeny of the ramiform elements is not known.

Pa ELEMENT SYMMETRY

The symmetry classification of Lane (1968) (Text-Fig. 10) provides a convenient means of discussing the pairing of Pa elements in conodont apparatuses. Lane (1967, 1968) discussed the phylogenetic significance of Pa element symmetry in some early Pennsylvanian taxa, and the differentiation of *Adetognathus* and *Cavusgnathus* on the basis of Pa element symmetry illustrates its potential taxonomic significance. Pa element symmetry varies both within and between genera of the Cavusgnathidae (Table 1) and may prove to be a useful character in any systematic revision of the family. Pa element symmetry also has considerable functional significance and may provide evidence in determining whether conodont apparatuses performed a grasping or filter-feeding function (Aldridge, 1987; Nicoll, 1987).

Pa elements that are herein considered to be *T. varians* have previously been assigned to symmetry Class I (Lane, 1968; Druce, 1973; Austin *in* Austin and Mitchell, 1975) and Class II (Austin *in* Austin and Mitchell, 1975). The present collection of more than 400 *T. varians* Pa elements has enabled a detailed reassessment of their symmetry. On the basis of curvature and blade position, Pa elements were assigned to one of thirteen categories (Text-Fig. 7). Morphotype III elements (Text-Fig. 11; categories H–M)

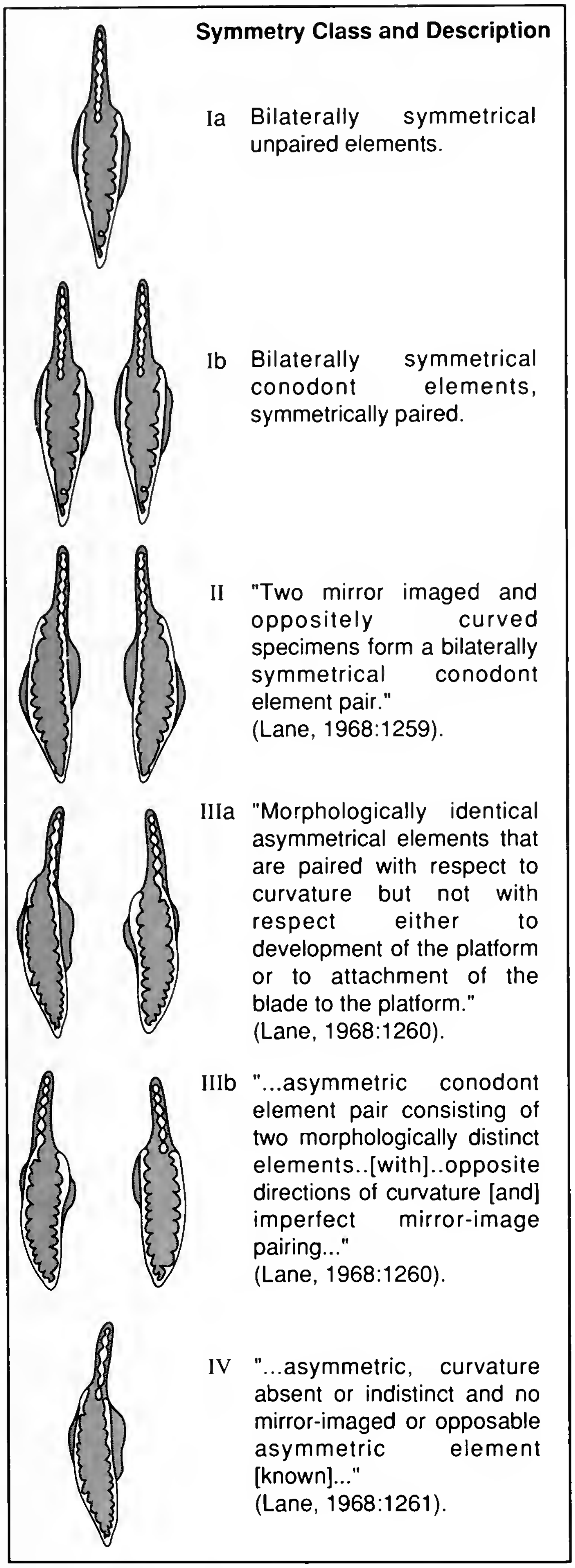


TEXT-FIG. 9. Ontogeny of Pa and Pb elements of *Taphrognathus varians*. Figures based on actual specimens with broken parts restored: a) ROM 48831; b) ROM 48828; c) ROM 48830; d) NG2/267; e) TG1/569; f) ROM 48829; g) ROM 48824; h) ROM 48825; i) ROM 48822; j) ROM 48834; k) TG1/439; l) ROM 48832.

far outnumber morphotype I and II elements (Text-Fig. 11; categories A–G). This disproportionate representation and the absence of morphotype III elements in the collection of Austin and Mitchell (1975) suggests that morphotype II elements did not pair with morphotype III elements (Class IIIa symmetry). Too few morphotype II specimens were available to test this hypothesis statistically. Not enough morphotype I specimens have been recovered in this study to assess their symmetry in the Northumberland trough. Pa element pairing in *T. varians* morphotype III can, however, be statistically analyzed. Because it cannot be assumed that the data for each of the categories H to M are normally distributed and do not have significantly different variances, nonparametric procedures were used.

Of the 288 morphotype III Pa elements that have been categorized, 133 are sinistral (H, I, J) and 155 are dextral (K, L, M). Spearman's rank correlation indicates a positive relationship between the distributions of sinistral and dextral elements ($P < 0.01$) (see Purnell, 1989, for all Spearman's rank correlation data and results). This may be interpreted in two ways: either *T. varians* that bore morphotype III Pa elements existed in two forms, one with dextral and the other with sinistral Pa elements, which were numerically balanced and had a consistent pattern of co-occurrence; or Pa elements were paired sinistral with dextral and in the same animal. Although some cavusgnathids may have had Pa elements that were asymmetrically paired in terms of curvature (Rexroad, 1981), the possibility of a consistent 1:1 relationship between animals with dextral pairing and those with sinistral seems remote.

Thus elements assigned to categories H, I, and J were paired with K, L, and M (Text-Fig. 12). H, J, and M are the most common and abundant element forms (Text-Fig. 11). H and J must have paired with M (Text-Fig. 12), and the hypothesis that the combined distribution of H and J is unrelated to that of M is rejected ($P < 0.01$). A relationship between J and M is supported statistically ($P < 0.001$), but the distributions of H and M are not significantly correlated ($P > 0.05$). Given that sinistral and dextral



Symmetry Class and Description	
Ia	Bilaterally symmetrical unpaired elements.
Ib	Bilaterally symmetrical conodont elements, symmetrically paired.
II	"Two mirror imaged and oppositely curved specimens form a bilaterally symmetrical conodont element pair." (Lane, 1968:1259).
IIIa	"Morphologically identical asymmetrical elements that are paired with respect to curvature but not with respect either to development of the platform or to attachment of the blade to the platform." (Lane, 1968:1260).
IIIb	"...asymmetric conodont element pair consisting of two morphologically distinct elements..[with]..opposite directions of curvature [and] imperfect mirror-image pairing..." (Lane, 1968:1260).
IV	"...asymmetric, curvature absent or indistinct and no mirror-imaged or opposable asymmetric element [known]..." (Lane, 1968:1261).

TEXT-FIG. 10. Symmetry classification of Lane (1968) illustrated by hypothetical *Taphrognathus varians* Pa element pairing.

elements were paired, however, this lack of correlation is puzzling as there is little other than M type elements with which H forms could have paired (Text-Fig. 11). The relationship between H and L is supported statistically ($P < 0.05$) but because of the small numbers of L type elements, H:L pairing was probably less common. None of the six remaining pairing permutations is supported by significant Spearman's rank correlations but, unless elements could be unpaired, at least some of them must have occurred. Only two are considered unlikely because of the rarity of both elements of the pair (Text-Fig. 12). In the majority of cases, therefore, *T. varians* morphotype III paired with Class IIIb symmetry. Class II symmetry (see Text-Fig. 10) is also possible but, given the variability of Pa elements of the species and their tendency to develop a higher right anterior parapet, was probably rare.

The 16 specimens in the Austin and Mitchell (1975) collection considered herein to be *T. varians* morphotypes I and II are inadequate for a detailed analysis of symmetry. The range of blade positions and curvature exhibited by these specimens and the morphotype II material of this study is, however, consistent with Class IIIb symmetry (Text-Fig. 13).

European collections of *T. varians* contain few morphotype I Pa elements. They may have paired together or with morphotype II or III elements (Class IIIb symmetry dominant), but the small number of known specimens precludes more rigorous analysis. Most American *T. varians* faunas are, however, dominated by morphotype I elements. The original collection of Branson and Mehl (1941b) includes 70 specimens from the Sylvan Beach locality. Of these, 61 elements have determinable curvature of which 30 are sinistral, 16 are dextral, and 15 are straight. These numbers suggest that sinistral-dextral and sinistral-straight pairing (Class IIIb symmetry) were most common; dextral-dextral pairing and straight-straight pairing (Class Ib symmetry) were rare (Text-Fig. 14). Again, the morphological variability of these specimens and the tendency to develop a higher right anterior parapet suggests that Class II was rarely if ever developed.

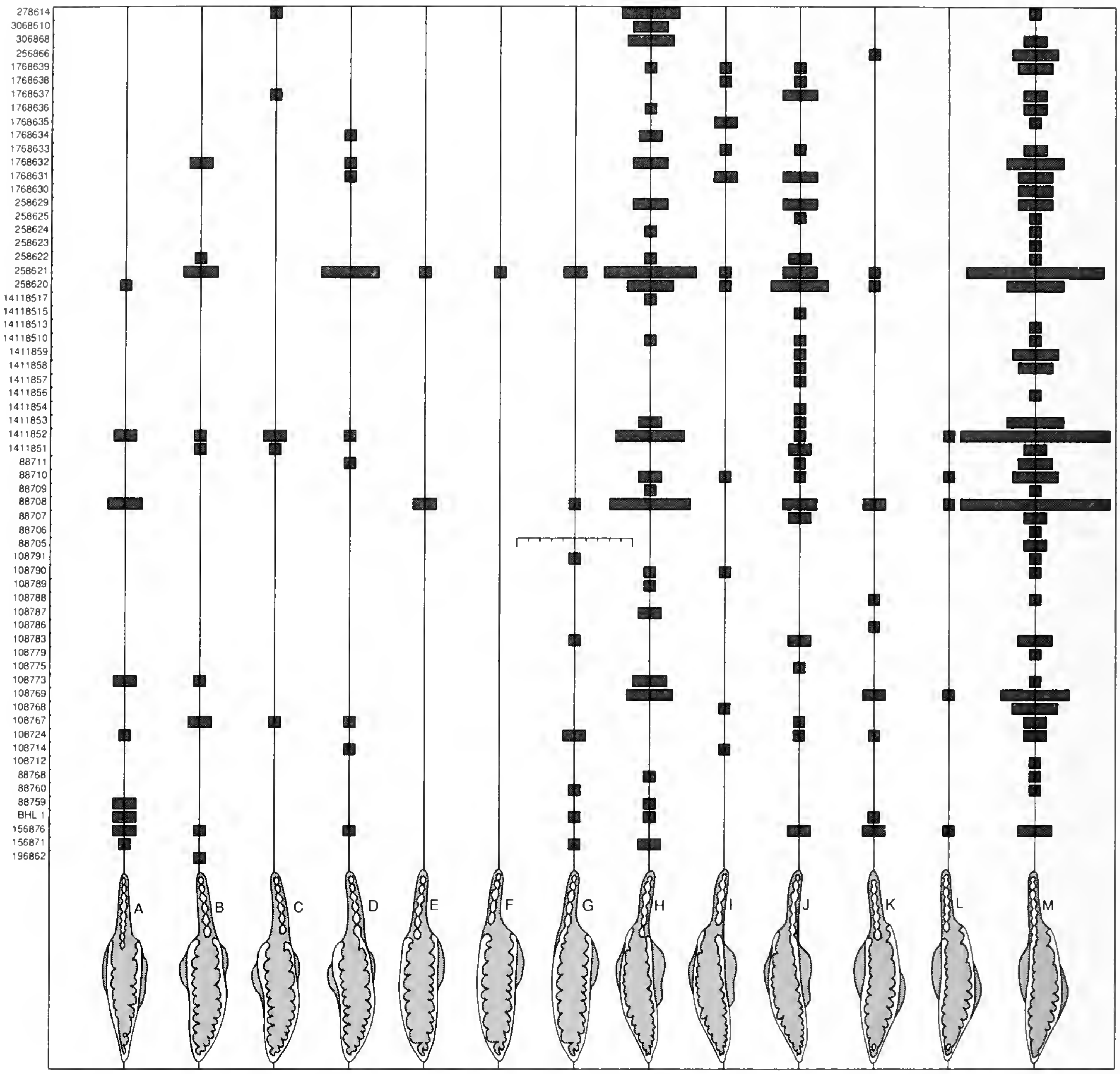
Taphrognathus cf. *varians*

MATERIAL STUDIED

Two Pa elements from the Cementstone Group in the Rothbury and Kielder areas.

DISCUSSION

These specimens differ from *T. varians* only in exhibiting a marked lateral bulging of the anterior end of the right parapet. Whether such specimens represent a distinct taxon or variant *T. varians* Pa elements is unclear.



TEXT-FIG. 11. Distribution of *Taphrognathus varians* blade position/curvature categories in the Lower Border and Cementstone groups. Scale bar equals 10 Pa elements; sample numbers at left. N.B. Diagram includes only *T. varians*-yielding samples.

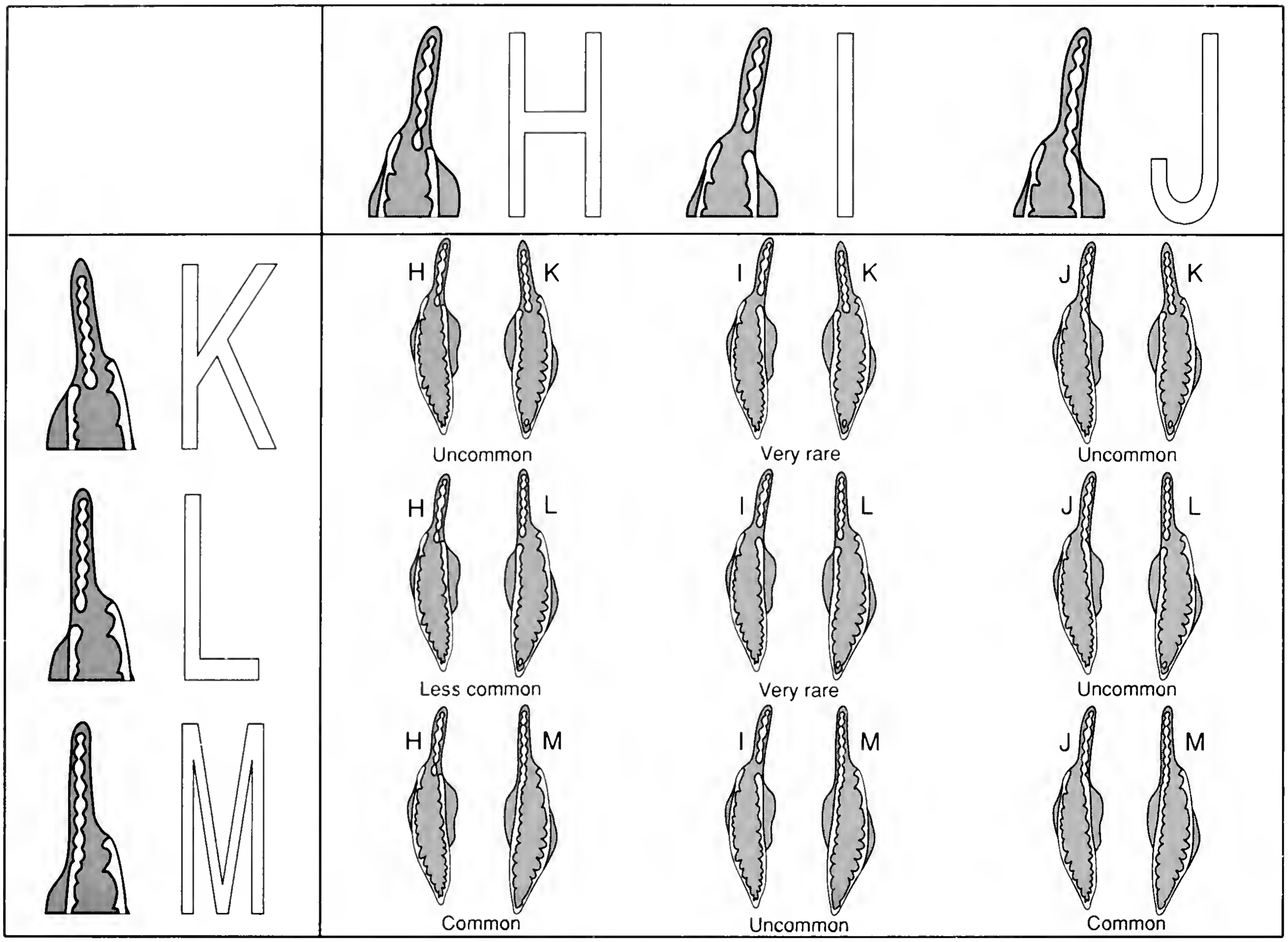
***Taphrognathus* sp. a**
Plate 5, Figs. 5a, b

MATERIAL STUDIED

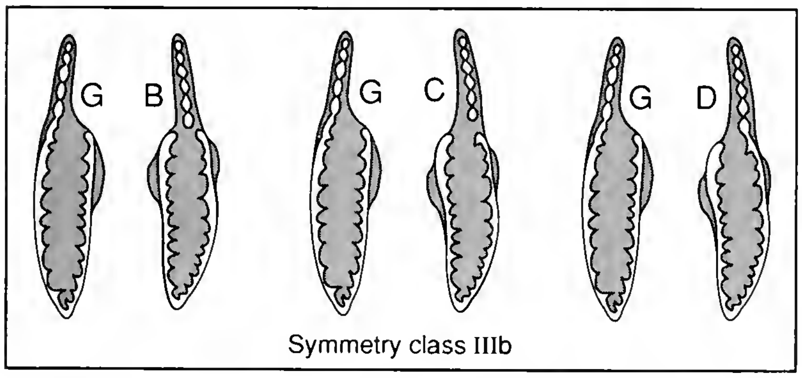
One Pa element from the Harden Member, Middle Border Group, superjacent to the Black Burn Formation.

DESCRIPTION

The apparatus of this species is unknown. The anterior blade of the Pa element is located on the left side. The blade is continuous with the outer parapet and bears four blunt denticles, the middle two of which are largest. The denticles are fixed apart from their tips and are not laterally compressed. The blade is free for its entire length and makes up one-quarter of the length of the element. The platform is sinistral, the outer parapet convex, the inner more or less straight. The parapets have rounded crests and bear weak transverse ridges which increase slightly in strength posteriorly. The right parapet is slightly higher than the left in the anterior half. The medial trough is shallow and unornamented. It is open anteriorly and shallows towards the bluntly pointed posterior end of the element. In lateral view the element is gently arched, the platform height slightly decreasing posteriorly. Platform width is just over one-quarter of its length, widest in the anterior half. The basal cavity is lanceolate and subsymmetrical,



TEXT-FIG. 12. The nine possible pairings of Pa elements of *Taphrognathus varians* morphotype III in the present study. Relative frequency categories based on the results of Spearman's rank correlation of blade position/curvature categories.

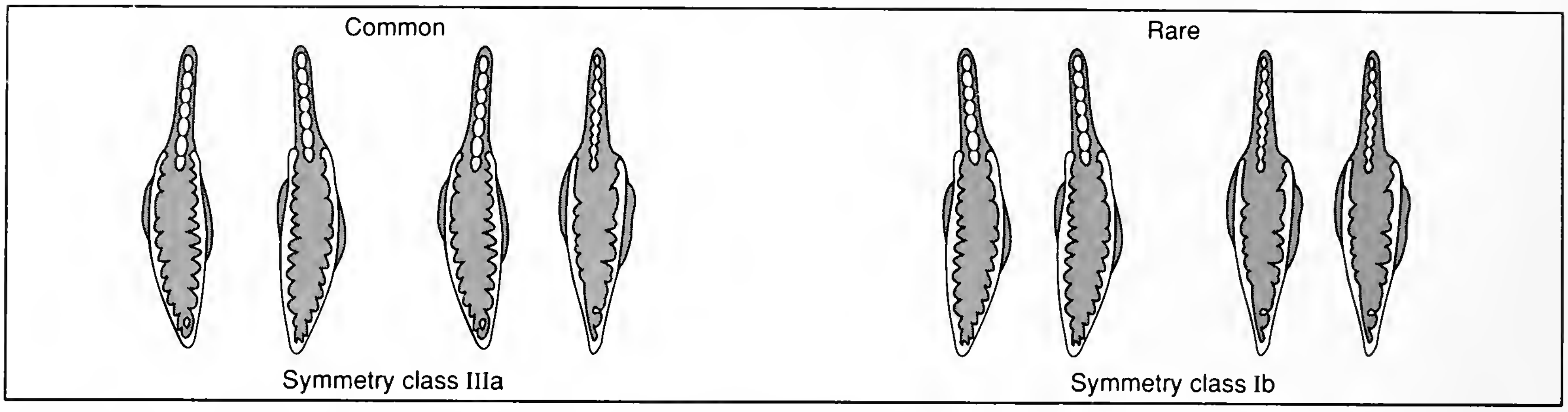


TEXT-FIG. 13. Likely Pa element pairing in *Taphrognathus varians* morphotype II (based on the collection of Austin and Mitchell, 1975; and this study). Letters indicate blade position/curvature categories.

and occupies most of the lower surface of the element. It is widest and deepest at element midlength and bears a medial groove. Posteriorly the cavity tapers gently to the end of the element.

DISCUSSION

The single Pa element of *Taphrognathus* sp. a differs from other species of *Taphrognathus* chiefly in the form of the anterior blade, the roundedness of the parapet crests, and the shallowness of the medial trough. It is very similar to specimens identified as *Cloghergnathus* sp. A and *Taphrognathus* sp. B, in Marchant (1978) and Rees (1987) respectively.



TEXT-FIG. 14. Likely Pa element pairing in *Taphrognathus varians* morphotype I (based on the collection of Branson and Mehl, 1941b). Symmetry classes after Lane (1968; see Text-Fig. 10).

***Taphrognathus*? *transatlanticus* (von Bitter and Austin, 1984)?**
Plate 5, Figs. 4a, b

MATERIAL STUDIED

One Pa element from the Bogside Limestone Member of the Bewcastle Formation, Lower Border Group.

DESCRIPTION

See von Bitter and Austin (1984:101–106). The Pa element recovered from the Bogside Limestone differs from *T.*? *transatlanticus* in bearing an anterior blade that does not increase in height posteriorly.

DISCUSSION

Because of the differences from typical *T.*? *transatlanticus* noted above, and its poor state of preservation, the single specimen recovered has been assigned to *T.*? *transatlanticus*?.

In erecting *T. transatlanticus*, von Bitter and Austin (1984:100) noted that neither *Taphrognathus* nor *Cavusgnathus* were "... sufficiently broad to comfortably and unequivocally include the new species." The same is true of the revised concept of *Taphrognathus*. Both *T. varians* and *T. carinatus* bore M elements, whereas *T.*? *transatlanticus* did not. No other species of *Taphrognathus* has the posteriorly enlarging Pa element blade denticles or the unornamented parapets of *T.*? *transatlanticus*.

A single specimen of *Taphrognathus* sp. A was recovered by Davies (1980), figured by Austin and Davies (1984, pl. 1, fig. 3), and considered by von Bitter and Austin (1984) to be *T. transatlanticus*. This element appears to have incipient ornament on the right parapet and is probably a juvenile *T. varians* element. Similar specimens have been recovered in this study (e.g., Pl. 4, Fig. 7). Given the resemblance between juvenile *T. varians* Pa and Pb elements (Pl. 4, Figs. 7, 8, 10, 14) and their mature counterparts in *T.*? *transatlanticus*, the latter species may have evolved progenetically from *T. varians*.

Family Gnathodontidae Sweet, 1988

Genus *Gnathodus* Pander, 1856

Gnathodus Pander, 1856:33.
[non] *Gnathodus* Fieber, 1866.
Dryphenotus Cooper, 1939:386.
Westfalicus Moore and Sylvester-Bradley, 1957:21.

DIAGNOSIS

(After Lane, Sandberg, and Ziegler, 1980; Austin and Rhodes *in* Robison, 1981.) Apparatus probably seximembrate: Pa element carminiscaphate; basal cavity asymmetric, inner side bears parapet and is narrower and extends further anteriorly than the more expanded outer side. Pb elements angulate; M elements dolabrate; Sa element alate; Sb elements bipennate; Sc elements bipennate. Pa elements paired with Class II symmetry; other elements, except the Sa, paired symmetrically.

TYPE SPECIES

Polygnathus bilineatus Roundy (1926) by subsequent designation (I.C.Z.N. opinion 1415, Tubbs, 1986).

***Gnathodus cuneiformis* Mehl and Thomas, 1947**
Plate 5, Fig. 7

Gnathodus cuneiformis Mehl and Thomas, 1947:10, pl. 1, fig. 2.

Gnathodus cuneiformis—Ziegler *in* Ziegler, 1981:123–6, *Gnathodus*—pl. 1, figs. 1–5 [with full synonymy].

DIAGNOSIS

See Lane, Sandberg, and Ziegler (1980:130).

HOLOTYPE

University of Missouri, C654-4 (Mehl and Thomas, 1947, pl. 1, fig. 2).

TYPE HORIZON AND LOCALITY

Greenish-grey and red argillaceous limestone, Fern Glen Formation, units 9–11 of Mehl and Thomas (1947); bluff of the Meramec River at Castlewood, Missouri, U.S.A.

MATERIAL STUDIED

A single Pa element from a loose sample of the Glebe Limestone Member, Cementstone Group.

DESCRIPTION

Apparatus unknown. See Mehl and Thomas (1947:10) for Pa element description.

DISCUSSION

Only the Pa elements of this species are known. The specimen recovered closely resembles the holotype, considered by Lane, Sandberg, and Ziegler (1980) to represent a younger morphotype of the species.

Gnathodus? simplicatus (Rhodes, Austin, and Druce, 1969)
Plate 5, Fig. 6

Gnathodus simplicatus Rhodes, Austin, and Druce, 1969:107, pl. 8, fig. 5; pl. 18, figs. 2–5.

DIAGNOSIS

See Rhodes, Austin, and Druce (1969:107).

HOLOTYPE

British Museum, X89 (Rhodes, Austin, and Druce, 1969, pl. 18, fig. 4).

TYPE HORIZON AND LOCALITY

Sample ZLA 33 of Rhodes, Austin, and Druce (1969), North Crop, South Wales Coalfield, U.K. (precise locality details are confused in Rhodes, Austin, and Druce, 1969).

MATERIAL STUDIED

A single Pa element from the Harden Member, Middle Border Group, superjacent to the Black Burn Formation.

DESCRIPTION

Apparatus unknown. See Rhodes, Austin, and Druce (1969:107) for description of Pa elements.

DISCUSSION

See Davies (1980) for the only recent synonymy for this species. Only the Pa elements are known. The specimen recovered in this study is very similar to the holotype, but does not have the regularly sloping upper surface considered to be diagnostic by Rhodes, Austin, and Druce (1969). It is also similar to *G. simplicatus* from Ireland figured by Johnston and Higgins (1981).

According to Lane, Sandberg, and Ziegler (1980), an expanded asymmetric basal cavity and the development of an inner parapet are diagnostic of *Gnathodus*. The simple carminiscaphate Pa elements of this species should probably be referred to another genus, but without knowledge of the apparatus this new generic assignment cannot be determined.

Family Mestognathidae Austin and Rhodes *in* Robison, 1981

Genus *Mestognathus* Bischoff, 1957

Mestognathus Bischoff, 1957:36.

DIAGNOSIS

See von Bitter, Sandberg, and Orchard (1986:32).

TYPE SPECIES

Mestognathus beckmanni Bischoff, 1957, by original designation.

Mestognathus beckmanni Bischoff, 1957
Plate 5, Figs. 8, 9

Mestognathus beckmanni Bischoff, 1957:37, pl. 2, figs. 4–6, 8, 9 [Pa elements].

[(?)] *Ozarkodina macra* Branson and Mehl—Metcalfe, 1980:173, fig. 3 (table) [Pb elements] [not figured].

[v.] *Ozarkodina macra*—Metcalfe, 1981, pl. 19, fig. 6 [Pb element].

Mestognathus beckmanni—von Bitter, Sandberg, and Orchard, 1986:35–37, pl. 1, figs. 1–8, 23; pl. 2, figs. 1–5, 9; pl. 3, figs. 1–5, 9; pl. 4, figs. 1–5, 9; pl. 12, figs. 1–6; pl. 13, figs. 1–9; pl. 14, figs. 1–12; pl. 15, figs. 1–12; pl. 16, figs. 1–12; pl. 17, figs. 1–13; pl. 19, figs. 1–5; pl. 20, figs. 3, 6, 10, 12; pl. 23, figs. 1–3; pl. 25, figs. 7–9; pl. 26, fig. 4; pl. 27, figs. 3, 4, 7 [Pa elements] [with full synonymy for Pa element].

[v.p] *Cavusgnathus unicornis* Youngquist and Miller—Armstrong and Purnell, 1987, pl. 1, fig. 13 only [Pb element].

[vnon] *Mestognathus beckmanni*—Armstrong and Purnell, 1987, pl. 3, figs. 4, 5, 6, 7.

DIAGNOSIS

See von Bitter, Sandberg, and Orchard (1986:37).

HOLOTYPE

Phillips University (Marburg), Bi 1957/35 (Bischoff, 1957, pl. 2, fig. 4).

TYPE HORIZON AND LOCALITY

Lower *Goniatites* Stufe, cu III α, small quarry 1 km north of Lethmathe, immediately north of the Waldcafé, on the road between Lethmathe and Schwerte, Topographic Sheet Hohenlimburg, Germany.

MATERIAL STUDIED

Pa elements, 86(3); Pb elements, 1; from the Bogside Limestone Member of the Bewcastle Formation, Lower Border Group, and the Cementstone Group, Akenshaw Burn. Unpublished material, including 5 Pb elements, collected by Dr. N. J. Riley from the Craven basin was also examined.

DESCRIPTION

Pa elements. See von Bitter, Sandberg, and Orchard (1986:3–7, 36–37).

Pb elements. The anterior process is straight and bears eight to ten laterally compressed, slightly reclined denticles with sharp triangular tips. The denticles are all fused for more than half their length but become more fused towards the cusp; they are largest and least fused immediately anterior of the process midlength. The process is laterally thickened with a distinct rib or ridge developed below the base of the denticles, especially on the outer side. This rib thins towards the anterior end and the sharp lower edge, and extends along the long axis of the cusp. The cusp is as much as two or three times the length and width of the largest process denticles. It is strongly reclined at an angle of 150° from the long axis of the anterior process and, in mature specimens, has an irregularly stepped or weakly serrated anterior edge. The serration appears to be caused by the incorporation of two or three anterior denticles into the cusp during ontogeny. The posterior process is straight and is deflected downwards at an angle of approximately 40° from the anterior process. It is similar to the anterior process in terms of length, denticle size and shape, and the thin lower margin, but is less thickened and slightly lower. The posterior end is commonly missing, but the process bears as many as nine or more denticles which are increasingly reclined posteriorly. The basal cavity is narrow and elongate; it is situated beneath the cusp and does not extend along the thin lower edges of the processes, both of which bear a zone of recessive basal margin (eversion strips). White matter is developed along the growth axes of the cusp and posterior denticles especially.

DISCUSSION

von Bitter, Sandberg, and Orchard (1986) were uncertain if *Mestognathus* bore nonplatform elements, but did not rule out the possibility that they may have been present under optimum conditions. The present study suggests that in certain environments *M. beckmanni* bore a pair of Pb elements similar in form to *"Ozarkodina macra."* In the Northumberland trough this distinctive Pb element has been recovered with *M. beckmanni* Pa elements from the Bogside Limestone Member (Appendix IIb) and from the 3 m thick Tombstone Limestone, which has also yielded *M. beckmanni* (Armstrong and Purnell, 1987). Metcalfe (1980) recorded seven specimens of *"O. macra"* associated with *M. beckmanni* in five samples through the Embsay Limestone Member in the Craven basin. A further three specimens were reported by Metcalfe (1981), two occurring with *M. beckmanni,* one within 2 m of a *M. beckmanni*-yielding sample. Five specimens of *"O. macra"* collected by Dr. N. J. Riley from the Craven basin were all associated with *M. beckmanni* Pa elements. The rest of the fauna recovered by Metcalfe (1980, 1981) and Riley is made up of species of *Gnathodus* and *Kladognathus* Rexroad with *Patrognathus capricornis* (Druce) and rare *Polygnathus bischoffi* Rhodes, Austin, and Druce. None of these conodonts bore Pb elements of *"O. macra"* form. In addition to this evidence of association, certain aspects of the morphology of these Pb elements, notably the anterior process denticles and cusp, are similar to *M. beckmanni* Pa elements (compare Pl. 5, Fig. 9 with von Bitter, Sandberg, and Orchard, 1986, pl. 16, fig. 7, for example). The small basal cavity, the well-developed eversion strips, and the overall robust structure of the element are also reminiscent of *M. beckmanni* Pa elements.

Mestognathus bipluti Higgins probably also bore Pb elements similar to those described above. Five such Pb elements were assigned to *Clydagnathus windsorensis* (Globensky) by Plint and von Bitter (1986, table 1) and by von Bitter and Plint (1987, table 1), but were recovered from a sample which contains no Pa elements of *Cl.*

windsorensis (sample IDM-3-21). This sample does, however, contain nine Pa elements of *M. bipluti* and *Mestognathus* spp.

Mestognathus praebeckmanni **Sandberg, Johnston, Orchard, and von Bitter, 1986**

Plate 5, Fig. 10

Mestognathus praebeckmanni Sandberg, Johnston, Orchard, and von Bitter *in* von Bitter, Sandberg, and Orchard, 1986:34, 35, pl. 1, figs. 32–34; pl. 7, figs. 1–5; pl. 8, figs. 1–11; pl. 9, figs. 1–11; pl. 10, figs. 1–7, 10, 11; pl. 11, figs. 1–10 [with full synonymy].

[vp] *Mestognathus beckmanni*—Armstrong and Purnell, 1987, pl. 3, fig. 4 only.

DIAGNOSIS

See von Bitter, Sandberg, and Orchard (1986:35).

HOLOTYPE

United States National Museum 257757 (von Bitter, Sandberg, and Orchard, 1986, pl. 8, figs. 1–4, 8, 10).

TYPE HORIZON AND LOCALITY

Facies de Leffe, Banc 60 of Groessens (1971, log 6, section 8), route between Salet and Bioul, 8 km NW of Dinant, Belgium.

MATERIAL STUDIED

Pa elements, 9(2) from the lower Lynebank Formation, Lower Border Group.

DESCRIPTION

Pa elements. See von Bitter, Sandberg, and Orchard (1986:3–7, 34, 35).

DISCUSSION

Many of the specimens of *M. praebeckmanni* from the Northumberland trough are transitional to *M. beckmanni*, with similar overall proportions and a vertical anterior left parapet termination. All other taxonomic characters are, however, typical of *M. praebeckmanni* and similar specimens were included in this species by von Bitter, Sandberg, and Orchard (1986, pl. 10, figs. 1–7, pl. 11, figs. 1–3, 5, 6). In general, *M. praebeckmanni* Pa elements from this study resemble morphotype 2 of von Bitter, Sandberg, and Orchard (1986) more closely than they do morphotype 1 or 3.

Mestognathus praebeckmanni–M. beckmanni **intermediates**

Plate 5, Figs. 11, 12

Mestognathus cf. *beckmanni*—von Bitter, Sandberg, and Orchard, 1986:27, pl. 23, figs. 1, 2.

[vp] *Mestognathus beckmanni*—Armstrong and Purnell, 1987, pl. 3, fig. 6 only.

MATERIAL STUDIED

Pa elements, 8(1); from the Bogside Limestone Member of the Bewcastle Formation and the Lynebank Formation, Lower Border Group, and from the Cementstone Group, Akenshaw Burn.

DISCUSSION

The Northumberland trough represents an area where *M. beckmanni* and *M. praebeckmanni* co-existed. In such areas, von Bitter, Sandberg, and Orchard (1986) expected considerable morphologic intergradation between the two species, and this has proved to be the case in this study. One group of intermediate forms are close to *M. praebeckmanni* in morphology but have an anterior left parapet area, the most important criterion in differentiating species of *Mestognathus*, which approaches that of *M. beckmanni* (Pl. 5, Figs. 11a, b). In most of these specimens, the anterior left parapet termination is vertical with a small anterior denticle developed. Occasionally the parapet area is more raised than that developed by *M. praebeckmanni*. Other intermediate specimens are close to *M. beckmanni* in morphology but possess a low parapet area and/or a relatively large, only slightly everted basal cavity similar to *M. praebeckmanni* (Pl. 5, Figs. 12a–c). These characteristics are also exhibited by juveniles of *M. beckmanni*; consequently, only specimens longer than 0.7 mm are considered intermediate. Specimens below this size are assigned to *Mestognathus* sp.

Genus *Polygnathus* Hinde, 1879

Polygnathus Hinde, 1879:361.
Hindeodella Bassler, 1925:219.
Ctenopolygnathus Müller and Müller, 1957:1084.

DIAGNOSIS
(After Klapper and Philip, 1971; Klapper et al. *in* Robison, 1981.) Apparatus seximembrate; Pa elements carminiplanate (carminiscaphate in earliest species); Pb elements angulate; M elements dolabrate; Sa element alate; Sb elements digyrate; Sc element bipennate.

TYPE SPECIES
Polygnathus dubius Hinde, 1879, by subsequent designation of Miller (1889:520).

Polygnathus bischoffi **Rhodes, Austin, and Druce, 1969**
Plate 6, Figs. 1, 3

[v*] *Polygnathus bischoffi* Rhodes, Austin, and Druce, 1969:184–5, pl. 13, figs. 8–11.
Polygnathus bischoffi—Klapper *in* Ziegler, 1975:275–6, *Polygnathus*—pl. 4, fig. 5 [with synonymy].

DIAGNOSIS
See Rhodes, Austin, and Druce (1969:184).

HOLOTYPE
British Museum, X349 (Rhodes, Austin, and Druce, 1969, pl. 13, fig. 11).

TYPE HORIZON AND LOCALITY
Sample SCC of Rhodes, Austin, and Druce (1969), South Wales Coalfield, Fall Bay, Gower, South Wales.

MATERIAL STUDIED
Pa elements, 28(6); M elements, 1(1); from the lower Lynebank Formation, Lower Border Group. In addition, the type specimens of Rhodes, Austin, and Druce (1969) and the collection of Austin and Mitchell (1975) were examined.

DESCRIPTION
Pa elements. See Rhodes, Austin, and Druce (1969: 184–5).
M elements. See Rhodes, Austin, and Druce (1969:158–9) under *Neoprioniodus confluens*.

DISCUSSION
The Pa elements from the Northumberland trough have deeper anterior adcarinal troughs and larger basal cavities with more pronounced lips than the holotype and paratypes of *P. bischoffi*. These differences are almost certainly ontogenetic; no specimens that would have exceeded 0.8 mm in total length were found in this study, whereas the holotype is 1.32 mm long and both paratypes are over 1 mm. The other figured specimen (hypotype) of Rhodes, Austin, and Druce (1969) is, however, 0.725 mm long and has a larger basal cavity. Austin and Mitchell (1975) recorded, but did not figure, *P. bischoffi* Pa elements from the Lower Carboniferous Shale, Northern Ireland. These elements range in length between 0.4 mm and 1.6 mm; only specimens of over 0.75 mm develop small basal cavities.

Although the adcarinal troughs of the Pa elements from the Lower Border Group are deeper than those of larger specimens, they can still be distinguished from Pa elements of *P. inornatus* E. R. Branson in lacking the conspicuously high right anterolateral margin characteristic of the latter species.

Small Pa elements of *P. bischoffi* with their larger basal cavities resemble Pa elements of *Pseudopolygnathus minutus* Metcalfe, the holotype of which is only 0.56 mm long. Metcalfe (1981) suggested that *P. bischoffi* evolved from *Ps. minutus*, presumably peramorphically; alternatively, although the ranges of the two species are not completely concurrent (Higgins and Austin, 1985:250–1, table 6), *Ps. minutus* Pa elements may be immature *P. bischoffi* elements.

The single complete M element recovered that probably belongs to *P. bischoffi* is of *"Neoprioniodus confluens"* form. The posterior process is less downwardly deflected than it is in the M elements of *P. mehli* Thompson (see below) but, from the available material, *P. bischoffi* M elements cannot be distinguished from *Patrognathus capricornis* (Druce) M elements.

Polygnathus mehli **Thompson, 1967**
Plate 6, Figs. 2, 4–7, 9–11

[?] *Bryantodus planus* Huddle, 1934:75–6, pl. 10, fig. 8 [Pb element].
Polygnathus mehli Thompson, 1967:47, 48, pl. 2, figs. 1–6 [Pa elements].
[?p] *Neoprioniodus confluens* (Branson and Mehl)—Rhodes,

Austin, and Druce, 1969:158, pl. 21, fig. 2 only [M element].

Polygnathus lacinatus Huddle—Higgins, 1971, pl. 1, figs. 6, 8 [Pa elements].

Polygnathus mehli—Klapper *in* Ziegler, 1975:307–8, *Polygnathus*—pl. 6, fig. 4 [Pa element] [with Pa element synonymy].

Polygnathus lacinatus—Austin *in* Austin and Mitchell, 1975:52, pl. 1, figs. 28, 29, 31, 32 [Pa elements].

Polygnathus aff. *P. lacinatus sensu* Rhodes, Austin, and Druce—Nicoll and Druce, 1979:29, pl. 16, fig. 10 [Pa element].

[(?)] *Polygnathus lacinatus asymmetricus* Rhodes, Austin, and Druce—Metcalfe, 1981, pl. 9, fig. 5 [Pa element].

Polygnathus mehli latus Johnston and Higgins, 1981:92, 94, figs. 5.11–5.15 [Pa elements] [with partial synonymy].

"Polygnathus" mehli—Chauff, 1981, pl. 2, figs. 9, 10, 22–25, 35, 36 [Pa elements].

Polygnathus mehli—Austin and Davies, 1984, pl. 1, fig. 2; pl. 2, fig. 33(?); pl. 3, figs. 10, 12 [Pa elements].

Polygnathus lacinatus—Austin and Davies, 1984:196, text-fig. 1, pl. 2, figs. 1, 32 [Pa elements].

Polygnathus mehli latus—Varker and Sevastopulo, 1985:192, pl. 5.2, figs. 9, 10 [Pa elements].

Polygnathus mehli mehli—Varker and Sevastopulo, 1985:192, pl. 5.2, figs. 11, 12, 15, 18 [Pa element].

Polygnathus mehli—Belka, 1985, pl. 14, fig. 13 [Pa element].

DIAGNOSIS

Pa element diagnostic, see Thompson (1967:48).

HOLOTYPE

University of Missouri, C-994-17 (Thompson, 1967, pl. 2, figs. 1, 2).

TYPE HORIZON AND LOCALITY

Pierson Formation, Unit 19; Roaring River State Park south entrance, road cut on west side of State Highway 112, locality F of Thompson (1967), Barry County, Missouri, U.S.A.

MATERIAL STUDIED

Pa elements, 165(14); Pb elements, 13(5); M elements, 9; Sa elements, 2(4); Sc elements, 6(2); from the Liddel Formation, Lower Border Group, and the Harden Member, Middle Border Group.

DESCRIPTION

Pa elements. See Thompson (1967:48) under *P. mehli*, and Rhodes, Austin, and Druce (1969:188–91) under *P. lacinatus*.

Pb elements. The anterior and posterior processes are subequal in length and are downcurved and slightly incurved. The anterior process bears four or five large laterally compressed, triangular denticles, free for most of their length. They are largest towards the middle of the process and increasingly reclined towards the cusp. The length of the denticles commonly exceeds the depth of the process beneath them, which exceeds them only slightly in thickness. The reclined cusp is similar in shape to the anterior denticles but is higher and wider, although sometimes only slightly so. The posterior process bears six to eight smaller less compressed and less discrete denticles. They are subequal in size and become increasingly reclined posteriorly. The elongate basal cavity is widest and deepest beneath the cusp, tapering to a point at or near the anterior tip of the element and to halfway along the posterior process.

M elements. See Rhodes, Austin, and Druce (1969:158) under *Neoprioniodus confluens*.

Sa element. The lateral processes diverge anteriorly at an angle of slightly less than 180° in a horizontal plane, and at 90° to 100° in a vertical plane. They are relatively short and have a thick wedgeshaped cross-section. Process height and width are subequal towards the cusp, but width gradually decreases laterally. The processes are slightly curved downwards, with an inflection point at midlength, and each bears four discrete isolated denticles that are rounded in cross-section. The upper part of the recurved and slightly reclined cusp is also round in cross-section, but becomes more laterally compressed towards the base. The posterior process joins the cusp at a higher level than the lateral processes. It is wedgeshaped in cross-section and tapers posteriorly in height and slightly in width. The figured specimen (Pl. 6, Figs. 10a, b) bears only a single small broken denticle, but the posterior process may be more denticulate. The basal cavity is shallow and everted, and tapers along the lateral processes to narrow grooves flanked by recessive basal margins. It continues along the posterior process as a slightly broader groove.

Sb elements. The Sb elements of *P. mehli* are unknown.

Sc elements. Two morphotypes occur, differing in the form of the anterior process. The more common form of process (Pl. 6, Fig. 11) extends anteriorly from the cusp and is flexed outwards slightly, then gently inwards through about 45°. It is laterally compressed and bears six discrete slightly laterally compressed denticles that increase in size anteriorly. The process also thins and curves slightly downwards towards the anterior end. The other form (Pl. 6, Fig. 9) is sharply deflected downwards and inwards through 90°. It is also laterally compressed, thinning anteriorly, and bears at least five discrete slightly incurved denticles. Apart from one or two minor denticles adjacent to the cusp, these denticles decrease in size along the process. In all other respects, these two morphotypes are similar. The recurved and slightly reclined cusp is laterally compressed towards the base but becomes more rounded in cross-section upwards. It is wider and longer than the largest process denticles. The laterally compressed posterior process is over twice the length of the anterior. It is straight and bears slightly laterally compressed reclined denticles, which alternate in size with one to three minor denticles between each major denticle. There is an overall increase in the size of the major denticles toward the posterior, the posteriormost two being considerably larger than the others. The posterobasal termination of the process is deflected downwards. The shallow elongate basal cavity is widest and deepest beneath the cusp, where a slight lip is developed on the outer side. The cavity tapers posteriorly to a groove that extends along the process to the posterobasal deflection. Anteriorly it tapers to a point halfway along the process.

DISCUSSION

The reconstruction of the apparatus of this species is based chiefly on the abundant but monospecific fauna from sample 108763. The apparatus is very similar to that of other *Polygnathus* species (e.g., Nicoll, 1985; Klapper and Philip, 1971).

Pa elements of *P. mehli* from the Northumberland trough vary in the width and posterior extension of the basal cavity, the degree of cavity eversion, the prominence of the recessive basal margin, the strength of the pseudokeel, the strength of the platform ornament, the degree of expansion of the posterior half of the platform, and the pointedness of the posterior tip. *Polygnathus mehli mehli* is distinguished from *P. mehli latus* Johnston and Higgins, in having fainter ribs, a narrower basal cavity, and a narrower platform (Johnston and Higgins, 1981). These characters were found to vary discordantly and the elements have not been assigned to subspecies. Marchant (1978) noted the variability of *P. mehli* Pa elements in his Irish material, but was also unable to recognize *P. mehli mehli* and *P. mehli* n. subsp. of Johnston (1976)(= *P. mehli latus*).

M elements of *P. mehli* are similar to those of *Patrognathus capricornis* (Druce) but have a more strongly downwardly deflected posterior process with a broader groove along its lower surface. Sa elements resemble "*Hibbardella macrodentata* Thomas"; Sc elements with a downflexed incurved anterior process resemble "*Hindeodella corpulenta* Branson and Mehl."

Family Spathognathodontidae Hass, 1959

Genus *Lochriea* Scott, 1942

Lochriea Scott, 1942:298.
Paragnathodus Meischner, 1970:1173 (nom. nud.).
Paragnathodus Higgins, 1975:70.

DIAGNOSIS

(After Norby, 1976.) Apparatus at least quinquemembrate; Pa elements carminiscaphate with free anterior blade and large posterior basal cavity, the upper surface of which is either unornamented or bears one or two nodes. Pb elements angulate; M elements dolabrate; Sa element alate; Sc elements bipennate. The Pb, M, Sc, and probably the Pa elements, were symmetrically paired.

TYPE SPECIES

Lochriea montanaensis Scott, 1942, by original designation (a subjective junior synonym of *Spathognathodus commutatus* Branson and Mehl, 1941c).

DISCUSSION

The generic concept followed herein is the same as that of Norby (1976) and Rexroad and Horowitz (1990). The multielement composition of the genus was reconstructed on the evidence of bedding plane assemblages (Scott, 1942; Norby, 1976).

Lochriea scotiaensis (Globensky, 1967)

Plate 6, Figs. 12a, b

[v*] *Gnathodus scotiaensis* Globensky, 1967:441, pl. 58, figs. 2–7, 10, 12 [Pa elements].
[v*?] *Ozarkodina acadiensis* Globensky, 1967:445, pl. 55, figs. 6, 9–11, 14 [Pb elements].
[v] *Neoprioniodus singularis* (Branson and Mehl)—Globensky, 1967:444–5, pl. 55, figs. 23, 24 [M elements].
[v.] *Gnathodus scotiaensis*—von Bitter and Plint-Geberl, 1982:202, pl. 6, figs. 13–15 [Pa elements], fig. 20 [M element].

HOLOTYPE

University of New Brunswick, 64-F-266 (Globensky, 1967, pl. 58, figs. 2, 10).

TYPE HORIZON AND LOCALITY

Windsor Limestone, sample KD12 of Globensky (1967). On the Atlantic coast between the village of Skir Dhu and North Shore, about 330 m SW of Skir Dhu fisherman's wharf, Skir Dhu, Cape Breton Island, Nova Scotia, Canada.

MATERIAL STUDIED

A single Pa element from the lower Lynebank Formation, Lower Border Group, and the specimens from the Codroy Group of Newfoundland, Canada, in the collection of von Bitter and Plint-Geberl (1982).

DESCRIPTION

Pa element. See Globensky (1967:441) under *Gnathodus scotiaensis*.

M element. This element, although identified and figured by von Bitter and Plint-Geberl (1982), has not been described.

DISCUSSION

No diagnosis exists for this species. Only the Pa and M elements are known; *"Ozarkodina acadiensis"* may be the Pb element. These elements resemble the homologous elements of *L. commutata* much more closely than they do *Gnathodus*; Norby (1976:149) suggested that *G. scotiaensis* was probably a "variety or subspecies" of *L. commutata*. Consequently, these elements are assigned to *Lochriea* herein.

The single Pa element recovered from the Northumberland trough differs from the description and the comparatively large figured specimens of Globensky (1967:441, pl. 58, figs. 2–7, 10, 12; holotype is 0.74 mm long) chiefly in the straightness of the upper posterior part of the blade, and in bearing fewer denticles. It is, however, very similar to some specimens from the Codroy Group of SW Newfoundland (von Bitter and Plint-Geberl, 1982). Superficially, some Pa elements of *L. scotiaensis* resemble those of *G.? simplicatus* (Rhodes, Austin, and Druce) but the two species can be easily distinguished by the size of the basal cavity.

***Lochriea* sp. indet.**

Plate 6, Fig. 13

MATERIAL STUDIED

Pb elements, (3); M elements, 10(1); mostly from the Cementstone Group, Akenshaw Burn, but also from the Cambeck Formation, Lower Border Group.

DESCRIPTION

Pb elements. See Higgins (1961:218, 219) and Rhodes, Austin, and Druce (1969:198, 199) under *Subbryantodus subequalis*.

M elements. See Hass (1953:88) and Rhodes, Austin, and Druce (1969:160) under *Prioniodus singularis* and *Neoprioniodus montanaensis* respectively.

DISCUSSION

Rexroad and Horowitz (1990) include a full synonymy for multielement *L. commutata*. Other species of *Lochriea* probably bore nonplatform elements indistinguishable from those of *L. commutata* (Norby, 1976). In the absence of associated Pa elements, the M and incomplete Pb elements from this study can only be assigned to *Lochriea* sp. indet.

Family Unknown

Genus *Vogelgnathus* Norby and Rexroad, 1985

Vogelgnathus Norby and Rexroad, 1985:2.

DIAGNOSIS

See Purnell and von Bitter (1992:316).

TYPE SPECIES

Spathognathodus campbelli Rexroad, 1957, by original designation.

***Vogelgnathus gladiolus* Purnell and von Bitter, 1992**

Plate 7, Figs. 1–8

[v*] *Vogelgnathus gladiolus* Purnell and von Bitter, 1992:320–23, figs. 8.1–8.5 [Pa elements], figs. 8.6, 8.10 [Pb elements], figs. 8.7, 8.9 [M elements], fig. 8.8 [Sb element], fig. 8.11 [Sc element] [with full synonymy].

DIAGNOSIS

See Purnell and von Bitter (1992:320).

HOLOTYPE
Royal Ontario Museum, ROM 48667 (Purnell and von Bitter, 1992, figs. 8.2, 8.4).

TYPE HORIZON AND LOCALITY
Bed 1.8–2.1 m above base of 40 cm shale unit exposed in quarry and waterfall section through Bogside Limestone Member, Bewcastle Formation, Lower Border Group, Ashy Cleugh, Bewcastle, Cumbria, U.K. (G.R. NY 56497700 to NY 56547695). Bed collected as sample 258624.

MATERIAL STUDIED
Pa elements, 127(3); Pb elements, 4; M elements, 7; Sb elements, 10(3); Sc elements, 14(17); almost all from the Bogside Limestone Member of the Bewcastle Formation, but also from the Cambeck Formation, Lower Border Group, and the Cementstone Group in Akenshaw Burn.

DESCRIPTION
See Purnell and von Bitter (1992:320–23).

DISCUSSION
Purnell and von Bitter (1992) include full description and discussion of *V. gladiolus* from the Northumberland trough.

Vogelgnathus kyphus **Purnell and von Bitter, 1992**
Plate 7, Figs. 9, 10, 12

[v*] *Vogelgnathus kyphus* Purnell and von Bitter, 1992:323–25, figs. 10.1–10.6 [Pa elements], fig. 10.7 [Sb element] [with full synonymy].

DIAGNOSIS
See Purnell and von Bitter (1992:323).

HOLOTYPE
Royal Ontario Museum, ROM 48677 (Purnell and von Bitter, 1992, figs. 10.3–10.5).

TYPE HORIZON AND LOCALITY
Bed 2.6–3.0 m above base of Birky Cleugh Limestone Member, Main Algal Formation, Lower Border Group, Birky Cleugh, Bewcastle, Cumbria, U.K. (G.R. NY 58997540 to NY 59017540. Bed collected as sample 88725.

MATERIAL STUDIED
Pa elements, 129(2); Sb elements, 2 (both broken during photography); 1 Sa element and 2 Sc element fragments which may belong to *V. kyphus* were also recovered.

DESCRIPTION
See Purnell and von Bitter (1992:323–25).

DISCUSSION
Purnell and von Bitter (1992) include full description and discussion of *V. kyphus* from the Northumberland trough.

Vogelgnathus pesaquidi **Purnell and von Bitter, 1992**
Plate 7, Fig. 11

[v*] *Vogelgnathus pesaquidi* Purnell and von Bitter, 1992:325–27, figs. 11.1–11.12 [Pa elements], figs. 11.13–11.15 [Pb elements], figs. 12.1–12.3 [M elements], figs. 12.4–12.7 [Sa elements], figs. 12.8, 12.9 [Sb elements], figs. 12.10, 12.11 [Sc elements] [with full synonymy].

DIAGNOSIS
See Purnell and von Bitter (1992:325).

HOLOTYPE
Royal Ontario Museum, ROM 48680 (Purnell and von Bitter, 1992, fig. 11.2).

TYPE HORIZON AND LOCALITY
Beds 2.1–3.7 m above apparent base of Sanford Limestone, Miller Creek Formation, lower Windsor Group, near Windsor, Nova Scotia, Canada.

MATERIAL STUDIED
Pa elements, 23(3); Sc elements, (4); from the Bewcastle, Main Algal, and Cambeck formations, Lower Border Group; the Orroland Lodge and Barlacco Heugh formations, Orroland Group; the Southerness Formation, Cementstone Group; and the Cementstone Group of Akenshaw Burn.

DESCRIPTION
See Purnell and von Bitter (1992:325–27).

DISCUSSION
With the exception of one poorly preserved specimen from the Bewcastle Formation, Pa elements from the Northumberland trough are *V. pesaquidi* morphotype II of Purnell and von Bitter (1992).

Vogelgnathus **cf.** ***pesaquidi***
Plate 8, Fig. 1

MATERIAL STUDIED
Pa elements, 4(1); from the Bewcastle Formation, Lower Border Group.

DESCRIPTION
Apparatus unknown. Pa elements are more elongate and have less laterally compressed denticles and processes than those of *V. pesaquidi*. The basal cavity is shallower and less expanded laterally than morphotype II Pa elements of *V. pesaquidi*. The cavity is lanceolate in outline and in some specimens is not pointed posteriorly.

Order Prioniodinida Sweet, 1988
Family Prioniodinidae Bassler, 1925

Genus *Kladognathus* Rexroad, 1958

[non] *Cladognathus* Burmeister, 1847:364.
Cladognathus Rexroad, 1957:28.
Kladognathus Rexroad, 1958a:19.
Lambdagnathus Rexroad, 1958a:19, 20.
Cladognathodus Rexroad and Collinson, 1961:6.
Magnilaterella Rexroad and Collinson, 1963:11–14.

DIAGNOSIS
(Modified from Rexroad, 1981:11.) Platform elements not developed; M elements dolabrate with prominent anticusp; Sa elements alate; Sb elements bipennate; Sc elements bipennate; Sd elements tertiopedate. The S elements have discrete pointed denticles.

TYPE SPECIES
Cladognathus prima Rexroad, 1957, by original designation.

DISCUSSION
The concept of *Kladognathus* employed herein is based on that of Rexroad (1981), Horowitz and Rexroad (1982), and Rexroad and Horowitz (1990). Apparatus reconstruction is based on the statistical studies of Horowitz and Rexroad (1982), confirming the tentative suggestion of Norby (1976).

Kladognathus tenuis (Branson and Mehl, 1941a)
Plate 8, Figs. 2, 3

[p] *Prioniodus peracutus* Hinde, 1900:343, pl. 10, fig. 22 only [M β element].
Ligonodina tenuis Branson and Mehl, 1941a:170, pl. 5, figs. 13, 14 [Sc α elements].
Prioniodus scitulus Branson and Mehl, 1941a:173–4, pl. 5, figs. 5, 6 [M α elements].
Ligonodina levis Branson and Mehl, 1941b:185, pl. 6, fig. 10 [Sc β element].
Lambdagnathus fragilidens Rexroad, 1958a:19, pl. 6, figs. 10–16 [Sd elements].
Kladognathus tenuis—Rexroad, 1981:13, pl. 2, figs. 19, 21, 24–26 [Sc α elements], fig. 20 [Sc β element].
Kladognathus tenuis—Rexroad and Horowitz, 1990:505–6, pl. 3, figs. 28–30 [M elements], 21–24 [Sa elements], 25–27, 33 [Sb elements], 16–20 [Sc elements], 12–15 [Sd elements] [with full synonymy].

DIAGNOSIS
See Rexroad (1981:13).

HOLOTYPE
University of Missouri, C543-3 (*Ligonodina tenuis* Branson and Mehl, 1941a, pl. 5, fig. 13).

TYPE HORIZON AND LOCALITY
The Caney Shale immediately below the higher of the two conspicuous bands of concretions; steep bank of black fissile shales at the side of State Highway 48, about 6 miles south of Ada, Pontotoc County, Oklahoma, U.S.A.

MATERIAL STUDIED
Sa elements, 1; Sb elements, 1; Sc α elements, 3; indeterminate Sc elements, (4); from the Lower Lynebank and Cambeck formations, Lower Border Group, and the Cementstone Group of Akenshaw Burn.

DESCRIPTION
M elements. See Rhodes, Austin, and Druce (1969:161–3) under *Neoprioniodus peracutus* and *Neoprioniodus scitulus*.
Sa element. See Rexroad (1958a:18) and Rhodes, Austin, and Druce (1969:113) under *Hibbardella milleri* and *Hibbardella (Hibbardella) milleri* respectively.
Sb elements. See Rexroad and Collinson (1963:14–17) under *Magnilaterella robusta*.
Sc α elements. See Branson and Mehl (1941a:170) and Rhodes, Austin, and Druce (1969:138) under *Ligonodina tenuis*, and Rexroad (1957:32) under *L. hamata*.
Sc β elements. See Rhodes, Austin, and Druce (1969:134) under *Ligonodina levis*.
Sd elements. See Rexroad (1958a:19) under *Lambdagnathus fragilidens*.

DISCUSSION
Nicoll and Rexroad (1975) recovered "*Neoprioniodus tulensis* (Pander)," "*Hibbardella abnormis* Branson and Mehl," "*Magnilaterella* sp.," "*Ligonodina magnilaterina*

Rhodes, Austin, and Druce," and "*L. levis* Branson and Mehl" from the Sanders Group of Indiana and Kentucky. Table 1 of Nicoll and Rexroad (1975) shows that these elements co-occur in approximately the same proportions relative to each other, independently of the abundance of other species, in four formations. The elements closely resemble those of Chesterian *K. tenuis* and were probably borne by Meramecian *K. tenuis* or a closely related species. This reconstruction is partly supported by the statistical analysis of Nicoll and Rexroad (1975:15).

Order Unknown
Family Unknown

Genus *"Apatognathus"*

[non] *Apatognathus* Branson and Mehl, 1934a:201.

DISCUSSION

Branson and Mehl (1934a) erected *Apatognathus* as a monotypic genus for sharply arched conodont elements with an apical cusp and two denticulate parallel or slightly divergent processes. Elements with this morphology occur in the Devonian and Lower Carboniferous but are absent from the lowest part of the Carboniferous (Scott and Collinson, 1961; Varker, 1967). The majority of conodont workers have regarded the Carboniferous forms as probable homeomorphs (e.g., Rexroad and Collinson, 1963) or morphic equivalents (Varker, 1967) which should be assigned to a different genus (e.g., Rexroad and Collinson, 1963; Klapper, 1966; Varker, 1967). The Devonian and Carboniferous apatognathid elements almost certainly belonged to markedly different apparatuses (Nicoll, 1980).

Despite the strength of the argument on both stratigraphic and morphological grounds, no genus has been formally erected to receive the Carboniferous species. Sweet (1988:115) "loosely referred" one Carboniferous apatognathid species to *Hindeodus*, but the reasoning behind this decision was not adequately explained. The Carboniferous apatognathid apparatus (see below) does not fit Sweet and Clark's diagnosis of the genus (*in* Robison, 1981) and lacks "the curious extensiform digyrate [Sb] element" that Sweet (1988:116) considered the most diagnostic feature of the apparatus of *Hindeodus*. Sweet (1988) conceded that his interpretation of *Hindeodus* was probably too broad; Carboniferous apatognathids are herein assigned to *"Apatognathus"* with order and family unknown.

Evidence for the apparatus of *"Apatognathus"* comes from a fused cluster (Austin and Rhodes, 1969) and the recurrent association of elements (summarized by von Bitter, Sandberg, and Orchard, 1986:12, table 1). Rexroad and Thompson (1979) suggested that *"Apatognathus" scitulus* bore an apparatus composed of elements previously described as "*Spathognathodus scitulus* (Hinde)," "*Ozarkodina laevipostica* Rexroad and Collinson," "*Apatognathus porcatus* (Hinde)," and "*A. scalenus* Varker." Nicoll (1980) and Dean (1987) believed that the apatognathid elements of this apparatus were represented by elements of *"Apatognathus porcatus"* form and "*Apatognathus geminus* (Hinde)" form. These apparatus reconstructions, and that proposed for *"A." cuspidatus* Varker herein, are different from *Apatognathus varians* Branson and Mehl *sensu* Nicoll (1980), and the element notational scheme of Nicoll (1980) cannot be applied to *"Apatognathus."* The apatognathid elements of *"Apatognathus"* may have formed a symmetry transition series (Rexroad and Thompson, 1979; Sweet, 1988) and the element notation Sa, Sb, and Sc is used to indicate their increasing asymmetry, chiefly in terms of process incurvature (contra Nicoll, 1980; Austin et al. *in* Robison, 1981). This notation implies analogy rather than homology with the elements of other genera. Unlike those of the majority of conodonts, the Pa and Pb elements of *"Apatognathus"* represent the vicariously shared, conservative parts of the apparatus, and it is the S elements that evolved more rapidly. The distributional data, however, suggest that Pb elements were not always developed in the apparatus (see von Bitter, Sandberg, and Orchard, 1986:12).

Rexroad and Thompson (1979) suggested that *"Apatognathus varians,"* "*Hibbardella separata* (Branson and Mehl)," and "*Lonchodina* sp. a" *sensu* Rhodes, Austin, and Druce (1969) may have formed part of the *"Apatognathus"* apparatus. These elements were found by Druce, Rhodes, and Austin (1972) to be statistically associated in the Lower Carboniferous of the North Crop of the South Wales coalfield. However, considering the relative rarity of the "species" in this study (Druce, Rhodes, and Austin, 1972), and the lack of supporting distributional data, it is unlikely that all of these elements were borne by *"Apatognathus."*

N.B. Shortly after final submission of this manuscript, a new genus, *Synclydognathus* Rexroad and Varker, 1992, was erected to accommodate Carboniferous apatognathids.

"Apatognathus" cuspidatus Varker, 1967
Plate 8, Figs. 4–9

[p] *Apatognathus*? *porcata* (Hinde)—Rexroad and Collinson, 1963:8, pl. 1, fig. 8 [?Sc element], figs. 10, 11 [Sb elements] only.

[p?] *Ozarkodina laevipostica* Rexroad and Collinson, 1963:19, pl. 1, figs. 1, 2, 4 only [Pb elements].

[p?] *Spathognathodus scitulus* (Hinde)— Rexroad and Collinson, 1963:20, pl. 2, figs. 14, 31 only [Pa elements].

[p] *Apatognathus*? *porcata*—Globensky, 1967:438, pl. 56, fig. 24 only [Sa element].

Apatognathus? *cuspidata* Varker, 1967:131, pl. 17, figs. 4, 6–8, 10 [Sb elements].

Apatognathus? *librata* Varker, 1967:134, pl. 18, figs. 3, 6, 8, 9, 12, 13 [Sa elements].

Apatognathus? *petila* Varker, 1967:135, pl. 17, fig. 11; pl. 18, figs. 7, 10, 11 [Sc elements].

[(?)] *Apatognathus porcata*—Thompson and Goebel, 1969:21, pl. 2, fig. 1 [Sb element]; pl. 4, fig. 23 [Sc element].

Apatognathus petilus—Rhodes, Austin, and Druce, 1969:72, pl. 20, figs. 12–14, 17 [Sc elements].

Apatognathus cf. *libratus*—Rhodes, Austin, and Druce, 1969:75, pl. 20, fig. 8 [Sa element].

[p?] *Spathognathodus scitulus*—Rhodes, Austin, and Druce, 1969:232, pl. 8, fig. 10 only [Pa element].

[(?)] *Apatognathus*? *cuspidatus*— Reynolds, 1970:7, pl. 3, fig. 4 [Sb element].

[(?)] *Apatognathus*? *libratus*— Reynolds, 1970:7, pl. 3, fig. 9 [Sa element].

Apatognathus? *petilus*—Reynolds, 1970:7, pl. 3, fig. 5 [Sc element].

Apatognathus scalenus Varker—Austin and Aldridge, 1973, pl. 2, fig. 6 [Sc element].

Apatognathus petilus—Austin and Aldridge, 1973, pl. 2, fig. 9 [Sa element].

Apatognathus cuspidatus—Austin and Husri, 1974, pl. 10, figs. 8(?), 15 only [Sb elements].

[(?)] *Apatognathus libratus*—Austin and Husri, 1974, pl. 10, fig. 6 [?Sc element].

[(?)] *Apatognathus minutus* Austin and Husri, 1974:51, pl. 10, figs. 1, 2, 5, 9 [Pb elements?].

Apatognathus petilus—Austin and Husri, 1974, pl. 10, fig. 7 [Sc element].

Spathognathodus scitulus—Austin and Husri, 1974, pl. 7, fig. 10; pl. 8, fig. 6? [Pa elements].

[(?)] *Apatognathus cuspidatus*—Metcalfe, 1980:299, pl. 37, fig. 1 [Sb element?].

Apatognathus libratus—Metcalfe, 1980:300, pl. 37, fig. 4 [Sa element].

Spathognathodus scitulus—Metcalfe, 1980, pl. 38, fig. 7 [Pa element].

[p(?)] *Apatognathus libratus*—Metcalfe, 1981, pl. 13, fig. 1 only [Sa element].

[p] *Apatognathus petilus*—Metcalfe, 1981, pl. 13, figs. 4, 5 [Sc elements], 7 [Sc element?] only.

Apatognathus cuspidatus—Metcalfe, 1981, pl. 13, figs. 8 [Sb element], 9 [Sb element?].

Apatognathus sp. Metcalfe, 1981, pl. 13, fig. 10 [Sc element].

Prioniodina laevipostica—Metcalfe, 1981, pl. 19, fig. 1 [Pb element].

[v.] *Apatognathus cuspidatus*—Higgins and Varker, 1982, pl. 19, figs. 11, 13, 19 [Sb elements].

[v?] *Apatognathus libratus*—Higgins and Varker, 1982:157, pl. 19, fig. 12 [Sa element].

[v?] *Spathognathodus scitulus*—Higgins and Varker, 1982: 164, 165, pl. 19, fig. 14 [Pa element].

Apatognathus libratus—Austin and Davies, 1984, pl. 3, fig. 19 [Sb element].

[(?)] *Apatognathus petilus*—Austin and Davies, 1984, pl. 3, fig. 20 [Sc element?].

[p] *Spathognathodus scitulus*—Austin and Davies, 1984, pl. 3, fig. 18 only [Pa element].

'*Apatognathus*' *cuspidatus*—Varker and Sevastopulo, 1985:196, pl. 5.4, figs. 1, 2 [Sb elements] [fig. 2 cop. Varker, 1967, pl. 17, fig. 8].

'*Apatognathus*' *petilus*—Varker and Sevastopulo, 1985:198, pl. 5.4, figs. 3–5 [Sc elements] [figs. 4, 5 cop. Varker, 1967, pl. 18, fig. 10; pl. 17, fig. 11].

'*Apatognathus*' *libratus*—Varker and Sevastopulo, 1985:198, pl. 5.4, figs. 8–11 [Sa elements] [cop. Varker, 1967, pl. 18, figs. 6, 8, 12, 13].

[v.] '*Apatognathus*' *cuspidatus*—Armstrong and Purnell, 1987, pl. 1, fig. 1 [Sb element].

[v.] '*Apatognathus*' aff. *libratus*—Armstrong and Purnell, 1987, pl. 1, fig. 4 [Sa element].

[v.] '*Apatognathus*' *scandalensis* Higgins and Varker—Armstrong and Purnell, 1987, pl. 1, fig. 3 [Sa element].

REVISED DIAGNOSIS

Apparatus at least quinquemembrate: Pa elements carminiscaphate with large triangular anterior denticle; Pb elements angulate; Sa elements alate (lacking posterior process), symmetrical, apatognathid with recurved apical cusp; Sb elements bipennate, apatognathid with large incurved reclined cusp and incurved reclined anterior process denticles; Sc elements bipennate, apatognathid with incurved reclined cusp and strongly incurved anterior process.

HOLOTYPE

University of Sheffield, Department of Geology, 28(6) BB205 (Varker, 1967, pl. 17, fig. 7).

TYPE HORIZON AND LOCALITY

Great Limestone, Borrowdale Beck, Stainmore, Cumbria, U.K. (G.R. NY 834160).

MATERIAL STUDIED

Pa elements, 7(3); Pb elements, 1(1); Sa elements, 8(1); Sb elements, 7(3); Sc elements, 4(4); from the Bogside Limestone Member, Bewcastle Formation, and the Lynebank Formation, Lower Border Group.

DESCRIPTION

Pa elements. See Clarke (1960:21) and Rhodes, Austin, and Druce (1969:232) under *Spathognathodus scitulus.*
Pb elements. See Rexroad and Collinson (1963:19) under *Ozarkodina laevipostica,* and Rhodes, Austin, and Druce (1969:195) under *Prioniodina laevipostica.*
Sa elements. See Varker (1967:134) under *Apatognathus*? *librata.* Note differences in orientation terminology if elements are considered to be alate.
Sb elements. See Varker (1967:131) under *Apatognathus*? *cuspidata.*
Sc elements. See Varker (1967:135) under *Apatognathus*? *petila.*

DISCUSSION

The apparatus of *"A." cuspidatus* was reconstructed on the evidence of association of elements in samples 108768 and 108769 from the Lynebank Formation, Lower Border Group, and on the association of elements in previous studies. Because of the vicarious sharing of Pa and Pb elements between *"Apatognathus"* species, *"A." cuspidatus* is the oldest available name for this species.

The range charts and element abundances of Varker (1967), Davies (1980), and Dean (1987) suggest that elements of "*A. scalenus* Varker" form may sometimes have been present in the apparatus of *"A." cuspidatus,* possibly representing the M elements. No elements of this form were found in this study.

"Apatognathus" sp. a

MATERIAL STUDIED

Sb elements, 1(1); Sc elements, 2; from the Cambeck Formation, the Bogside Limestone Member, Bewcastle Formation, and the Lynebank Formation, Lower Border Group.

DESCRIPTION

Sb elements. See Higgins and Varker (1982:158) under *Apatognathus scandalensis.*
Sc elements. See Higgins and Varker (1982:157) under *Apatognathus asymmetricus.*

DISCUSSION

The partial reconstruction of this species is based on the limited evidence of association in this study and the concurrent ranges of the elements in Ravenstonedale, Cumbria (Higgins and Varker, 1982). This reconstruction is tentative and the species is placed in open nomenclature.

"Apatognathus" sp. indet.

Plate 8, Fig. 10

MATERIAL STUDIED

Pa elements, 3(3); from the Cambeck, Main Algal, and Lynebank Formations, Lower Border Group, and the Barlacco Heugh Formation, Orroland Group.

DESCRIPTION

Pa elements. See Clarke (1960:21) and Rhodes, Austin, and Druce (1969:232) under *Spathognathodus scitulus.*

DISCUSSION

Because of the vicarious sharing of Pa elements in *"Apatognathus,"* Pa elements that are not associated with identifiable S elements cannot be specifically assigned. Some of these elements (e.g., Pl. 8, Fig. 10) have greater posterior extension of the basal cavity than typical *"Apatognathus"* Pa elements.

Genus Indeterminate

Gen. a sp. a

Plate 8, Figs. 11, 12

MATERIAL STUDIED

Pa elements, 4(2); M elements, 1; from the Bewcastle and Cambeck formations, Lower Border Group.

DESCRIPTION

Pa elements. Pa elements are carminate, laterally compressed, and bladelike with slight arching and lateral curvature. The only complete specimen bears 14 denticles including a minor anterior "piggy-back denticle," but the broken specimens suggest that more may be developed. The denticles are laterally compressed and elongate, fused apart from their tips. They are rather bluntly pointed in the two larger specimens recovered (including Pl. 8, Fig. 11), more sharply so in smaller specimens. Apart from the minor denticle, the denticles are highest at the anterior end, decreasing in height towards the inconspicuous cusp, increasing slightly over the basal cavity then declining to the posterior end. The anterior termination of the element is straight and almost vertical with an anterobasal angle of approximately 70° to 80°. The basal cavity is elongate and subsymmetrical, the outer lip slightly more flared than the inner. It is widest and deepest just posterior of midlength, tapering gradually to the anterior and posterior, and bears a medial groove. The cavity extends to the posterior end of the element as a groove, but does not reach the posterior tip. White matter is present through the length of the four or five denticles over the basal cavity but is absent from the others.

M elements. The single M element recovered is dolabrate with a long recurved cusp, the tip of which is missing. The anterobasal corner is also broken and the element may have possessed a short anticusp. The large symmetrical basal cavity occupies the whole of the lower surface of the element. It is sharply elliptical in outline, deepest and widest under the posterior margin of the cusp, and bears a medial groove. The upper posterior surface of the cavity is continuous with the posterior margin of the cusp and bears three broken reclined denticles forming the posterior process.

DISCUSSION

The generic assignment of Lower Carboniferous species that bore a simple carminate Pa element is problematic (see Rexroad and Thompson, 1979; Norby and Rexroad, 1985, for discussion). Pa elements similar to those described above but stratigraphically older were tentatively given the generic name *Synprioniodina* Bassler by Rexroad and Thompson (1979) on the basis of probable M element morphology. The probable M element of this species, however, is not of *"Synprioniodina"* form. When the apparatuses containing Pa elements of this type have been reconstructed, new generic names will be required, as was the case with *Vogelgnathus* Norby and Rexroad. Consequently open nomenclature has been used in preference to an obsolete or inappropriate name.

Pa elements of Gen. a sp. a were found in association with *Cavusgnathus unicornis*, *Vogelgnathus gladiolus*, and *V. pesaquidi*, none of which have M elements like that described above. The M element probably belongs to Gen. a sp. a.

ACKNOWLEDGMENTS

This research was undertaken as part of a NERC funded Ph.D. project at the University of Newcastle upon Tyne. I am indebted to Dr. Howard Armstrong (now at the University of Durham) for his supervision of all conodont-related areas of this project, and particularly for lengthy discussions regarding problems of conodont taxonomy. Dr. R. J. Aldridge (University of Leicester), Dr. R. L. Ethington (University of Missouri-Columbia), Dr. N. J. Riley (BGS Keyworth), Dr. J. E. Whittaker (British Museum (Natural History)), and Dr. P. H. von Bitter (Royal Ontario Museum) are thanked for access to and/or loan of material in their care. The assistance provided by Peter von Bitter and Joan Burke (Royal Ontario Museum) is also gratefully acknowledged. Dr. G. K. Merrill and Dr. C. A. Sandberg are thanked for their reviews of the manuscript. The manuscript was completed during tenure of a Leverhulme Trust Study Abroad Studentship at the Royal Ontario Museum.

Appendices

APPENDIX I: LOCALITY DETAILS

1. Whitton Glebe Farm. Five metres of Glebe Limestone Member exposed in disused quarry. Grid reference: NU 051005. References: Garwood, 1931; Fowler, 1936.

2. Birky Hill. Birky Hill Limestone Member. No *in situ* exposure, loose blocks on site of old workings. Grid reference: NZ 048991. References: Garwood, 1931.

3. Allerdene. Old workings south of Allerdene Farm. No *in situ* exposure, loose blocks of Glebe Limestone Member. Grid reference: NU 025009. References: Fowler, 1936.

4. Snitter Mill. Patchy exposure of Cementstone Group in stream. Grid reference: NU 03130296. References: Fowler, 1936.

5. Snitter. Patchy exposure of Cementstone Group in Back Burn. Grid reference: NU 03050358. References: Fowler, 1936.

6. Alwinton. Barrow Scar, Alwinton Gorge on the River Coquet. Approximately 50 m of Cementstone Group exposed. Samples taken from south side of gorge. Grid reference: NT 904062. References: Westoll, Robson, and Green, 1955.

7. Chattlehope Burn. Patchy exposure through upper Cementstone Group. Grid reference: NT 720020. References: Cater, Briggs, and Clarkson, 1989.

8. Kielder Burn. Very poor exposure of Cementstone Group in banks of burn. Grid reference: NY 636938. References: Fowler, 1936.

9. Akenshaw Burn. Faulted and folded exposure through approximately 80 m of upper Cementstone Group. Grid reference: NY 605895-611897. References: Fowler, 1936.

10. Ashy Cleugh. Section through almost all of the Bewcastle Formation, Lower Border Group (locality 25 of Leeder, 1974b). Grid reference: NY 56497700-58087665. References: Day, 1970; Leeder, 1974b.

11. Antonstown Burn. Section through 7 m of Bogside Limestone Member, Bewcastle Formation, Lower Border Group. Grid reference: NY 56577739. References: Day, 1970.

12. Birky Cleugh. Section through uppermost Bewcastle Formation, whole of Main Algal Formation, and Lower Antiquatonia Member of Cambeck Formation, Lower Border Group (locality 33 of Leeder, 1974b). Grid reference: NY 58857540-59437542. References: Day, 1970; Leeder, 1974b.

13. Whitberry Burn. Section through all but the lower part of Cambeck Formation, Lower Border Group. Grid reference: NY 52207403-52027407. References: Day, 1970.

14. Ellery Sike. Section through lower Lynebank Formation, Lower Border Group (locality 21 of Leeder, 1974b). Grid reference: NY 54337584-54507575. References: Day, 1970; Leeder, 1974b.

15. Bothrigg Burn. Section through lower Lynebank Formation, Lower Border Group (locality 22 of Leeder, 1974b). Grid reference: NY 54587591-54807598. References: Day, 1970; Leeder, 1974b.

16. River Black Lyne SE of Holmhead Farm. a) Common Flat Limestone Member, Lynebank Formation. b) Section through upper Lynebank Formation and Bogside Limestone Member, Bewcastle Formation, Lower Border Group. Grid references: a) NY 54377851; b) NY 54167822-54117821. References: Day, 1970.

17. Harden Burn. Patchy exposure through Liddel Formation, Lower Border Group, and Harden Member, Middle Border Group (locality 15 of Leeder, 1974b). Grid reference: NY 51709070-52149015. References: Leeder, 1974b.

18. Black Burn. Patchy exposure through possible Arnton Fell Formation?, Lower Border Group (locality 11 of Leeder, 1972, 1974b). Grid reference: NY 47878880-48768869. References: Leeder, 1972, 1974b.

19. Black Burn. Folded and faulted section through Black Burn Formation, Lower Border Group, and Harden Member, Middle Border Group (localities 7, 8, and 9 of Leeder, 1974b). References: Leeder, 1974b.

20. Black Pool, Tweeden Burn. Uppermost exposed limestone of the Liddel Formation, Lower Border Group (part of locality 18 of Leeder, 1974b). Grid reference: NY 48968643. References: Leeder, 1974b.

21. Ettleton Sike. Section through lower Arnton Fell Formation, Lower Border Group (locality 12 of Leeder, 1974b). Grid reference: NY 47108640. References: Leeder, 1974b.

22. West of Drum, near Kirkbean. Basal Cementstone Formation, Cementstone Group; patchy exposure in stream. Grid reference: NX 976612. References: Craig, 1956.

23. South of Brickhouse near Kirkbean. Basal Cementstone Formation, Cementstone Group; patchy exposure in stream. Grid reference: NX 979601. References: Craig, 1956.

24. Southerness Lighthouse. Basal beds of Gillfoot Formation, Cementstone Group. Grid reference: NX 978542. References: Craig, 1956.

25. Southerness Foreshore. Folded section through whole of Southerness Formation, Cementstone Group. Grid reference: NX 971521. References: Craig, 1956.

26. Portling outlier. Conglomerates, sandstone, and shales of Cementstone Group. Grid reference: NX 882535. References: Deegan, 1973.

27. Rerrick outlier, below Orroland. Section through Orroland Lodge and Barlacco Heugh formations, Orroland Group. Grid reference: NX 778463. References: Deegan, 1973.

APPENDIX II: CONODONT ELEMENTS RECOVERED

Group	Formation	Member	Locality	Sample number	Mass processed	Processing number	*"Apatognathus" sp.* Pa	*"Apatognathus" cuspidatus* Pa	*"Apatognathus" cuspidatus* Pb	*"Apatognathus" cuspidatus* Sa	*"Apatognathus" cuspidatus* Sb	*"Apatognathus" cuspidatus* Sc	*"Apatognathus" sp. a* Sc	*"Apatognathus" sp. a* Sb	*"Apatognathus" sp.* frags.	*Cavusgnathus hudsoni* Pa α	*Cavusgnathus hudsoni* Pa β	*Cavusgnathus hudsoni* Pa γ	*Cavusgnathus hudsoni* Pa int.	*Cavusgnathus hudsoni* Pa ind.	*Cavusgnathus hudsoni* Pb	*Cavusgnathus hudsoni* M	*Cavusgnathus hudsoni* Sa	*Cavusgnathus hudsoni* Sb	*Cavusgnathus hudsoni* Sc	*Cavusgnathus hudsoni* S	*Cavusgnathus sp.* Pa	*Cavusgnathus sp.* Pb	*Cavusgnathus sp.* S	*Clydagnathus windsorensis* Pa	*Clydagnathus windsorensis* Pb	*Clydagnathus windsorensis* M	*Clydagnathus windsorensis* Sa	*Clydagnathus windsorensis* Sb	*Clydagnathus windsorensis* Sc	*Clydagnathus windsorensis* S
Lower Border	Bewcastle	Bogside Ls	11	88712	1.37	1417	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls.	11	88711	1 37	1416	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	11	88710	1.33	1415	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls.	11	88709	1 35	1414	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls.	11	88708	1 29	1413	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	11	88707	1.36	1412	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	11	88706	1 36	1408	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	11	88705	1 32	1407	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	16b	108791	1 20	1449	—	1	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	16b	108790	1 32	1448	—	—	—	1(1)	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls.	16b	108789	1 36	1447	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	16b	108788	1 12	1446	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	16b	108787	1 31	1445	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	16b	108786	1 26	1444	—	2	—	—	(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	16b	108785	1 21	1443	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	16b	108784	0 82	1442	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	16b	108783	1 38	1441	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	16b	108782	1.38	1440	—	2	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	16b	108781	1 39	1439	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	16b	108780	1.18	1438	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	16b	108779	1 42	1437	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	16b	108778	1 42	1436	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls.	16b	108777	1 40	1435	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	16b	108776	1 45	1434	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	16b	108775	1 43	1433	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	U Lynebank	—	16b	108774	1 36	1432	—	—	—	—	(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	U Lynebank	—	16b	108773	1 33	1431	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	U Lynebank	—	16b	108770	1 12	1519(UF)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	U Lynebank	—	16b	108769	1 34	1518	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	U Lynebank	—	16b	108768	1 33	1517	—	2	—	6	6(1)	2(3)	1	1	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	U Lynebank	—	16b	108767	1 22	1516	—	4(1)	1	1	—	2	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	M Lynebank	Common Flat Ls	16a	108794	1 32	1460	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	L Lynebank	Rawney Ls	15	108729	1 39	1496	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	L Lynebank	—	15	108724	1 42	1495	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	L Lynebank	—	15	108722	0 67	1494	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	L Lynebank	—	15	108719	1 49	1493	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	L Lynebank	—	15	108714	1.38	1492	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	L Lynebank	—	15	108712	1 06	1491	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	L Lynebank	—	14	88768	1 27	1484	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	L Lynebank	—	14	88763	1 45	1483	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	L Lynebank	Ellery Sike Ls	14	88761	1 11	1426	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	L Lynebank	Ellery Sike Ls	14	88760	1 04	1425	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	L Lynebank	Ellery Sike Ls	14	88759	1 39	1424	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	L Lynebank	Ellery Sike Ls	14	88758	1 38	1423	—	—	—	—	—	(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10(2)	(5)	—	—	1	8	(7)
Lower Border	L Lynebank	Ellery Sike Ls	14	88757	1 42	1422	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	2	2	2	(1)	(2)	(8)
Lower Border	L Lynebank	Ellery Sike Ls	14	88756	1 32	1421	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6(1)	13(1)	6	1	6	4(4)	(16)
Lower Border	L Lynebank	Ellery Sike Ls	14	88755	1 44	1482(UF)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	L Lynebank	—	14	88754	1 35	1481	—	—	—	—	—	—	—	—	—	12	2	—	—	(2)	8	7	(1)	1	2	17	(1)	—	—	—	—	—	—	—	—	—
Lower Border	L Lynebank	—	14	88751	1 23	1420	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1(1)	—	—	—	—	—	—
Lower Border	L Lynebank	—	14	88750	1 34	1419	—	—	(1)	—	—	—	—	—	1	2	—	—	—	—	—	—	—	—	—	—	—	(1)	—	—	—	—	—	—	—	—
Lower Border	L Lynebank	—	14	88748	1 20	1418	—	—	—	—	—	—	—	—	—	(1)	1	—	1	—	—	—	—	—	—	—	(1)	—	(2)	—	—	—	—	—	—	—

APPENDIX IIa. Conodont elements recovered from the Lynebank Formation and the Bogside Limestone Member, Bewcastle Formation, localities 11, 14–16. UF residue not completely picked; ˆ juvenile elements; † juvenile cavusgnathid; ¢ cavusgnathid; * includes 9 immature elements; r rare.

Kladognathus tenuis Sa	*Kladognathus tenuis* Sb	*Kladognathus tenuis* Sc	*Kladognathus tenuis* Sc α	*Lochriea scotiaensis* Pa	*Mestognathus praebeckmanni* Pa	*M. praebeck.-beck.* intermediate Pa	*Mestognathus beckmanni* Pa	*Mestognathus* sp. Pa	*Patrognathus capricornis* Pa	*Patrognathus capricornis* M	*Patrognathus capricornis* Sc	*Patrognathus* sp. (juvenile) Pa	*Polygnathus bischoffi* Pa	*Polygnathus bischoffi* M	*Polygnathus* sp. Pb	*Polygnathus* sp. Sc	*Polygnathus* sp. S	*Taphrognathus carinatus* Pa	*Taphrognathus varians* Pa I	*Taphrognathus varians* Pa II	*Taphrognathus varians* Pa III	*Taphrognathus varians* Pa ind.	*Taphrognathus varians* Pb	*Taphrognathus varians* M	*Taphrognathus varians* Sa	*Taphrognathus varians* Sb	*Taphrognathus varians* Sc	*Taphrognathus varians* S	*Vogelgnathus gladiolus* Pa	*Vogelgnathus gladiolus* M	*Vogelgnathus gladiolus* Sc	*Vogelgnathus gladiolus* S	*Vogelgnathus pesaquidi* Pa	Genus indeterminate Pa	Genus indeterminate Pb	Genus indeterminate Sc	S fragments	Indeterminate fragments	Fish teeth	Ostracodes
—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—
—	—	—	—	—	—	—	—	—	—	(1)	—	—	—	—	—	—	—	—	—	1	4	—	1	3	—	—	—	(12)	1	1	—	(1)	—	—	—	1	—	—	●	●
—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	9	8	(2)	—	—	—	—	—	—	—	—	—	—	—	—	—	8	6	●	●
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1(1)	—	1	—	—	—	(4)	—	—	—	—	—	—	—	—	—	—	—	●	●
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	2(1)	26	10(9)	(4)	3	(1)	(1)	—	—	—	—	—	—	—	—	—	1	50	44	●	●
—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	4	—	—	1(1)	—	—	—	(6)	—	—	—	—	—	—	—	—	—	9	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	(1)	—	1	—	—	—	(5)	—	—	—	—	—	—	—	—	—	4	●	—
—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	2	(5)	—	—	1	—	—	—	—	—	—	—	(1)	—	—	—	—	5	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	(1)c	—	—	—	10	●	●
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	1	3	2	1	2(1)	2	(11)	—	—	—	—	—	—	—	—	—	6	—	●
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	●	●
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1(1)	1(1)	—	(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	2	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1(4)	2	(1)	—	—	(3)	—	—	—	—	—	—	—	—	—	—	14	●	●
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3(6)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	18	●	●
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(1)	—	(1)	(4)	—	—	—	—	(3)	—	—	—	—	—	—	(1)	—	—	—	4	●	●
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	r	●
—	—	—	—	—	—	—	—	(1)	—	(1)	—	—	—	—	—	—	—	—	—	1	4(1)	2(3)	(1)	—	1(1)	—	(6)	—	—	—	—	—	—	—	—	—	13	2	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	r	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3(8)	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	●	●
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	●	—
—	—	—	—	—	—	1	—	—	1	1	(3)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	r	—
—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	r
—	—	—	—	—	—	—	—	(1)	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	(9)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	7	r	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1(1)	1	2(2)	(4)	2	—	—	1	(1)	(15)	—	—	—	—	—	—	—	—	—	5	●	●
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12(1)	(4)	—	—	—	—	(1)	—	—	—	—	—	—	—	—	—	—	17	●	●
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4(1)	6(9)	1	—	2	—	1	—	—	—	—	—	—	—	—	—	11	25	●	●
—	—	—	—	—	—	—	—	—	—	—	—	(1)^	—	—	—	—	—	—	—	4	3	1^(1)	3	(2)	—	2	2	(5)	—	—	—	—	—	—	—	—	—	12	●	●
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1(1)	—	2	—	—	—	—	—	—	—	●	●
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	2(2)	2^(2)	(2)	—	3	—	—	—	—	—	—	—	—	—	—	—	15	10	●	●
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(1)	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	(1)	(1)	—	—	2(1)	—	—	—	—	—	—	—	—	—	4	—	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	—	—	—	—	—	(1)	—	—	—	—	—	—	—	—	—	2	—	●
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1(1)	(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	●
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—
—	—	—	—	—	3	—	—	19*(4)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1(1)	—	(5)	—	2	●	r
—	—	—	—	1	1	—	—	(1)	—	—	—	—	—	—	—	—	—	—	—	(1)	1	—	—	—	—	—	—	—	—	—	—	—	—	—	(1)	—	3	1	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	(1)	—	—	—	—	—	—	—	—	—	—	—	—	1†(1)	—	—	1	5	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	8	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(1)	—	2	r	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1	1	(3)	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	●	●
—	—	—	—	—	2(1)	1	—	2(1)	—	—	—	—	14(6)	(1)	(1)	—	(8)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	10	●	●
—	—	(1)	1	—	3(1)	1	—	1(1)	—	—	—	—	14	1	—	(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(5)	1	(1)	—	8	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	●

Group	Formation	Member	Locality	Sample number	Mass processed	Processing number	*"Apatognathus" cuspidatus* Pa	*"Apatognathus" cuspidatus* Sb	*M. praebeck.-beck.* intermediate Pa	*Mestognathus beckmanni* Pa	*Mestognathus beckmanni* Pb	*Mestognathus* sp. Pa	*Patrognathus capricornis* Pa	*Patrognathus capricornis* Pb	*Patrognathus capricornis* M	*Patrognathus capricornis* Sb	*Patrognathus capricornis* Sc	*Patrognathus capricornis* S	*Patrognathus* sp. (juvenile) Pa	*Patrognathus* sp. Pa
Lower Border	Bewcastle	Bogside Ls.	10	1768640	1.30	1147	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls.	10	1768639	1.29	1146	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls.	10	1768638	1.25	1145	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls.	10	1768637	1.19	1144	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls.	10	1768636	1.23	1143	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls.	10	1768635	1.40	1142	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls.	10	1768634	1.29	1141	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls.	10	1768633	1.35	1140	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls.	10	1768632	1.40	1139	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	10	1768631	1.37	1138	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls.	10	1768630	1.37	1137	—	—	1	1	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls.	10	*	1.00	1344	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls.	10	258629	1.28	1057	—	—	—	(1)	1	—	—	—	1	—	(3)	—	—	(1)
Lower Border	Bewcastle	Bogside Ls.	10	*	1.21	1343	—	—	—	—	—	—	—	—	1(1)	—	(1)	—	—	—
Lower Border	Bewcastle	Bogside Ls	10	258628	1.15	1056	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	10	258627	1.15	1055	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	10	258626	1.20	1054	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls.	10	258625	1.30	1053	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls.	10	258624	1.36	1052	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls.	10	258623	1.37	1051	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	10	258622	1.34	1050	—	—	—	—	—	—	—	—	—	—	—	—	1	—
Lower Border	Bewcastle	Bogside Ls	10	*	1.90	1271-5	—	—	—	—	—	—	—	—	—	—	—	(1)	—	—
Lower Border	Bewcastle	Bogside Ls.	10	258621	1.25	1049	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	10	258620	1.29	1048	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls.	10	14118519	0.34	947	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls.	10	14118518	0.38	945	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	10	14118517	1.21	944	—	—	—	1(1)	—	(1)	—	1	1	—	5	—	—	—
Lower Border	Bewcastle	Bogside Ls	10	*	1.93	1266-70	—	—	—	3(1)	—	2	—	1	1(1)	—	(4)	—	1	—
Lower Border	Bewcastle	Bogside Ls	10	14118516	1.10	943	—	—	(1)	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	10	14118515	1.29	942	—	—	—	—	—	—	2	—	—	—	(1)	(1)	—	—
Lower Border	Bewcastle	Bogside Ls	10	14118514	0.35	946	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	10	14118513	1.24	941	—	1	1	—	—	—	2	1(1)	2	—	(3)	(1)	6(1)	2(1)
Lower Border	Bewcastle	Bogside Ls	10	14118512	1.20	940	—	—	—	—	—	(1)	2	—	1(1)	—	(2)	(2)	1(1)	—
Lower Border	Bewcastle	Bogside Ls	10	14118511	1.23	939	—	—	—	—	—	—	1	1	—	—	(2)	—	—	—
Lower Border	Bewcastle	Bogside Ls	10	14118510	1.22	938	1	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	10	1411859	1.25	937	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	10	1411858	1.12	936	—	—	—	—	—	—	2	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	10	1411857	1.24	935	—	—	—	—	—	—	1(1)	1	—	—	—	—	1	—
Lower Border	Bewcastle	Bogside Ls	10	1411856	1.17	934	—	—	—	—	—	—	—	—	1	(1)	(2)	—	3	1
Lower Border	Bewcastle	Bogside Ls	10	1411855	1.16	933	—	—	—	—	—	—	—	—	—	—	—	—	2	—
Lower Border	Bewcastle	Bogside Ls	10	1411854	1.16	932	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	10	1411853	1.33	931	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	10	1411852	1.19	930	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Bogside Ls	10	1411851	1.19	929	—	—	—	—	—	—	—	—	—	—	—	—	—	—

APPENDIX IIb. Conodont elements recovered from the Bogside Limestone Member, Bewcastle Formation, locality 10.

Taphrognathus carinatus Pa	*Taphrognathus varians* Pa I	*Taphrognathus varians* Pa II	*Taphrognathus varians* Pa III	*Taphrognathus varians* Pa ind.	*Taphrognathus varians* Pb	*Taphrognathus varians* M	*Taphrognathus varians* Sa	*Taphrognathus varians* Sb	*Taphrognathus varians* Sc	*Taphrognathus varians* S	*Taphrognathus? transatlanticus?* Pa	*Vogelgnathus gladiolus* Pa	*Vogelgnathus gladiolus* Pb	*Vogelgnathus gladiolus* M	*Vogelgnathus gladiolus* Sb	*Vogelgnathus gladiolus* Sc	*Vogelgnathus gladiolus* S	Genus indeterminate Pb	Genus indeterminate M	Genus indeterminate Sa	Genus indeterminate Sc	S fragments	Indeterminate fragments	Fish teeth	Ostracodes
—	—	—	—	—	—	—	—	—	(2)	—	—	3	—	—	—	—	(1)	—	—	—	—	—	—	●	—
—	—	—	6	(3)	—	2	—	—	(8)	—	—	11	—	—	1	(1)	—	—	—	—	—	—	1	●	—
—	—	—	2	(3)	(2)	—	—	—	—	—	—	(1)	—	—	—	—	—	—	—	—	—	1	—	●	—
—	—	1	4(1)	—	—	1	—	—	(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	r
—	—	—	3	2(2)	—	4	(2)	—	(7)	—	—	3	—	—	—	(1)	—	—	—	—	—	8	—	●	—
—	—	—	3	—	—	1	1	—	(7)	(1)	—	3	1	1	—	3	—	—	—	—	—	—	1	●	r
—	—	1	2	—	1(1)	—	—	—	(4)	—	—	1	—	—	1	—	—	—	—	—	—	—	—	●	—
—	—	—	4	(2)	(1)	1	—	—	(6)	—	—	1	—	—	—	—	—	—	—	—	—	—	1	●	—
—	—	3	6(2)	(4)	(2)	—	—	—	(1)	—	—	—	—	—	—	—	—	—	—	—	(1)	—	4	●	—
—	—	1	7(1)	(3)	—	2	—	—	(6)	—	—	—	—	—	—	—	—	—	—	—	—	1	3	●	—
—	—	—	2	—	2(2)	3	(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	4	●	—
—	—	—	1	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	(2)	—	—	●	—
—	—	—	5	(1)	(2)	—	(1)	—	(3)	—	—	1	—	—	1	—	—	—	(1)	—	1(10)	—	4	●	—
—	—	—	3(1)	—	1(1)	—	—	—	(3)	—	—	1	—	—	—	—	—	—	—	—	—	4	2	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—
—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	●	—
—	—	—	2(1)	—	1	1	—	—	(4)	—	—	10	—	—	—	—	1	—	—	—	—	—	—	●	●
—	—	—	2	(6)	(1)	—	—	—	—	—	—	4	—	—	—	—	(4)	—	—	—	—	2	7	●	—
—	—	—	1	—	—	—	—	—	—	—	—	5	—	—	1	(3)	(3)	—	—	—	—	—	—	●	—
—	—	1	—	3	—	(1)	—	—	—	—	—	34	1	2	1(3)	5(3)		—	—	—	—	2	2	●	—
—	—	—	2(2)	—	(1)	—	—	—	—	—	1	30	1	3	2	(3)	(1)	—	—	—	—	2	1	●	—
—	—	11(1)	21(4)	(14)	—	—	—	—	—	(14)	—	—	—	—	1	—	(2)	—	—	—	—	—	14	●	—
1	1	—	14(2)	1(12)	7	3	—	3	2(10)	—	—	1	—	—	—	1	—	—	—	—	—	28	16	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	?
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●
—	—	—	—	—	1	2	—	—	(2)	—	—	6(1)	1	—	—	2(3)	(1)	—	—	—	1(2)	6	1	●	—
—	—	—	(1)	—	—	—	—	—	—	—	—	4	—	—	1	—	—	—	—	—	(14)	—	1	●	—
—	—	—	—	—	—	1	—	—	—	—	—	1	—	—	—	—	—	(2)	—	(1)	(1)	2	—	●	—
—	—	—	1	—	—	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	(1)	2	2	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●
—	—	—	1	(1)	—	—	1	(1)	(1)	—	—	—	—	—	—	(1)	—	—	—	(2)	(9)	12	13	●	●
—	—	—	—	1(1)	—	—	(1)	—	(3)	(1)	—	—	—	—	—	—	—	—	—	(1)	(3)	10	9	●	●
—	—	—	—	—	—	2(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1	●	●
—	—	—	3	—	—	(1)	—	—	1(1)	—	—	—	—	—	—	—	—	—	—	—	—	3	5	●	●
—	—	—	5	(2)	(1)	—	—	—	3(2)	(2)	—	—	—	—	—	—	—	—	—	—	—	3	5	●	●
—	—	—	4	(2)	—	—	—	—	—	(1)	—	—	—	—	—	—	—	(1)	—	—	—	2	5	●	●
—	—	—	1	(2)	(1)	1	(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	(1)	—	3	●	●
—	—	—	1	—	(2)	3(1)	—	—	—	—	—	—	—	—	—	—	—	(1)	—	—	(1)	7	5	●	●
—	—	—	—	1	2(1)	—	—	(1)	(1)	—	—	—	—	—	—	—	—	—	—	—	—	9	1	●	●
—	—	—	1	1	(1)	—	—	—	—	(1)	—	2	—	—	1	1(2)	—	—	—	—	—	2	—	r	●
—	—	—	8	(5)	(1)	1	—	—	1(1)	—	—	—	—	—	—	—	—	—	—	—	—	18	10	●	●
—	2	2(2)	20(1)	(8)	2	—	—	—	2(6)	—	—	—	—	—	—	—	—	—	—	—	—	8	19	●	●
—	—	2	4	(3)	2	1(2)	—	2(1)	1	(4)	—	—	—	—	—	—	—	—	—	—	—	4	8	●	●

Group	Formation	Member	Locality	Sample number	Mass processed	Processing number	"*Apatognathus*" sp. Pa	"*Apatognathus*" sp. a Sb	"*Apatognathus*" sp. fragments	*Cavusgnathus unicornis* Pa α	*Cavusgnathus unicornis* Pa β	*Cavusgnathus unicornis* Pa γ	*Cavusgnathus unicornis* Pa int.	*Cavusgnathus unicornis* Pa ind.	*Cavusgnathus unicornis* Pb	*Cavusgnathus unicornis* M	*Cavusgnathus unicornis* Sa	*Cavusgnathus unicornis* Sc	*Cavusgnathus* cf. *hudsoni* Pa	*Cavusgnathus* cf. *unicornis* Pa	*Cavusgnathus* sp. a Pa	*Cavusgnathus* sp. Pa	*Cavusgnathus* sp. S	*Clydagnathus windsorensis* Pa	*Clydagnathus* sp. Pa
Lower Border	Cambeck	—	13	108707	1.29	1490	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Cambeck	Syringothyris Ls.	13	108705	1.36	1427	—	(1)	1	4	2(2)	(1)	(1)	(12)	—	5	1	(1)	—	—	—	—	—	—	—
Lower Border	Cambeck	—	13	108704	1.22	1489	—	—	—	1	—	—	1	(1)	—	—	—	—	—	—	—	—	(3)	—	—
Lower Border	Cambeck	Whitrigg Serpula	13	108702	1.40	1488	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(1)
Lower Border	Cambeck	—	13	108701	1.37	1487	—	—	1	—	4	—	2	—	1	(3)	—	—	—	—	2(1)	(4)	—	5	(1)
Lower Border	Cambeck	—	13	88776	1.30	1486	—	—	—	6	—	—	3	1(7)	(2)	5	1	—	—	—	—	—	(5)	—	—
Lower Border	Cambeck	U Antiquatonia	13	88773	1.33	1485	—	—	—	—	—	—	—	(1)	(2)	—	—	—	—	—	—	—	—	—	—
Lower Border	Cambeck	L Antiquatonia	12	LA6	1.34	1522	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Cambeck	L Antiquatonia	12	LA5	1.39	1521	(1)	—	(1)	1	—	—	—	(2)	—	—	—	—	—	1	—	—	(6)	—	—
Lower Border	Cambeck	L Antiquatonia	12	LA1	0.70	1383	—	—	—	—	—	—	—	(1)	—	—	—	—	—	—	—	—	—	—	—
Lower Border	MA/CAM	—	12	88747	1.25	1480	—	—	1	—	—	—	—	—	—	2	—	—	—	—	—	(1)	(8)	—	—
Lower Border	Main Algal	Main Algal 13	12	88744	1.17	1479	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Main Algal	Main Algal 12	12	88743	1.23	1478	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Main Algal	Main Algal 11	12	88740	1.44	1477	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Main Algal	Main Algal 10	12	88735	1.40	1476	—	—	—	—	—	1	1	—	—	2(1)	(1)	—	—	—	—	—	(7)	—	—
Lower Border	Main Algal	Main Algal 9	12	88732	1.36	1475	—	—	—	—	1	—	—	(1)	1	1	—	—	—	—	—	(1)	—	—	—
Lower Border	Main Algal	Main Algal 8	12	88729	1.44	1474	—	—	—	—	—	—	—	1	(2)	1	—	—	—	—	—	—	(8)	—	—
Lower Border	Main Algal	Birky Cleugh Ls.	12	88727	1.34	1473	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(5)	—	—
Lower Border	Main Algal	Birky Cleugh Ls.	12	88726	1.36	1472	2	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Main Algal	Birky Cleugh Ls.	12	88725	1.28	1471	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Main Algal	Birky Cleugh Ls.	12	88724	1.35	1470	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(5)	—	—
Lower Border	Main Algal	Birky Cleugh Ls	12	88723	1.35	1469	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Main Algal	Birky Cleugh Ls.	12	88722	1.22	1468	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Main Algal	Birky Cleugh Ls.	12	88721	1.36	1467	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Main Algal	Main Algal 4	12	88720	1.37	1466	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Main Algal	Main Algal 2	12	88718	1.43	1465	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Main Algal	Main Algal 1	12	88717	1.34	1464	—	—	—	—	1	2	3	—	—	—	(1)	—	—	—	—	(4)	(5)	—	—
Lower Border	Main Algal	Main Algal 1	12	88715	1.36	1463	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Junction Ls.	12	88713	1.28	1462	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Junction Ls.	10	88704	1.33	1406	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Peel LS.	10	88702	1.30	1405	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
Lower Border	Bewcastle	Stack Cleugh Oolite	10	88701	1.33	1404(UF)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Rigghead Ls.	10	1988610	1.29	1251	—	—	(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	—	10	188868	1.31	1250	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	—	10	188865	1.36	1381	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Ashy Cleugh Ls.	10	168863	1.32	1249	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Ashy Cleugh Ls.	10	168861	1.30	1380	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	—	10	78866	1.17	1379	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	—	10	78864	1.06	1248	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	—	10	*	1.31	1342	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	New House Ls.	10	58862	1.43	1247	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	New House Ls	10	58861	1 25	1378	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	—	10	117861	1.09	1377	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	—	10	87865	1.32	1376	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	—	10	87862	1.28	1375	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	U Holmhead	10	278626	1.32	1246	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	—	10	278622	1.11	1373(UF)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	L Holmhead	10	278619	1.24	1372	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	(1)	(4)	—	—
Lower Border	Bewcastle	L Holmhead	10	*	1.23	1459	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	Kitty Beck Ls.	10	278614	1.28	1245	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	—	10	3068610	0.91	1371	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	—	10	306868	1.10	1370	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	—	10	256866	1.23	1369	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Bewcastle	—	10	256862	1 19	1368	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

APPENDIX IIc. Conodont elements recovered from the Bewcastle, Main Algal, and Cambeck formations, localities 10, 12, and 13. UF residue not completely picked; ¢ cavusgnathid; † *Hindeodus* fragments?; r rare.

Hindeodus crassidentatus? Pa	*Kladognathus* sp. Sc	*Lochriea* sp. M	*Patrognathus capricornis* Pa	*Patrognathus capricornis* M	*Taphrognathus varians* Pa II	*Taphrognathus varians* Pa III	*Taphrognathus varians* Pa ind.	*Taphrognathus varians* Pb	*Taphrognathus varians* M	*Taphrognathus varians* Sa	*Taphrognathus varians* Sb	*Taphrognathus varians* Sc	*Taphrognathus varians* S	*Vogelgnathus gladiolus* Pa	*Vogelgnathus kyphus* Pa	*Vogelgnathus kyphus* Sa	*Vogelgnathus kyphus* Sb	*Vogelgnathus kyphus* Sc	*Vogelgnathus kyphus* S	*Vogelgnathus pesaquidi* Pa	*Vogelgnathus pesaquidi* Sc	*Vogelgnathus pesaquidi* S	*Vogelgnathus* cf. *pesaquidi* Pa	Gen. a sp. a Pa	Gen. a sp. a M	Genus indeterminate Pa	Genus indeterminate Pb	Genus indeterminate M	Genus indeterminate Sc	S fragments	Indeterminate fragments	Fish teeth	Ostracodes
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	3	●	●
—	1	1(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	(3)	—	—	—	—	—	—	—	—	28	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	—	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	1	(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(1)	—	—	—	14		●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1(2)	—	(2)	—	4	1	—	—	—	—	62	7	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(1)¢	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	23	5	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	(2)	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9	●	●
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	●	●
(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	(1)	—	(1)	—	11	9	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	86	—	—	—	(7)	1	—	—	—	—	—	—	—	—	—	—	3	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	26	—	2	(1)	—	—	—	—	—	—	—	—	—	—	(1)	—	3	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	14(1)	(1)	—	—	(1)	—	—	—	—	—	—	—	—	—	—	—	—	r	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	●	●
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	r	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	4	●	●
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	r	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	●
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	●	●
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	●	r
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(1)¢	—	—	—	1	—	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—
1(2)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(3)¢	—	—	—	7	8	●	—
1(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2†	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—
—	—	—	—	—	—	—	(2)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(1)	2	6	—	●
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	(1)	(1)	—	—	(2)	(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	●
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(1)	—	(2)	—	—	—	—	30	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(1)	—	—	1	—	—	6	13	●	●
—	—	—	—	—	1	6	(4)	(1)	1	—	—	(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13	—	—
—	—	—	—	—	—	3	(1)	2	3	1	1	3(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	23	—	—
—	—	—	—	—	—	5(1)	3(8)	1(1)	(2)	(2)	—	(1)	(9)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	28	—	—
—	—	—	—	—	—	4(2)	1(10)	5(2)	1(1)	(1)	3	6(3)	(2)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(1)	—	67	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4(1)	—	—	—	—	—	—	1	—	●	—

Group	Formation	Member	Locality	Sample number	Mass processed	Processing number	*Cavusgnathus hudsoni* Pa α	*Cavusgnathus hudsoni* Pa β	*Cavusgnathus hudsoni* Pa γ	*Cavusgnathus hudsoni* Pa int.	*Cavusgnathus hudsoni* Pa ind.	*Cavusgnathus hudsoni* Pb	*Cavusgnathus hudsoni* M	*Cavusgnathus hudsoni* Sa	*Cavusgnathus hudsoni* Sb	*Cavusgnathus hudsoni* Sc	*Cavusgnathus hudsoni* S	*Cavusgnathus* sp. Pa	*Cavusgnathus* sp. M
Lower Border	Liddel	—	20	108792	1.44	1450	—	20	3	33	11(25)	5	3(1)	(1)	—	—	—	—	—
Middle Border	—	Harden	17	108766	1.31	1430	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Liddel	—	17	108764	1.23	1515	1	13	4	5	4(16)	—	2	—	—	1	(1)	(5)	(1)
Lower Border	Liddel	—	17	108763	1.30	1514	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Liddel	—	17	108760	1.40	1512	1	2	—	—	—	—	—	—	—	—	—	(5)	—
Lower Border	Liddel	—	17	108758	1.40	1511	5	16	4	16	8	10	2	3	—	—	(7)	1(3)	—
Lower Border	Liddel	—	17	108756	1.43	1509	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Liddel	—	17	108754	1.42	1508	1	—	—	2	(3)	(1)	3	—	—	—	(7)	(2)	—
Lower Border	Liddel	—	17	108752	1.49	1507	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Liddel	—	17	108751	1.43	1506^	25	11	—	49	5(18)	24(14)	6	3	2	2(1)	(10)	—	—
Lower Border	Liddel	—	17	108747	1.34	1505	—	—	—	—	—	—	—	—	—	—	—	—	—
Middle Border	—	Harden	19	108745	1.20	1429	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	U Black Burn	—	19	108742	0.86	1504	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	U Black Burn	—	19	108739	0.93	1503	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	L Black Burn	—	19	108737	0.96	1502	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	L Black Burn	—	19	108735	1.09	1501	—	—	—	—	—	—	—	—	—	—	—	—	—
Lower Border	Arnton Fell	—	21	108734	1.02	1428	—	—	—	—	—	—	—	—	—	—	—	—	—

APPENDIX IId. Conodont elements recovered from the Liddel, Black Burn, and Arnton Fell formations and the Harden Member, localities 17, 19–21. † juvenile; ¢ cavusgnathid; * includes 2 juveniles; ^ 18 anterior platform and blade fragments included in *C. hudsoni* Pa elements.

Gnathodus? simplicatus Pa	*Polygnathus mehli* Pa	*Polygnathus mehli* Pb	*Polygnathus mehli* M	*Polygnathus mehli* Sa	*Polygnathus mehli* Sc	*Polygnathus mehli* S	*Polygnathus* sp. Pa	*Polygnathus* sp. Sc	*Polygnathus* sp. S	*Taphrognathus* sp.a Pa	Genus indeterminate Pa	Genus indeterminate Pb	Genus indeterminate Sc	S fragments	Indeterminate fragments	Fish teeth	Ostracodes
—	4	(1)	—	1	—	—	1	—	—	—	—	—	—	27	13	—	—
—	24(3)	2	—	(1)	(1)	—	(5)	—	(11)	—	—	—	—	—	1	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	1	●	—
—	60	9	7	1(1)	6(1)	(15)	(12)*	—	—	—	—	—	—	15	8	●	—
—	29(1)	2(1)	—	—	—	—	—	(1)	(3)	—	—	(1)	—	—	8	●	●
—	—	—	—	—	—	—	—	—	—	—	—	—	—	29	1	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	14	3	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	1†	—	—	—	—	—	—	66	11	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	●
1	47(10)	(3)	2	(2)	—	—	(2)	2	(14)	1	1¢	—	—	—	5	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●
—	—	—	—	—	—	—	—	—	—	—	—	—	1	3	—	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	●
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Group	Formation	Member	Locality	Sample number	Mass processed	Processing number	"*Apatognathus*" sp. Pa	"*Apatognathus*" sp. fragments	*Cavusgnathus hudsoni* Pa	*Cavusgnathus unicornis* Pa α	*Cavusgnathus unicornis* Pa β	*Cavusgnathus unicornis* Pa γ	*Cavusgnathus unicornis* Pa int.	*Cavusgnathus unicornis* Pa ind.	*Cavusgnathus unicornis* Pb	*Cavusgnathus unicornis* M	*Cavusgnathus unicornis* Sa	*Cavusgnathus unicornis* Sb	*Cavusgnathus unicornis* Sc	*Cavusgnathus unicornis* S	*Cavusgnathus* sp. Pa	*Clydagnathus windsorensis* Pa	*Clydagnathus windsorensis* Pb	*Clydagnathus windsorensis* M	*Clydagnathus windsorensis* Sa	*Clydagnathus* sp. Pa	*Gnathodus cuneiformis* Pa	*Hindeodus crassidentatus?* Pa	*Kladognathus tenuis* Sc α	*Lochriea* sp. M	*Lochriea* sp. Pb
Cementstone	—	Glebe Ls.	1	156876	1.43	1389	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cementstone	—	Glebe Ls.	1	156874	1.36	1388	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cementstone	—	Glebe Ls.	1	156873	1.48	1387	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cementstone	—	Glebe Ls.	1	156871	1.32	1386	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cementstone	—	Glebe Ls.	1	246861	1.38	1221	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cementstone	—	Glebe Ls.	1	246862	0.87	1228	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cementstone	—	Birky Hill Ls.	2	BHL 1	1.38	1461	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cementstone	—	Glebe Ls.	3	196863	1.34	1226	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Cementstone	—	—	4	196862	0.69	1225	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cementstone	—	—	5	196861	1.34	1224	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cementstone	—	—	6	284874	0.91	1385	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—
Cementstone	—	—	6	284871	0.65	1384	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	1	—	—	—	—	—
Cementstone	—	—	7	1538701	0.94	1523	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cementstone	—	—	8	186861	1.48	1227	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3(1)	(1)	(1)	—	—	—	—	—	—	—
Cementstone	—	—	8	•	1.11	1411	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2(4)	(1)	—	—	—	—	—	—	—	—
Cementstone	—	—	9	209861	0.88	1254	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cementstone	—	—	9	209862	1.34	1255	(1)	1	—	3	3(3)	3	2(1)	(1)	7(1)	2	(5)	—	1	(13)	(38)	—	—	—	—	—	—	—	—	2	(1)
Cementstone	—	—	9	209863	1.14	1256	—	1	—	1	—	—	—	4	1	5	—	—	—	—	—	—	—	—	—	—	—	—	—	7	(2)
Cementstone	—	—	9	108733	1.30	1500	—	—	—	1	—	—	—	—	—	—	—	—	—	—	(1)	—	—	—	—	—	—	—	1	—	—
Cementstone	—	—	9	108730	1.19	1497	—	—	—	—	1	1	—	—	—	1(1)	—	—	—	—	(1)	—	—	—	—	—	—	—	—	—	—
Cementstone	Arnton Fell ?	—	18	—	0.97	1253	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	—	—	1	—	—	—	—	—	—
Cementstone	Arnton Fell ?	—	18	37862	1.58	1222	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(2)	—	—	—	8	—	—	—	—	—
Cementstone	Basel Cementstone	—	22	1968701	0.83	1397	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5(3)	—	—	—	—	—	—	—	—	—
Cementstone	Basal Cementstone	—	23	1968703	1.34	1398	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cementstone	Gillfoot	—	25	1868705	1.30	1396	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cementstone	Gillfoot	—	25	1868704	0.79	1395	—	—	—	(1)	—	—	—	—	—	—	—	—	—	—	(1)	—	—	—	—	—	—	—	—	—	—
Cementstone	Southerness	—	25	1968712	1.19	1403	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cementstone	Southerness	—	25	1968710	1.30	1402	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
Cementstone	Southerness	—	25	1968708	0.82	1401	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cementstone	Southerness	—	25	1968706	1.07	1400	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cementstone	Southerness	—	25	1968704	1.19	1399	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
Cementstone	—	—	26	1868703	1.06	1394	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cementstone	—	—	26	1868701	0.67	1393	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Orroland	Orroland Lodge	—	27	1768701	1.26	1390	—	—	—	2	1	—	—	—	—	(2)	—	(1)	—	—	—	—	—	—	—	—	—	—	—	—	—
Orroland	Barlacco Heugh	—	27	1768703	1 29	1392	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Orroland	Barlacco Heugh	—	27	1768702	1.39	1391	(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

APPENDIX IIe. Conodont elements recovered from the Cementstone and Orroland groups, localities 1–9, 18, 22, 23, 25–27.

M. praebeck.-beck. intermediate Pa	*Mestognathus beckmanni* Pa	*Mestognathus* sp. Pa	*Patrognathus capricornis* Pa	*Patrognathus capricornis* M	*Patrognathus capricornis* Sc	*Polygnathus mehli* Pa	*Taphrognathus carinatus* Pa	*Taphrognathus carinatus* Pb	*Taphrognathus carinatus* M	*Taphrognathus carinatus* Sa	*Taphrognathus carinatus* Sb	*Taphrognathus carinatus* Sc1	*Taphrognathus carinatus* Sc2	*Taphrognathus carinatus* S	*Taphrognathus varians* Pa I	*Taphrognathus varians* Pa II	*Taphrognathus varians* Pa III	*Taphrognathus varians* Pa ind.	*Taphrognathus varians* Pb	*Taphrognathus varians* M	*Taphrognathus* cf. *varians* Pa	*Taphrognathus* sp. Pa	*Taphrognathus* sp. Sc	*Vogelgnathus gladiolus* Pa	*Vogelgnathus kyphus* Pa	*Vogelgnathus pesaquidi* Pa	*Vogelgnathus pesaquidi* Sc	Genus indeterminate Pa	Genus indeterminate Pb	Genus indeterminate M	Genus indeterminate Sa	S fragments	Indeterminate fragments	Fish teeth	Ostracodes
—	—	—	—	—	—	—	3(1)	4	2	11	3	—	2	—	2	2	4(3)	3(9)	3	4	1	—	(9)	—	—	—	—	—	—	—	—	—	67	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	●	—
—	—	—	—	—	—	—	2(2)	—	—	—	(1)	4(6)	3	—	1	1	2	1	(1)	3	—	—	—	—	—	—	—	—	—	—	—	—	16	r	—
—	—	—	—	—	—	—	1	1	—	3(1)	—	1	—	(1)	—	—	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	●	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	1/1 cf	—	—	2	—	—	2	—	—	1	1(1)	2(3)	—	—	—	(2)	—	—	—	—	—	—	—	—	—	—	23	—	—
—	—	—	—	—	—	—	(1)	1	—	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—
—	—	—	—	—	—	—	—	1	—	2	—	—	—	—	—	(1)	(1)	1(1)	—	—	—	(1)	—	—	—	—	—	—	—	—	—	4	1	●	—
—	—	—	—	—	—	—	7	4	1	3	1	—	4(2)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—
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Plates

PLATE 1, FIGS. 1–14

Figs. 1a, b. *Hindeodus crassidentatus* (Branson and Mehl)?. Lateral and upper views of Pa element ROM 48777, sample 78864, x100.

Figs. 2–14. *Cavusgnathus hudsoni* (Metcalfe) x60.

2a–c. Lateral, lower, and upper views of sinistral Pa β element ROM 48778, sample 108751.

3a, b. Lateral and upper views of immature sinistral Pa α element ROM 48779, sample 108751.

4a, b. Lateral and upper views of immature sinistral Pa element ROM 48780, sample 108751.

5a–c. Lateral, upper, and lower views of sinistral Pa α/β element ROM 48781, sample 108751.

6. Upper view of aberrant dextral Pa element ROM 48782, sample 108758.

7a, b. Lateral and upper views of variant dextral Pa β/γ element ROM 48783, sample 108764.

8. Lateral view of dextral Pa γ element ROM 48784, sample 108764.

9. Lateral view of Pb element ROM 48786, sample 108751.

10. Lateral view of Sc element ROM 48785, sample 88754.

11. Posterior view of Sa element ROM 48787, sample 108751.

12. Lateral view of Sc element ROM 48788, sample 108751.

13. Lateral view of Sb element ROM 48789, sample 108751.

14. Lateral view of M element ROM 48790, sample 108754.

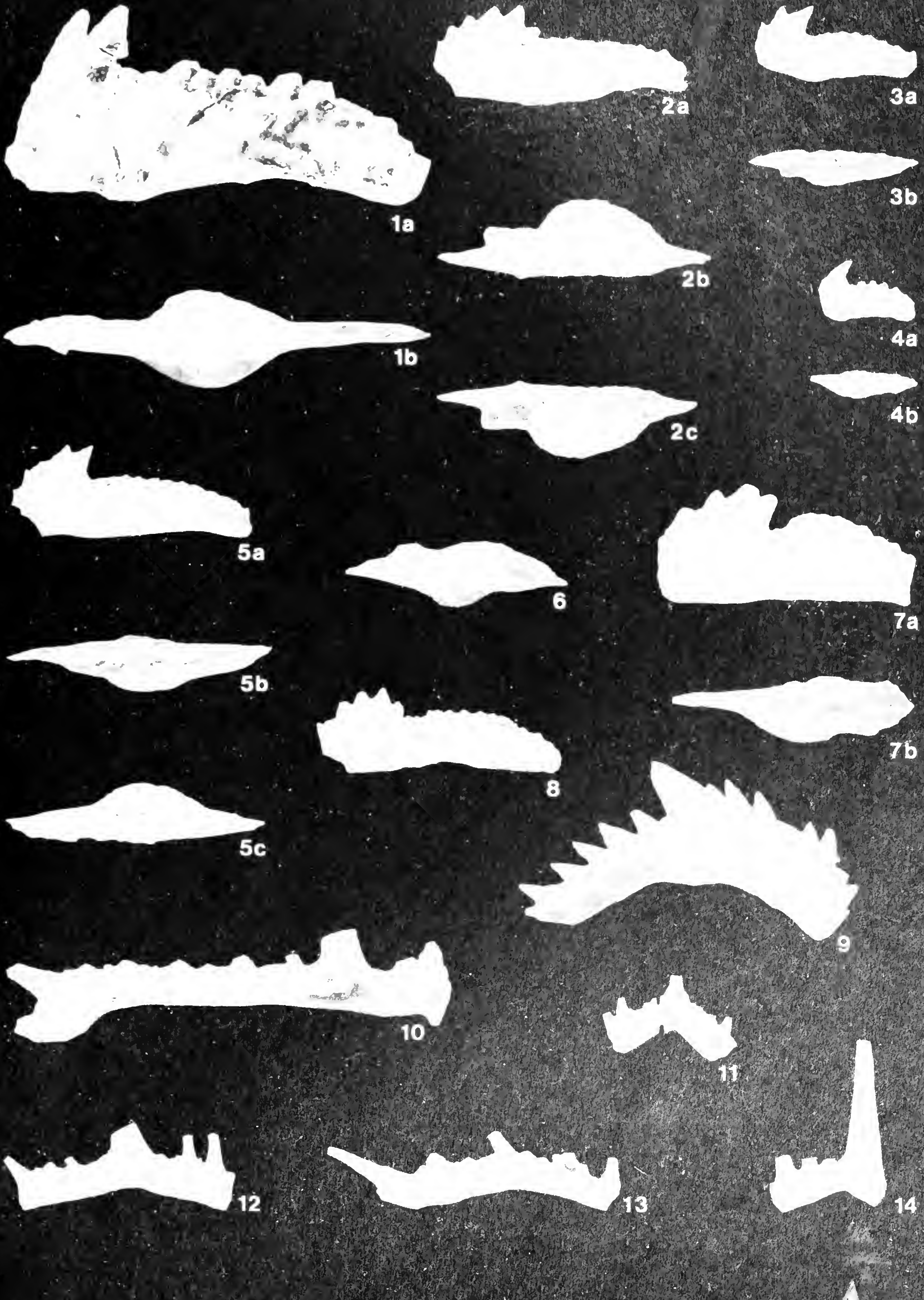
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PLATE 2, FIGS. 1–15

Figs. 1–5, 7. *Cavusgnathus unicornis* Youngquist and Miller x60.

1a, b. Upper and lateral views of dextral Pa β/γ element ROM 48791, sample 88717.

2. Upper view of sinistral Pa β element ROM 48792, sample 88776.

3. Lateral view of straight Pa α element ROM 48793, sample 88776.

4. Lateral view of aberrant sinistral Pa element ROM 48794, sample 209862.

5. Lateral view of sinistral Pa γ element ROM 48795, sample 209862.

7. Lateral view of M element ROM 48796, sample 209863.

Figs. 6a, b. *Cavusgnathus* cf. *unicornis* Youngquist and Miller. Upper and lateral views of dextral Pa element ROM 48797, sample LA5, x60.

Fig. 8. *Cavusgnathus*? sp. a. Upper view of sinistral Pa element ROM 48798, sample 108701, x60.

Figs. 9–15. *Clydagnathus windsorensis* (Globensky) x100.

9. Lateral view of dextral Pa element ROM 48799, sample 88758.

10a, b. Lateral and upper views of sinistral Pa element ROM 48800, sample 88757.

11. Lateral view of Pb element ROM 48801, sample 88756.

12. Lateral view of M element ROM 48802, sample 88756.

13. Posterior view of Sa element ROM 48803, sample 88756.

14. Lateral view of Sb element ROM 48804, sample 88756.

15. Lateral view of incomplete Sc element ROM 48805, sample 88756.


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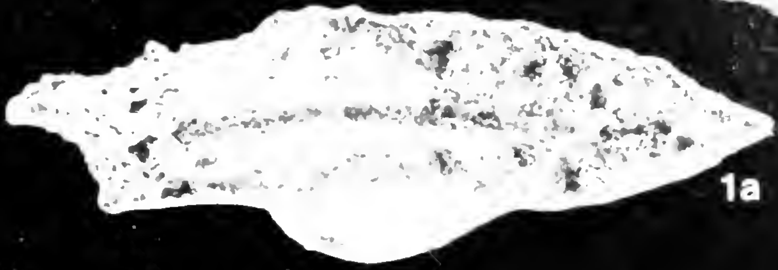
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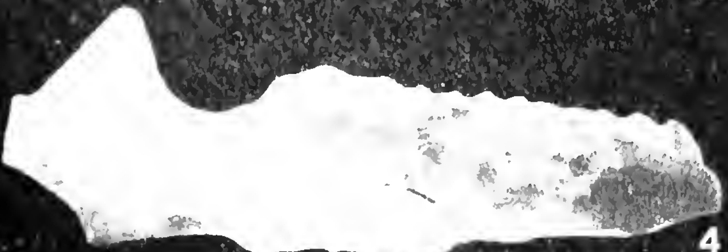
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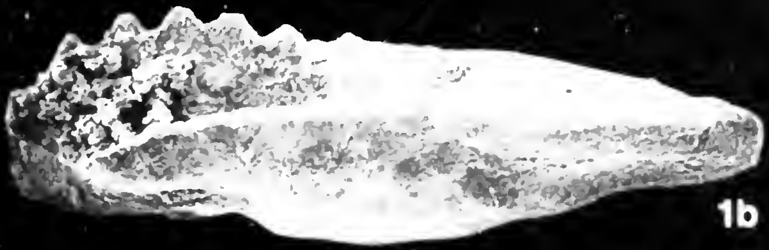
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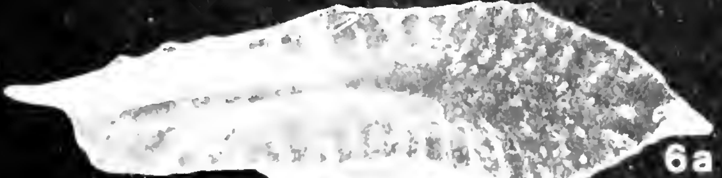
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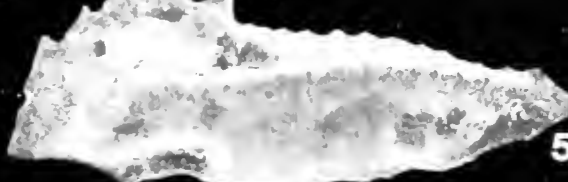
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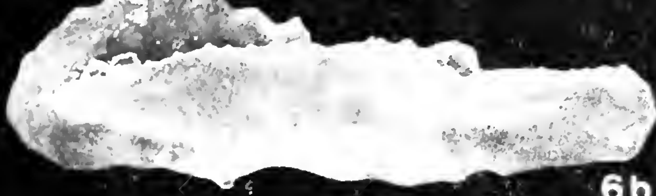
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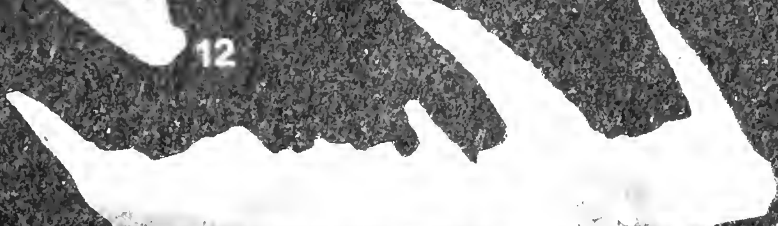
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PLATE 3, FIGS. 1–15

Figs. 1–9. *Patrognathus capricornis* (Druce) x100.
1. Lateral view of M element ROM 48806, sample 108778.
2. Upper view of Pa element ROM 48807, sample 1968710.
3a, b. Lateral and upper views of immature Pa element ROM 48813, sample 14118513.
4. Upper view of immature Pa element ROM 48814, sample 14118513.
5. Lateral view of M element ROM 48808, sample 1768701.
6a, b. Lateral and upper views of Pa element ROM 48809, sample 108701.
7a, b. Lateral and upper views of Pa element ROM 48810, sample 14118513.
8. Lateral view of Pb element ROM 48811, sample 14118517.
9. Lateral view of incomplete Sc element ROM 48812, sample 14118517.

Figs. 10–15. *Taphrognathus carinatus* (Higgins and Varker) x80.
10. Posterior view of Sa element ROM 48815, sample 156876.
11. Lateral view of Sc_2 element ROM 48816, sample 156871.
12. Posterior/lateral view of Sb element ROM 48817, sample 196861.
13. Posterior view of Sa element ROM 48818, sample 196861.
14. Lateral view of Pb element ROM 48819, sample 196861.
15. Lateral view of M element ROM 48820, sample 196861.

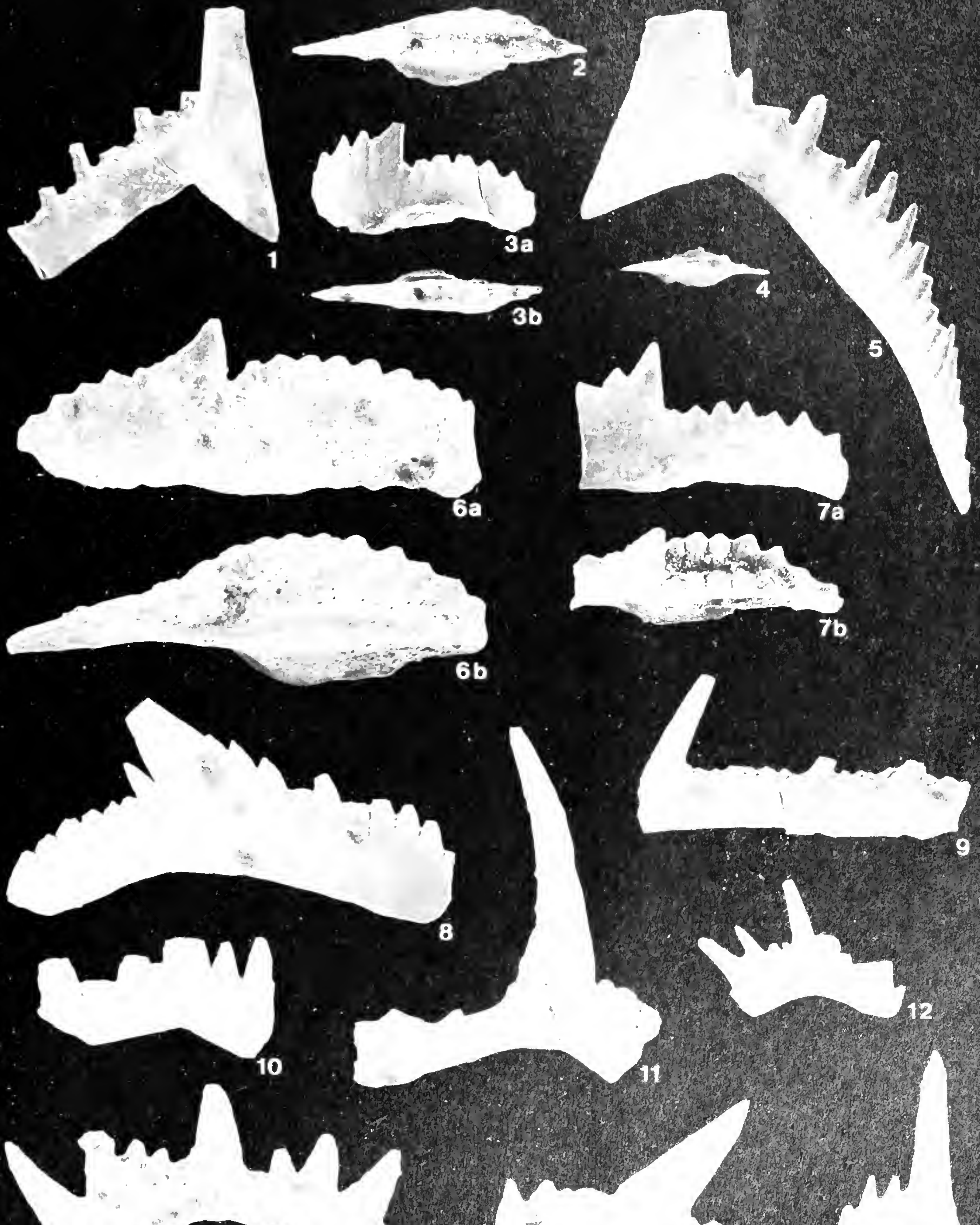
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PLATE 4, FIGS. 1–15

Fig. 1a, b. *Taphrognathus carinatus* (Higgins and Varker). Lateral and upper views of Pa element ROM 48821, sample 196861, x80.

Figs. 2–15. *Taphrognathus varians* Branson and Mehl x80.
2. Upper view of dextral morphotype II Pa element ROM 48822, sample 1768631.
3a, b. Lateral and upper views of sinistral morphotype III Pa element ROM 48823, sample 88710.
4a–c. Lateral, upper, and lower views of dextral morphotype III Pa element ROM 48824, sample 1768633.
5. Upper view of slightly sinuous morphotype I Pa element ROM 48825, sample 108773.
6. Upper view of dextral morphotype II/I Pa element ROM 48826, sample 258621.
7. Upper view of immature Pa element ROM 48827, sample 1411852.
8. Lateral view of immature Pa element ROM 48828, sample 258622.
9. Upper view of dextral morphotype II Pa element ROM 48829, sample 108767.
10. Upper view of immature Pa element ROM 48830, sample 256866.
11a, b. Lateral and upper views of immature Pa element ROM 48831, sample 258620.
12. Lateral view of Pb element ROM 48832, sample 1768634.
13. Lateral view of Pb element ROM 48833, sample 258620.
14. Lateral view of immature Pb element ROM 48834, sample 258625.
15. Lateral view of M element ROM 48835, sample 14118511.


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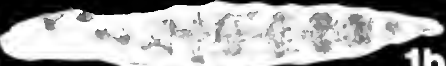
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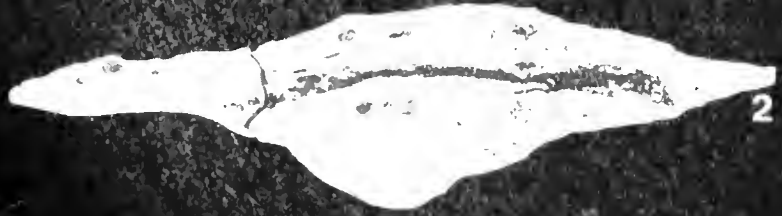
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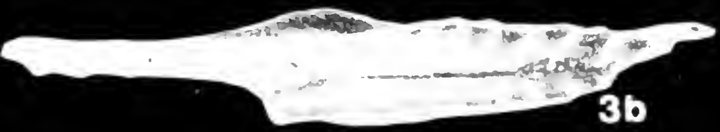
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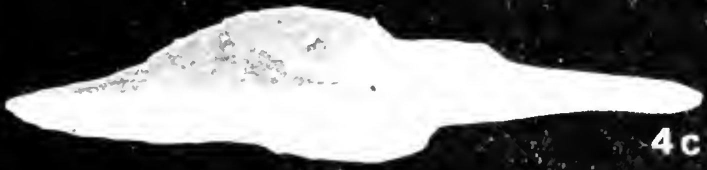
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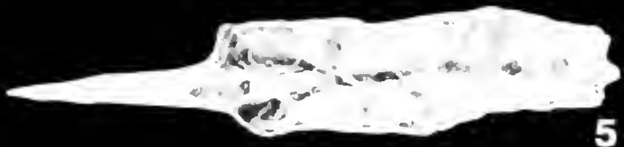
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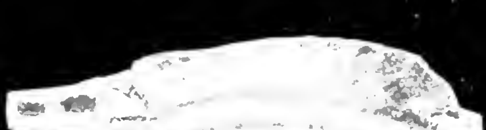
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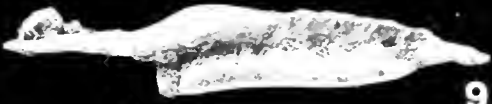
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PLATE 5, FIGS. 1–12

Figs. 1–3. *Taphrognathus varians* Branson and Mehl x80.
  1. Posterior view of Sa element ROM 48836, sample 108790.
  2. Lateral view of Sb element ROM 48837, sample 108790.
  3. Lateral view of Sc element ROM 48838, sample 108790.

Figs. 4a, b. *Taphrognathus*? *transatlanticus* (von Bitter and Austin)?. Oblique lateral view of Pa element ROM 48839, sample 258622, a x80, b x340.

Figs. 5a, b. *Taphrognathus* sp. a. Lateral and upper views of sinistral Pa element ROM 48840, sample 108745, x80.

Fig. 6. *Gnathodus*? *simplicatus* (Rhodes, Austin, and Druce). Lateral view of Pa element ROM 48841, sample 108745, x100.

Fig. 7. *Gnathodus cuneiformis* Mehl and Thomas. Upper view of Pa element ROM 48842, sample 196863, x100.

Figs. 8, 9. *Mestognathus beckmanni* Bischoff x60.
  8a, b. Lower and upper views of sinistral Pa element ROM 48843, sample 209862.
  9. Lateral view of Pb element ROM 48844, sample 258629.

Fig. 10. *Mestognathus praebeckmanni* Sandberg, Johnston, Orchard, and von Bitter. Oblique upper view of dextral Pa element ROM 48845, sample 439 of Armstrong and Purnell (1987), x60.

Figs. 11, 12. *Mestognathus praebeckmanni–M. beckmanni* intermediates x60.
  11a, b. Lower and lateral views of dextral Pa element ROM 48846, sample 88750.
  12a–c. Lateral, upper, and oblique lower views of dextral Pa element ROM 48847, sample 1768630.


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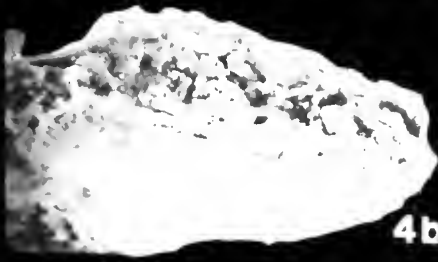
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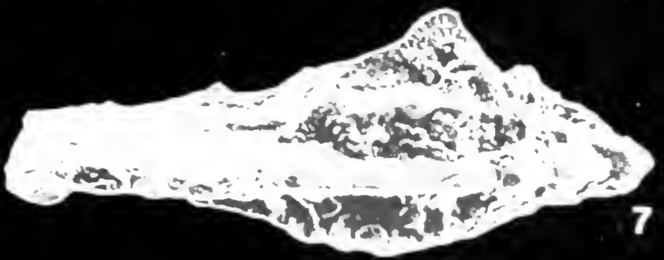
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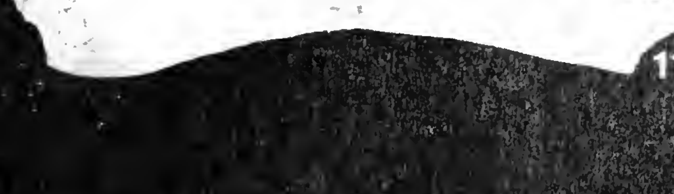
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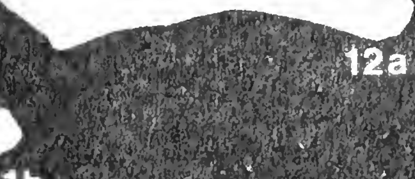
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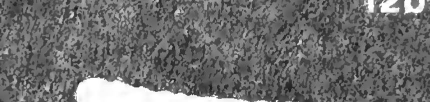
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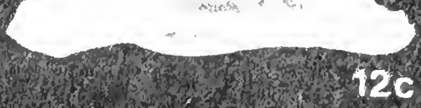
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PLATE 6, FIGS. 1–13

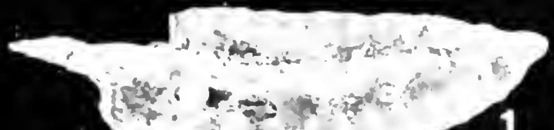
Figs. 1, 3. *Polygnathus bischoffi* Rhodes, Austin, and Druce x80.
1. Upper view of Pa element ROM 48848, sample 88751.
3. Lower view of Pa element ROM 48849, sample 88750.

Figs. 2, 4–7, 9–11. *Polygnathus mehli* Thompson x80.
2. Oblique upper view of Pa element ROM 48850, sample 108760.
4. Lower view of Pa element ROM 48851, sample 108745.
5. Lateral view of M element ROM 48852, sample 108763.
6. Lateral view of Pb element ROM 48853, sample 108763.
7. Lateral view of Pb element ROM 48854, sample 108763.
9. Lateral view of Sc element ROM 48855, sample 108763.
10a, b. Posterior and oblique lateral views of Sa element ROM 48856, sample 108763.
11. Lateral view of Sc element ROM 48857, sample 108763.

Fig. 8. *Polygnathus* sp. Lateral view of immature Pa element ROM 48858, sample 108745, x80.

Figs. 12a, b. *Lochriea scotiaensis* (Globensky). Lower and lateral views of Pa element ROM 48859, sample 88760, x100.

Fig. 13. *Lochriea* sp. Lateral view of M element ROM 48860, sample 209863, x60.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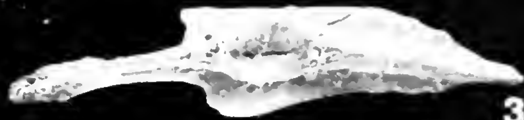
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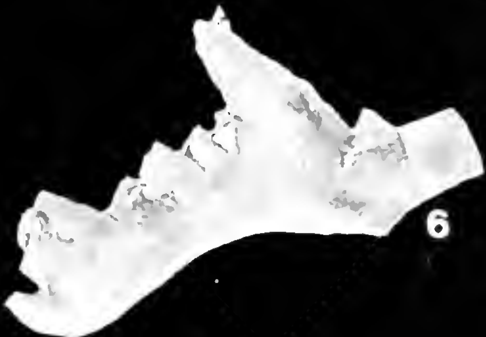
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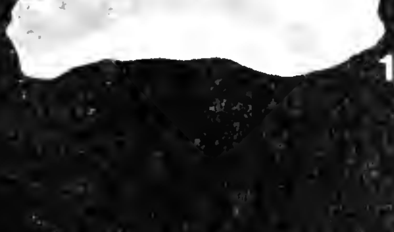
12a


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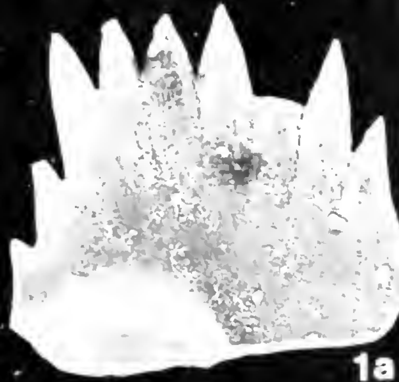
13

PLATE 7, FIGS. 1–12

Figs. 1–8. *Vogelgnathus gladiolus* Purnell and von Bitter x180.
- 1a, b. Lateral and upper views of Pa element ROM 48667, sample 258624.
- 2. Lateral view of Pa element ROM 48668, sample 258622.
- 3. Lateral view of variant Pa element ROM 48861, sample 1768636.
- 4. Oblique lower view of Pa element ROM 48669, sample 14118517.
- 5. Lateral view of Sb element ROM 48672, sample 1768634.
- 6. Lateral view of Sc element ROM 48675, sample 14118517.
- 7. Lateral view of Pb element ROM 48674, sample 1768635.
- 8. Lateral view of M element ROM 48673, sample 258622.

Figs. 9, 10, 12. *Vogelgnathus kyphus* Purnell and von Bitter x180.
- 9. Upper view of Pa element ROM 48676, sample 88727.
- 10a–c. Lateral, lower, and upper views of Pa element ROM 48677, sample 88725.
- 12. Lateral view of Sb element ROM 48679, sample 88726.

Figs. 11a, b. *Vogelgnathus pesaquidi* Purnell and von Bitter. Lateral and lower views of morphotype II Pa element ROM 48683, sample 1768701, x180.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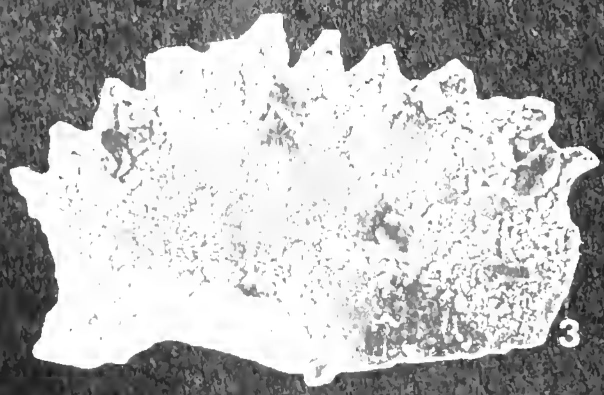
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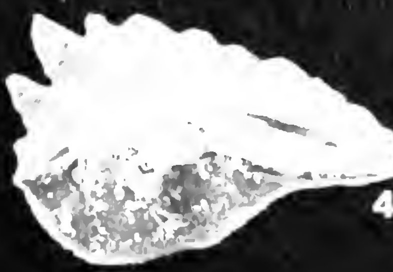
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11a


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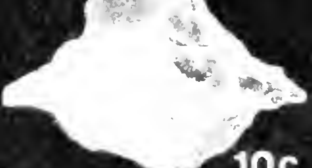
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PLATE 8, FIGS. 1–12

Fig. 1. *Vogelgnathus* cf. *pesaquidi* Purnell and von Bitter. Lateral view of Pa element ROM 48862, sample 256862, x180.

Figs. 2, 3. *Kladognathus tenuis* (Branson and Mehl) x80.
- 2a, b. Lower posterior and oblique lateral views of Sa element ROM 48863, sample 88754.
- 3. Lateral view of Scα element ROM 48864, sample 88754.

Figs. 4–9. *"Apatognathus" cuspidatus* Varker x100.
- 4. Posterior? view of Sa element ROM 48865, sample 108790.
- 5. Posterior? view of Sa element ROM 48868, sample 108768.
- 6. Lateral view of Sb element ROM 48866, sample 14118513.
- 7. Lateral view of Sc element ROM 48867, sample 108768.
- 8. Lateral view of Pa element ROM 48869, sample 108767.
- 9. Lateral view of Pb element ROM 48870, sample 108767.

Fig. 10. *"Apatognathus"* sp. Lateral view of Pa element ROM 48871, sample 1768702, x100.

Figs. 11, 12. Gen. a sp. a x100.
- 11. Lateral view of Pa element ROM 48872, sample 88776.
- 12. Lateral view of M element ROM 48873, sample 88776.


1


2a


2b


3


4


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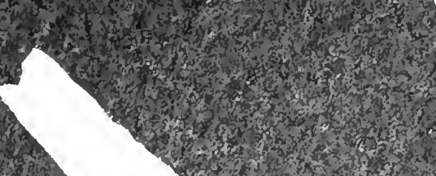
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