UNIVERSITY OF SOUTHAMPTON

ARUNDIAN (CARBONIFEROUS) CONODONTS FROM SOUTH WALES AND THE TECHNIQUES USED IN CONODONT STUDIES

A thesis presented for the degree of
Doctor of Philosophy

by

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UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF SCIENCE

GEOLOGY

Doctor of Philosophy

ARUNDIAN (CARBONIFEROUS) CONODONTS FROM SOUTH WALES AND THE TECHNIQUES USED IN CONODONT STUDIES

by Jeremy Jordan Stone

A relatively diverse conodont fauna has been recovered from a sample transect through the varied subenvironments of the carbonate ramp which existed to the south of St. George's Land during Arundian times. The fauna includes elements referred to the multielement species: Cavusgnathus altus, Clydagnathus gilwernensis, Gnathodus cuneiformis, G. aff. girtyi, G. texanus, G. homopunctatus, G. mermaidus, G. symmutatus, Hindeodus cristulus, ?H. scitulus, Idioprioniodus cf. healdi, Kladognathus aff. levis, Lochriea commutata, Mestognathus beckmanni, Patrognathus capricornis, Polygnathus bischoffi and Vogelgnathus cf. campbelli. Elements recovered which have not yet been referred to multielement species are: Angulodus cf. sp. nov. B of Rhodes et al. (1969), 'Apatognathus' cuspidatus, 'A.' libratus, 'A.' petilus, Geniculatus cf. claviger and Gen. et sp. nov.

The outer ramp fauna is the most abundant, and is dominated by species of Gnathodus. The cavusgnathoid genera and Polygnathus bischoffi are virtually confined to the more nearshore environments; and Vogelgnathus cf. campbelli and ?Hindeodus scitulus, although recovered from throughout the study area, were capable of living in extreme, euryhaline(?), littoral environments.

The Arundian outer ramp deposits have been divided into a series of three biostratigraphical zones on the basis of conodonts (Gnathodus cuneiformis Zone, G. texanus Zone and G. aff. girtyi Zone). This zonation does not correlate directly with any previously erected zonations, but parallels are drawn with the Arundian conodont faunas of the Craven Lowlands (Metcalfe 1981) and County Limerick (Austin and Husri 1974).

The reported stratigraphical ranges of the following species have been extended: Cavusgnathus altus, Clydagnathus gilwernensis, Gnathodus cuneiformis and Idioprioniodus healdi(?). Gnathodus girtyi is thought to have developed from a previously undescribed gnathodontan - here termed G. aff. girtyi, and it is suggested that the form species Angulodus cf. sp. nov. B and Gen. et sp. nov. existed together in the same apparatus which may have been ancestral to Aethotaxis advena.

Conodonts recovered from the Llanelly Formation are stratigraphically long-ranging forms, but are taken to imply a Chadian to mid-Arundian age.

The overall changes seen in the conodont fauna through Arundian times do not support the adoption of an event based philosophy of conodont biostratigraphy; but suggest that, in this instance, conodont evolution occurred as a cumulative mosaic of effects rather than as short sharp punctuations in a series of 'equilibria'.

A review is made of the variety of processing techniques available to conodont workers.

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It has been a pleasure to work alongside members of the present British "Carboniferous community" amongst whom John Simpson and John Scott were particularly benevolent. They introduced me to the sedimentology of South Wales, and their infectious enthusiasm for Carboniferous limestone and its study in the field has been a major plus throughout my work. I have been fortunate to discuss my project and its progress with Drs R. Waters, G. Sevastopulo and V.P. Wright, all of whom have made numerous useful suggestions.

The British Micropalaeontological Society Conodont Group provide a forum for interaction between British workers and I am grateful to have been able to take advantage of this. The enthusiasm and knowledge provided by Dr R. Aldridge has been invaluable; and M. Dean, R. Knight and A. Swift have all been most encouraging.

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Finally I thank Professor Nesbitt for use of facilities at the Department of Geology and acknowledge the University of Southampton for providing financial support through a University Scholarship; and my parents for providing financial support through their own munificence.

"...most of what I think I know about conodonts as animals is either conjecture or a highly personal interpretation of a still imperfect fossil record. So, with the caveat that what follows is only one way of viewing an important group, I offer my account..."

Sweet (1988).

PART ONE

GENERAL INTRODUCTION AND PREVIOUS WORK

1.1 CONTEXT AND ORGANISATION OF THIS THESIS.

It is anticipated that the production of this thesis will have provided a training in conodont studies, and that the finished work will provide a foundation for further investigation of (multielement) conodont evolution in the late Viséan, the palaeoecology of the different groups and the facies limitations on their distribution.

Research on Carboniferous conodonts and Viséan conodont biostratigraphy has reached a watershed. Over the last twenty years numerous empirical local zonations have been erected and a basic framework of conodont occurrence has been established. A more broadscale picture is now needed so that the lack of correlation between disparate localities can be evaluated and explained. Knowledge of facies limitations and the use of multielement taxonomy will help to clarify the profligate speciation reported in the literature.

In the present study the Arundian Stage of the Dinantian Subsystem is investigated in detail. The study encompasses the varied intertidal to outershelf carbonate environments of South Wales. The sampling programme is based on an understanding of the sedimentology of the shelf environment, thus permitting an investigation of the effect of facies control on conodont distribution.

The Arundian Stage type-section is within the study area and it is intended that concentration on this time interval will ensure a well confined and correlatable study. This Stage is of particular interest as it is not fully represented in the standard British Dinantian conodont reference section of the Avon Gorge (Rhodes et al. 1969). Further, there is no distinct Arundian macrofaunal assemblage, and use of archaediscid foraminifera to mark the base may prove problematical in areas of a palaeo-water depth greater than 40-50 m. The study will make an appreciable addition to the limited information which has been published on the conodonts of South Wales.

The thesis is divided into three parts, and does not necessarily follow the organisational pattern of previous conodont studies. Part one summarises the background information pertinent to this study, and reviews: the present state of knowledge about conodonts in general, previous work on Viséan conodonts, and the Arundian Stage and its correlation. Part two comprises a detailed study of Arundian conodonts from South Wales and the implications thereof for mid-Viséan multielement reconstructions, conodont biostratigraphy and palaeoecology. In part three a review is made of extractive techniques used in the study of conodonts.

NB, although Ph.D. theses are not recognised as valid references for taxonomic purposes (Article 9 [11], International Code of Zoological Nomenclature, Ed. Ride et al. 1985), the work of Norby (1976) is considered integral to the understanding of Carboniferous multielement taxonomy, and is referenced "informally" in the present work. Not to do this would be misleading.

1.2 INTRODUCTION TO CONODONTS.

1.2a The nature of conodonts.

Conodonts were a group of vermiform animals, at least some of which are known to have been about 4 cm long (Briggs et al. 1983). They formed an appreciable component of the marine biota throughout Palaeozoic times; and their zoological affinity is the subject of much debate (see section 1.2d). In general these animals are only represented in the fossil record by denticulate phosphatic skeletal elements thought to have been part of the ingestive apparatus. The term conodont has been used to refer both to the whole animal and to the skeletal elements alone; where there may be some ambiguity Aldridge and Briggs (1986) suggest calling the former "conodont animal" and the latter "conodont elements" (see also Jeppsson 1982, and Fåhræus 1983). Because the animal's soft parts are very rarely preserved, conodont elements have traditionally been studied in isolation. The elements range in length from 0.2 mm to 13 mm (Austin In: Higgins and Austin 1985, Aldridge et al. 1988) and are composed of calcium phosphate and organic matter.

Analysis of the non-organic component by Pietzner et al. (1968) revealed it to consist of francolite (a variety of apatite containing appreciable CO_2 and >1% fluorine) of the following specific formula:
$Ca_5Na_{0.14}(PO_4)_{3.01}(CO_3)_{0.16}F_{0.73}(H_2O)_{0.85}$. Within the organic matter, some identifiable amino acids have been reported (Armstrong and Halstead-Tarlo 1966, Pietzner et al. 1968, Fåhræus 1985).

Conodont elements can exhibit one of three modes of growth and associated levels of structural complexity (Bengtson 1976; Szaniawski 1987). Euconodont elements are the most common and the most widely studied; they grow centrifugally, and have been recovered from a wide variety of marine sediments. These range in age from the Dolgellian Stage of the Late Cambrian, which is equivalent to the Franconian in the United States of America (U.S.A.); to the Rhaetian Stage of the latest Triassic (Swift pers. comm. 1987). Paraconodont elements range from the mid-Cambrian to the Ordovician, they display a slightly different growth habit from euconodont elements (each successive growth lamella does not wholly encompass the entire element), and

contain more organic matter. **Protoconodont elements** range from the uppermost Pre Cambrian to the mid-Ordovician. They are thought to be the most primitive of the three groups as they contain the largest proportion of organic matter and exhibit the simplest growth habit. The evolutionary relationship between the three groups is uncertain; Bengtson (1983a) and Szaniawski (1987) place all three groups in one phylogenetic lineage. Dzik (1986) and Aldridge (1987) point out that the link between protoconodonts and paraconodonts is tenuous, and suggest that euconodonts may have evolved entirely separately from both.

Euconodont elements occur as a variety of morphological types which can be divided into three broad categories:

i) **coniform elements,** all of which are essentially cone-like but may exhibit different degrees of flexure and a variety of outlines in transverse section (fig. 1.2.1a and b).

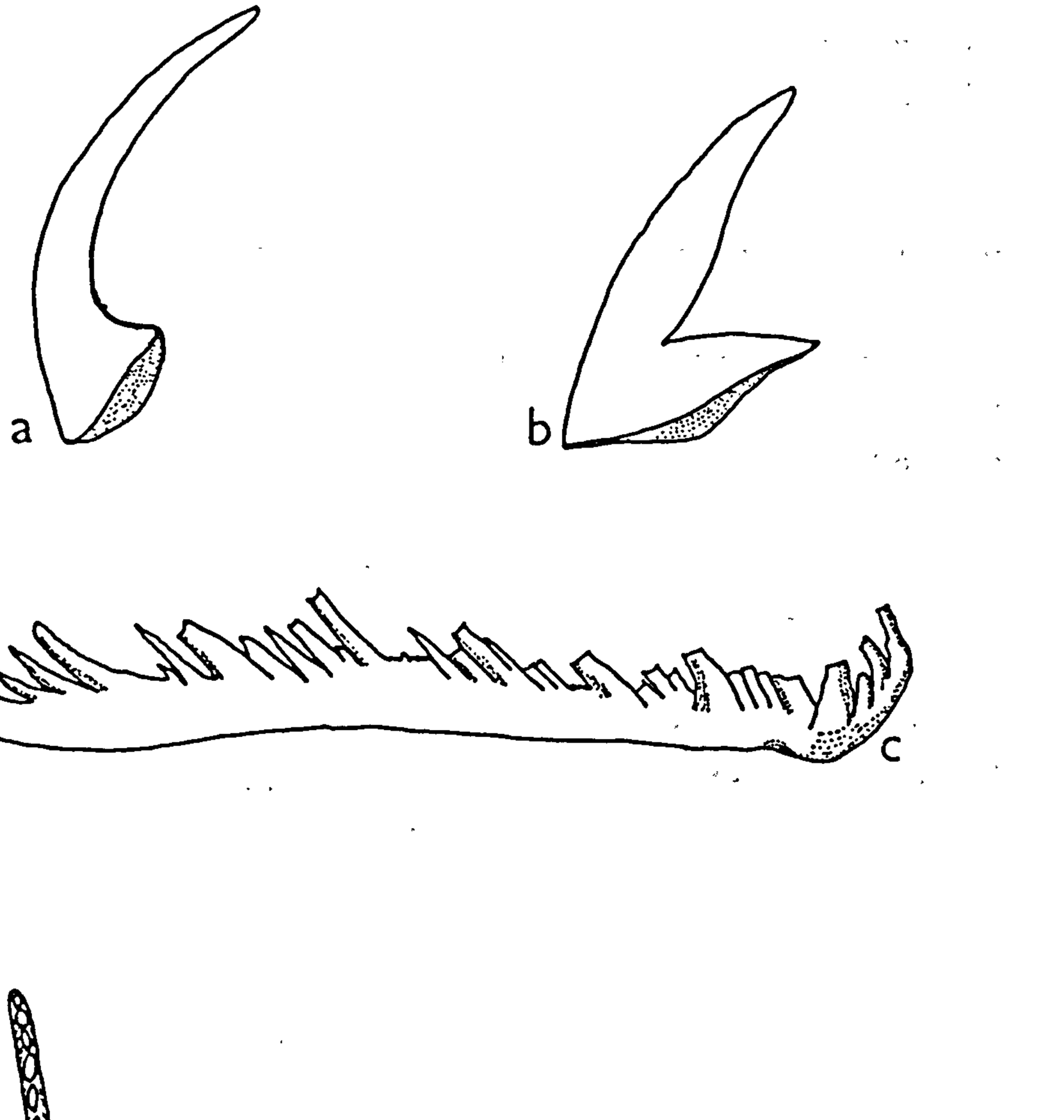
ii) **ramiform elements,** in which the base of the element is greatly extended longitudinally to form a long bar or bars which often support denticles (fig. 1.2.1c).

iii) **pectiniform elements,** in which the base of the element is extended downwards to produce "blades" (i.e. flattened bars), one of which may be expanded laterally to produce a "platform" (fig. 1.2.1d). Commonly the upper side of the platform is ornamented with nodes, ridges or "parapets" (or a combination of these).

1.2b Notation and nomenclature used in the study of conodonts.

In the earliest report and description of conodonts, Pander (1856) thought conodont elements to be fish teeth and that each "fish" contained only one type of element. Both these suppositions are now known to be incorrect, and much controversy and confusion has arisen as a result. Pander gave a Linnean binomial name to each individual type of element, assuming each to represent a separate species of fish. Work by Hinde (1879) and subsequent authors (see section 1.2e) has established that in most cases, any one species of conodont animal contained a range of element types which made up a single apparatus. Consequently **multielement taxonomy,** a more biologically based classification, has developed; in which different types of element are grouped together in apparatuses as they occurred in the individual conodont animals. Such apparatuses are named after the first described disjunct element they contain, as long as that name is not already in use. In some cases the existence of this dual nomenclature can cause confusion, and in this thesis use of single element taxonomy is denoted by the suffix s.f. (sensu formo), as suggested by Barnes and Poplawski (1973) and Chatterton (1974).

figure 1.2.1 Examples of the variety of types of conodont elements.
a) non-geniculate coniform element (after Lindström 1964).
b) geniculate coniform element (after Lindström 1964).
c) ramiform element.
d) pectiniform element, i-upper view.
ii-lateral profile.



The original disjunct element names can also be used informally for describing the individual elements of an ill-defined apparatus. The suffix "an" is added to generic names and the suffix "iform" is added to specific names (Klapper and Philip 1971). The formal use of single-element taxonomy is invalidated by the International Code of Zoological Nomenclature (Ride et al. 1985).

Although individual conodont elements seemingly exhibit a stunning variety of morphology, there are just fourteen shape categories to which all elements can be referred: two for coniform elements, seven for ramiforms and five for pectiniforms (Sweet, In: Clark et al. 1981). Coniform elements* may either be **geniculate**, in which cusp and base subtend an acute angle, or **non-geniculate** (fig. 1.2.1a and b).

Ramiform elements are classified according to the number and nature of their processes.

i) **Alate:** bilaterally symmetrical with a posterior process, and two symmetrical lateral processes which commonly form an arch beneath the cusp when viewed anteriorly. For example the Gnathodus Sa element (interpretive sketch 2.2.13 page 101).

ii) **Tertiopedate:** similar to alate elements except that the two lateral processes do not mirror each other. For example Gen. et sp. nov. of this study (interpretive sketch 2.2.46 page 171).

iii) **Digyrate:** another element with one posterior and two lateral processes, but the posterior process is short and adenticulate; and the lateral processes are markedly dissimilar in shape and orientation. For example the Idioprioniodus Pb element (interpretive sketch 2.2.24 page 125).

iv) **Bipennate:** one anterior and one posterior process only. Typically the latter is the longer, and the former may exhibit a degree of flexure. For example the Gnathodus Sd element (interpretive sketch 2.2.17 page 107).

v) **Dolabrate:** one posterior process only, often giving a pick-like lateral profile. A marked anticusp may be developed. For example the cavusgnathoid M element (interpretive sketch 2.2.2 page 77).

vi) **Quadriramate*:** rare ramiform element with four processes.

vii) **Multiramate*:** ramiform elements with more than four processes.

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* These elements are not represented in this study.

Classification of **pectiniform elements** is based primarily on the number of processes present.

i) **Stellate*:** elements with at least four primary processes.

ii) **Pastinate*:** elements with three primary processes.

iii) **Carminate:** elements with one anterior and one posterior process, exhibiting an essentially straight lateral profile. For example the Gnathodus Pa element (interpretive sketch 2.2.4 page 85).

iv) **Angulate:** similar to carminate elements but with an arched profile in lateral view. For example the Gnathodus Pb element (interpretive sketch 2.2.11 page 98).

vii) **Segminate*:** elements with just one, anterior, process.

At an informal level, pectiniform elements are commonly divided into those which do not exhibit any marked lateral expansion ("blades"); and those which do ("plates" or "platforms"). In the case of "platforms", one of two suffixes is added to the above terms:

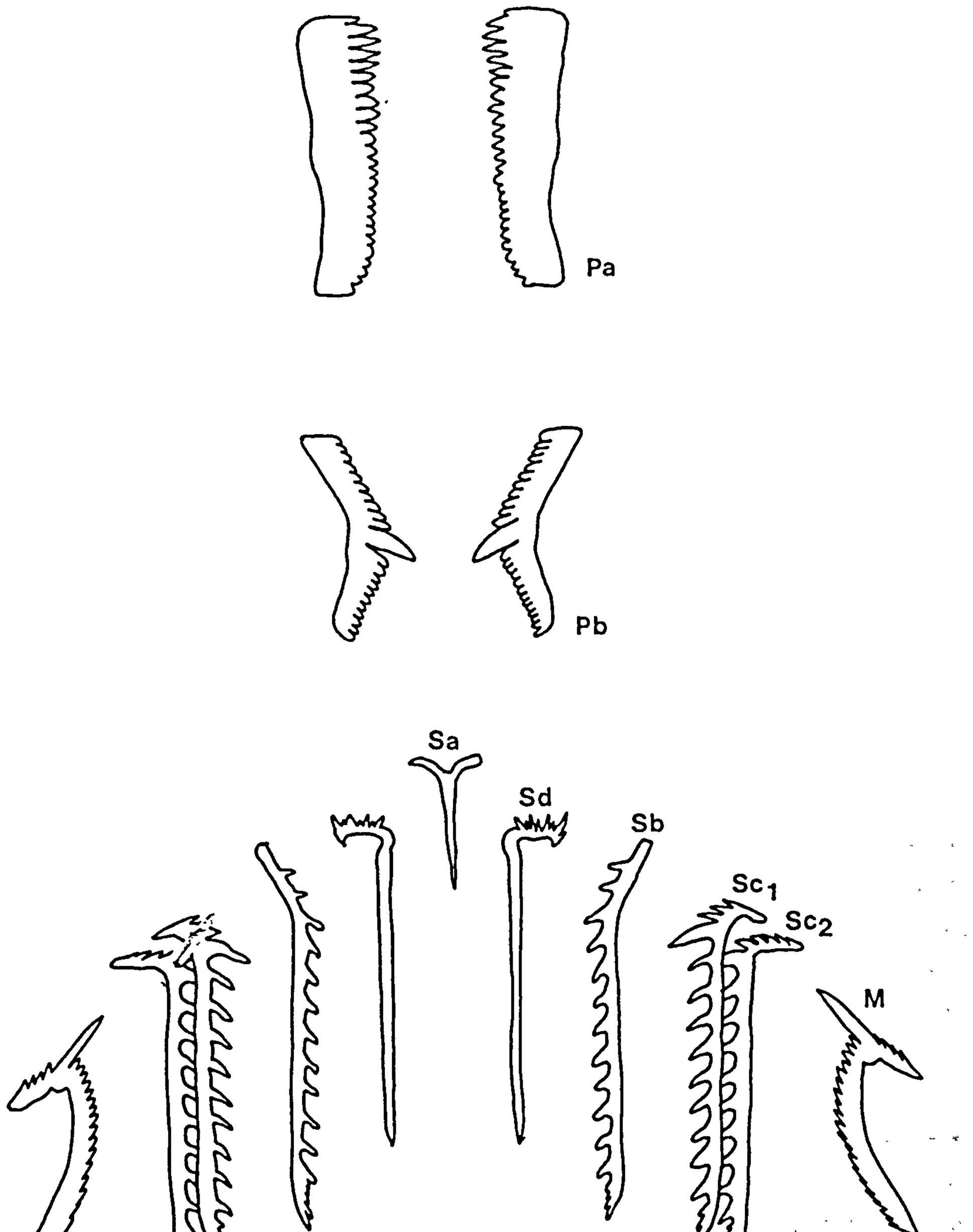
scaphate if the basal cavity is capacious, or

planate if the basal cavity is restricted.

For example the Gnathodus Pa element (e.g. interpretive sketches 2.2.4 and 2.2.5 page 85) is described as carminiscaphate.

Since the late 1960's and early 1970's researchers have endeavoured to work at the level of the conodont animal, and study entire apparatuses rather than single elements. Sweet (In :Clark et al. 1981) established terms to describe the number of types of element present in any apparatus. Essentially an apparatus may either be **unimembrate,** if only one type of element is present (as in some Cambrian animals); or **multimembrate,** where a variety of elements occur in an apparatus. Depending on the number of types of element, a multimembrate apparatus is termed: bimembrate, trimembrate, quadrimembrate, quinquimembrate, seximembrate or septimembrate. As most, but not all, types of element occur in pairs (left and right), this terminology implies nothing about the total number of discrete elements present in an apparatus. A study of preserved apparatuses and the reconstructions based on bedding-plane assemblages, reveals that multimembrate apparatuses are constructed on a limited number of recurring plans. The most common plan is either seximembrate or septimembrate, and is seen from Silurian to Triassic times (fig. 1.2.2). A number of authors have suggested notational schemes to describe the positions within this plan (e.g. Klapper and Philip 1971; Kozur and Mostler 1971; and Jeppsson 1971), however the system which has become widely adopted is that of Sweet (In :Clark et al. 1981). The component positions are divided into three categories (fig. 1.2.2):

figure 1.2.2 Schematic representation of the septimembrate apparatus of Gnathodus (after Norby 1976), showing the positional nomenclature used in this study. For a more likely interpretation of element orientation see figure 1.2.4.



i) **P positions** are occupied by paired pectiniform or specialised ramiform elements. Typically there are two types which are designated Pa and Pb.
ii) **M positions** are commonly occupied by a pair of dolabrate elements in polygnathacean apparatuses but in some groups bipennate, digyrate or coniform elements may occur.
iii) **S positions** are occupied by a series of ramiform elements. A single alate element typically occupies the Sa position and a series of paired ramiform elements complete a symmetry transition series through Sb, Sc and in the septimembrate apparatus Sd positions.

Although the above notation was originally intended to simply refer to positions in apparatuses, it is now common to use it when referring to the elements themselves. For example the dolabrate element in the Gnathodus apparatus is termed the Gnathodus M element or simply an M element - rather than "the element typically occupying the M position". When thinking of the apparatus as a functional whole, it may be divided into two semi-independent parts: the rather sturdy, paired P elements at the posterior; and the complex of more spindly ramiform M and S elements toward the anterior. The exact position of the M elements relative to the S elements is difficult to infer from preserved apparatuses. Aldridge (1987) and Nicoll and Rexroad (1987) propose that, in the polygnathacean apparatus, the M elements are toward the anterior and on the flanks of the complex of S elements.

1.2c Outline history of conodont studies.

Huddle (1972) suggests that the first known conodont reference is: Pander (1851), in which Silurian conodonts appearing as "very minute bodies not much larger than pin heads" were examined by Barrande, Carpenter and Pander; although these were assumed by Murchison (1854) to be "the ends of segments of some trilobite". It was not until 1856 that Christian Heinrich Pander first coined the term conodont and, in his monograph on Silurian fossil fish of the Baltic provinces of Russia, provided the earliest known descriptions and illustrations of conodont elements.

It is possible to delineate several major steps in an overall review of conodont research. Following the work by Pander, which included detailed structural examinations, conodont studies proceeded very slowly, mainly in Europe, until the 1920's when "the initiative in conodont research passed over to N. America" (Lindström 1964). An important publication describing many new species was "A classification of the toothlike fossils, conodonts, with descriptions of American, Devonian and Mississippian species" (Ulrich and Bassler 1926). This paper was the first to illustrate the great **biostratigraphical potential** of conodonts and since 1926 conodonts have played an important role as index

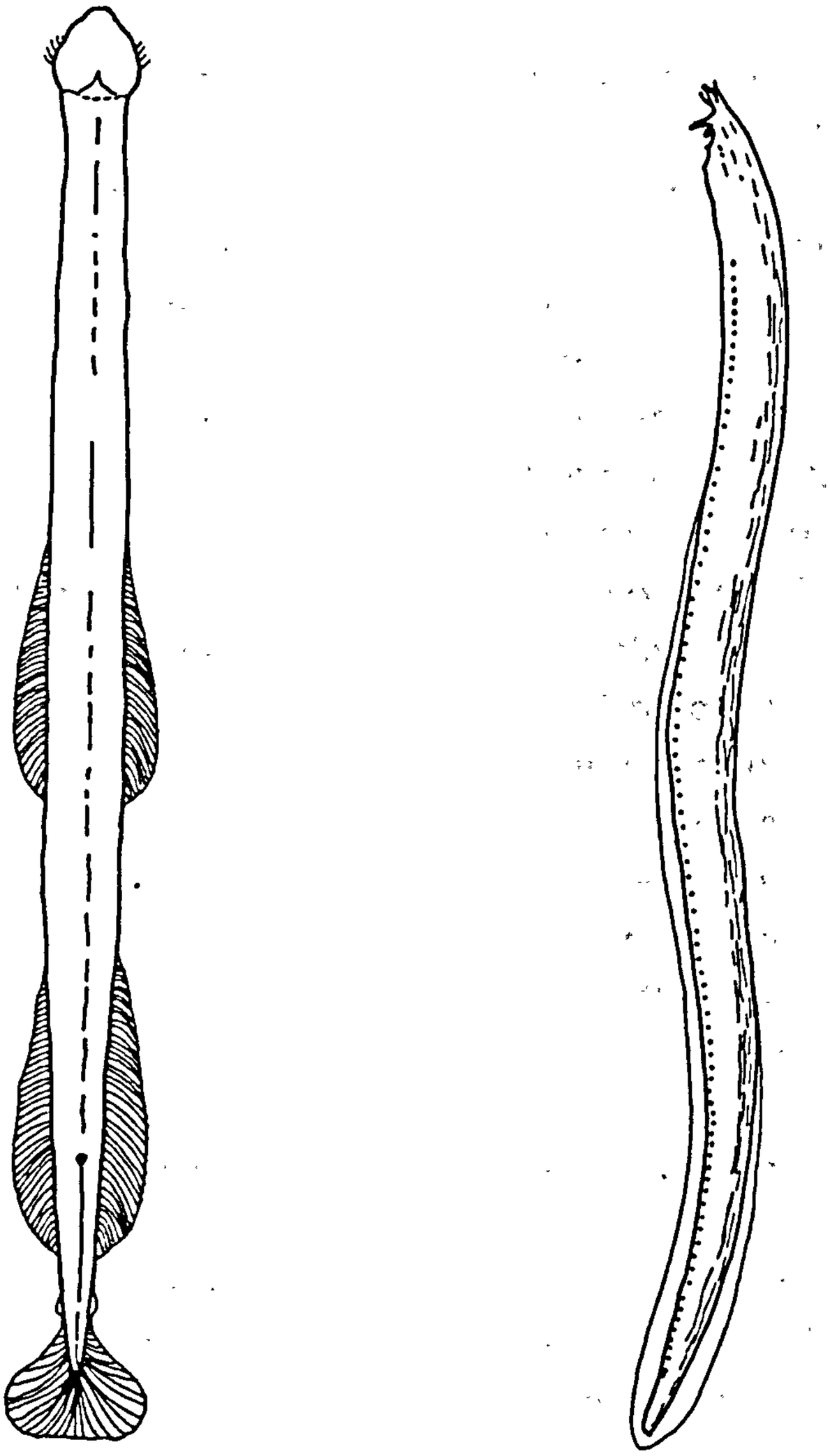
fossils. Branson and Mehl (1933-4, 1938, 1940, 1941) described entire conodont faunas from the Ordovician to the Mississippian, and the vast majority of these forms were new to science. An important advance was that they isolated their elements from the rock matrix (soft shale) to allow a true **three dimensional study.** Until about 1950 the majority of conodont work was purely descriptive and although each described fauna was related to its local stratigraphy there was no overall stratigraphical synthesis. In 1952 Fay published "a catalogue of conodonts" allowing future workers to interrelate the various unconnected studies, and to build up an overall **conodont biostratigraphy.** Graves and Ellison (1941) introduced the technique of dissolving limestone in acetic acid, to leave a conodont-rich residue, and by the early 1950's the technique had come into general use and allowed easy access to well preserved specimens from a great number of new localities.

With the publications of Beckmann (1949), Rhodes (1952, 1953, 1954), Sannemann (1954, 1955) and Lindström (1955), conodont research in Europe underwent a resurgence. Also, acceptance that most conodont animals had a **multielement apparatus,** ushered in a whole new area of study involving multielement reconstruction, and the functional morphology, palaeoecology and evolutionary lineages of the conodont animal. In the 1970's it became apparent that the occurrence of many conodonts was **facies related** and Seddon and Sweet (1971) and Barnes and Fåhræus (1975) erected opposing theories; suggesting a primarily depth stratified, pelagic habit, and a primarily nektobenthic habit respectively. It now seems likely that conodonts occupied a variety of life habits throughout their existence (Barnes 1976). The recent discovery of 10 specimens of **the conodont animal** (Briggs et al. 1983, Mikulic et al. 1985, Aldridge et al. 1986, Aldridge pers. comm. 1987) has sparked much interest and research into the palaeobiology and affinity of the conodont animal and the functional morphology of the conodont apparatus (see sections 1.2d, 1.2e and 1.2g).

1.2d Affinity of the conodont-bearing animal.

The suggested affinities of conodonts include plants, most of the invertebrate groups and the chordates (Müller In: Clark et al. 1981); and Clark (In: Clark et al. 1981) concluded that, awaiting further evidence, conodonts should be assigned to their own phylum "Conodonta". Recently the structural similarity between coniform conodont elements and chaetognath grasping spines has led to suggestions of taxonomic affinity (Bengtson 1983, Szaniawski 1987). A counter-proposal, to designate conodonts as primitive chordates, has arisen from the study of several completely preserved conodont animals (Briggs et al. 1983, Mikulic et al. 1985, Aldridge et al. 1986).

figure 1.2.3 Possible modern analogues for the conodont animal.
a) The chaetognath Sagitta elegans (after R.D. Barnes 1980) (ventral view).
b) The hagfish Myxine (after Romer and Parsons 1977) (lateral view).



a

b

The phylum Chaetognatha comprises some 50 species of mainly planktonic marine animals, commonly termed arrow worms (fig. 1.2.3a). Because of their mode of embryological development they are grouped with the deuterostomes which, in terms of evolutionary complexity, include the "higher" phyla (Echinodermata, Hemichordata and Chordata). Arrow worms are flattened dorso-ventrally, and range in length from 30 mm to 100 mm. Hanging down from each side of the head are from four to fourteen large grasping spines, and two rows of much shorter "posterior and anterior teeth", used for grasping prey; Barnes (R.D. 1980) says that contrary to earlier opinion, the spines are non-chitinous. The spines are enclosed in a fleshy hood during swimming, both for protection and streamlining. All arrow worms are voracious carnivores feeding on planktonic animals, it is thought they may inject poison to paralyse their prey, which they detect with highly adapted sensory hairs. Chaetognaths are hermaphrodite, have a post-anal tail, and have no specialised organs for gas exchange, excretion or internal transport. Szaniawski (1982, 1983) highlights the similarities between the structure of protoconodont elements and chaetognath grasping spines, and makes a strong case for their taxonomic affinity; further, he supports Bengtson (1976) in suggesting that protoconodont, paraconodont and euconodont elements are homologous, and therefore share a common lineage with the chaetognaths. However the complexities of Upper Palaeozoic conodonts are far removed from their simple coniform beginnings and Szaniawski (1987) suggests that euconodonts "are certainly not chaetognaths sensu stricto"; but instead represent an evolutionary offshoot from them, in which there was rapid diversification. Dzik (1986) emphasises that while chaetognath grasping spines and protoconodont elements may be very closely related, there is no histological justification for placing protoconodonts and euconodonts in the same lineage. Hence, any structural similarities between chaetognath grasping spines and early euconodont elements can be viewed as analagous rather than homologous.

Aldridge et al. (1986, 1987 and pers. comm. 1987) and Smith et al. (1987) have studied a series of exceptionally preserved whole specimens of the conodont animal, nine from the Lower Carboniferous of the Edinburgh district, and one from the Lower Silurian of Wisconsin in the U.S.A. The Scottish specimens are elongate worm-like animals approximately 40 mm long and 1.9 mm wide. The conodont apparatus occurs in the head region, just posterior to two lateral lobes which flank a central lumen. Two axial linear structures are preserved along the bodies of several specimens and may represent the gut, nerve cord or notochord. The body is divided into a series of V-shaped myotomes (muscle blocks separated by "myosepta"), with the apices pointing anteriorly. A series of fin rays are commonly preserved, arranged asymmetrically about the tail of the animal. The presence of caudal fins would suggest a swimming organism in which the body would probably be flattened

either dorso-ventrally or laterally. Following their studies of the fossilised soft tissue of the conodont animals, Briggs et al. (1983) and Aldridge et al. (1986) made comparisons with three similar extant groups: the Chaetognatha (see above), and two subdivisions of the Chordata; the Cephalochordata, and the agnathan craniates. Such studies might be expected to provide valuable information about the taxonomic affinity and life habit of the conodont animal. It is interesting to note that all of the extant groups considered similar to the conodont animal, in view of the recent whole-fossil finds, possess a relatively high level of evolutionary complexity.

The Cephalochordata constitute a subphylum of just 2 extant genera and 14 species, a well studied example is amphioxus (Branchiostoma). They are simple, laterally flattened "fish-like" organisms with a notochord (a stiffened but springy cartilagenous rod), and V-shaped myotomes which act against the notochord when swimming. In general they live on the continental shelf and juvenile forms can swim freely, although adults burrow into the substrate and live as sedentary filter feeders. The cilia are borne on internal skeletal rods which give support and increase the surface area available for food capture. There are also several complex skeletal filtering organs posterior to the skeletal rods.

The subphylum Craniata (Vertebrata) includes fish, amphibians, reptiles, birds, mammals and of course Homo sapiens. The most primitive class of the Craniata is Agnatha, the "jawless fish", of which there is fossil evidence from the Upper Cambrian. The hagfish (order Cyclostomata, suborder Myxinoidea) is an extant example (fig. 1.2.3b). Craniates are defined on the basis of possessing some form of cranium, some trace of vertebrae, an elaborated brain with associated sight smell and sound receptors, and a heart with at least three chambers (Young 1981). If the skeletal elements take the form of cartilagenous plates and nodes, as in the hagfish, none of these criteria are likely to be preserved in the fossil record, and assignment of an extinct organism to the subphylum must be done on the basis of secondary characteristics. Hagfish have an elongate, laterally flattened body with an asymmetrical tail fin. A series of myotomes act against a notochord which stops short of the head, thus allowing for development of the brain. The mouth is surrounded by sensory tentacles and has a lingual structure in which rows of teeth become opposed during eversion and act laterally to tear and fragment prey. The gut is simple with no specialised stomach. The circulatory system comprises a series of sinuses with several accessory hearts, and the gills are pouch-like with openings to the pharynx and the exterior.

Aldridge et al. (1986) reject a possible chaetognath affinity for the conodont animal on the basis of the V-shaped myotomes, the apparent lateral flattening of the body and the asymmetrical posterior fins. The conodont animal is considered closer to the craniates than the cephalochordates due to a number

of factors. The transversely acting teeth of the hagfish are much closer to the presumed function of the conodonts than the skeletal rods of amphioxus, and Janvier (1983) suggests that the lateral lobes on the head of the conodont animal could represent the eversible lingual structure of the hagfish. Further the lack of axial structures (notochord) in the head region of the conodont animal, its presumed actively swimming life habit and the lack of mineralised structures in any living cephalochordates all add weight to the proposal of a craniate affinity.

Work by Fåhræus and Fåhræus-van Ree (1987) involving fixing and staining of the soft tissue left after decalcification of conodont elements, has produced the oldest "stainable" cell ever found. The tissue contains an appreciable component of cells, and hence differs from any known examples of biomineralisation, all of which have an organic component totally dominated by collagen fibres. Consequently there is no definite link with any of the extant groups which contain francolite in their skeleton (chordates, inarticulate brachiopods and molluscs), although nothing is known of the structure of mineralised tissue in early chordates. Aldridge et al. (1986) review the available evidence and suggest that there is no longer any justification for retaining a separate phylum Conodonta, and that the conodont animal should be viewed as a primitive craniate.

1.2e The conodont apparatus and its function.

i) Introduction.

In separate bedding-plane studies Schmidt (1934), and Scott (1934) both described numerous sets of different conodont elements lying in close association. Subsequently several further such occurrences have been recorded: Scott (1942), Du Bois (1943), Schmidt (1950), Rhodes (1952), Schmidt and Müller (1964), Mashkova (1972), Collinson et al. (1972), Avcin (1974), Norby (1976), Nicoll (1977), Higgins (1981a), Puchkov et al. (1982), Rhodes and Austin (1985). Although some of these assemblages are chaotic and probably coprolitic in origin, many show consistent organisation and alignment of the elements. Comparison with the wholly preserved conodont animals found in Scotland and Wisconsin (Briggs et al. 1983, Mikulic et al. 1985) shows that, as suspected by their discoverers, the organised assemblages above reflect how the elements were situated in life. Such finds provide the best evidence on which to formally reconstruct conodont apparatuses, but unfortunately these occurrences are rare.

Several examples of fused clusters of different conodont elements have been reported from acid-insoluble limestone residues: Rexroad and Nicoll (1964), Barnes (1967), Lange (1968), Austin and Rhodes (1969), Pollock (1969),

Higgins (1975), Behnken (1975), Landing (1977), Ramovs (1978), Nowlan (1979), Repetski (1980), Aldridge (1982) and Nicoll and Rexroad (1987). The nature of the fusing is likely to be diagenetic in most cases (Nicoll and Rexroad 1987), although Rexroad and Nicoll (1964) suggest that if it occurred during life, the fusing could be pathogenetic. Some of these fused clusters probably represent coprolitic or chance associations, however many do represent at least partial apparatuses of single animals (Aldridge and Briggs 1986).

Due to the rarity of bedding-plane assemblages and fused clusters (particularly from non-Carboniferous rocks), many apparatuses have been reconstructed on the basis of statistical, distributional and morphological evidence (for example: Walliser 1964, Bergström and Sweet 1966 and Webers 1966). Problems can exist in statistical reconstructions due to the different preservation potential of different types of element from the same apparatus. The occurrence of vicarious elements (those which are common to a number of apparatuses) must also be accounted for. Much of the early work involving multielement reconstructions concentrated on Lower Palaeozoic faunas. These faunas lend themselves to such reconstruction as they often contain a fairly limited size range of elements and therefore components of the same apparatus have a similar preservation potential.

ii) Types of apparatuses.

Klapper and Philip (1971) were the first to attempt serious statistical reconstructions of Upper Palaeozoic conodont apparatuses. In view of the diversity of such faunas and the corresponding range in preservation potential of their constituent elements, Klapper and Philip concentrated on relatively simple and environmentally restricted Early and Mid-Devonian faunas. The basic apparatus plans arrived at were then compared with more complex Late Devonian faunas. One of the most interesting points to arise from their work was that despite studying "large and diverse mondial collections of Devonian conodonts", only four different types of apparatus plan were recognised. Further, these plans were found to be essentially similar to those occurring in other parts of the geological column. Studies of Missourian (Stephanian) conodont faunas from limestone and shale residues, led Baesemann (1973) to propose a fifth apparatus plan (Type 5) restricted to the monotypic taxon Aethotaxis advena.

Type 1 apparatus:

This is the standard polygnathid arrangement (e.g. Gnathodus) with paired platform (Pa), ozarkodinan (Pb) and neoprioniodontan (M) elements posterior to a symmetry transition series comprising a single symmetrical element (Sa) and paired hindeodellan elements (Sb, Sc and Sd). In some apparatuses the Sd element may be absent, and as originally defined for Devonian apparatuses the Sc element is angulodontan rather than hindeodellan. The compound (non-

platform) elements of this apparatus are often found to be vicarious; in contrast to the findings of workers reconstructing Ordovician apparatuses.

Type 2 apparatus: This is a less common arrangement (e.g. Parapolygnathus) and is similar to Type 1 (above) except for a different symmetry transition series, comprising one pair of ligonodinan elements and two pairs of lonchodinan elements. Also the element occupying the Pb position is not ozarkodinan but aversiform (from Prioniodina aversa s.f.) As with Type 1 apparatuses the compound elements are commonly vicarious.

Type 3 apparatus:

Identical with Type 2 (above) except for the total absence of a Pa element (e.g. Idioprioniodus).

Type 4 apparatus:

As defined by Klapper and Philip, this is fundamentally different from the previous three plans in that it only comprises a pair of icriodontan elements and two pairs of coniform elements. The accuracy of this plan is uncertain as subsequent workers have suggested that each apparatus may have included many coniform elements (Nicoll 1982).

Type 5 apparatus:

This plan comprises a pair of X elements (peculiar to Aethotaxis), and a peculiar symmetry transition series (Baesemann 1973).

In addition to these categories some Lower Palaeozoic apparatuses are entirely coniform, and may be unimembrate or multimembrate. Barnes et al. (1979) discuss these apparatus types in detail. The very different organisation of some of the early apparatuses may imply a slightly different function from the more complex apparatus types listed above. The elements recovered in this study are generally referable to the Type 1 and Type 3 apparatus plans.

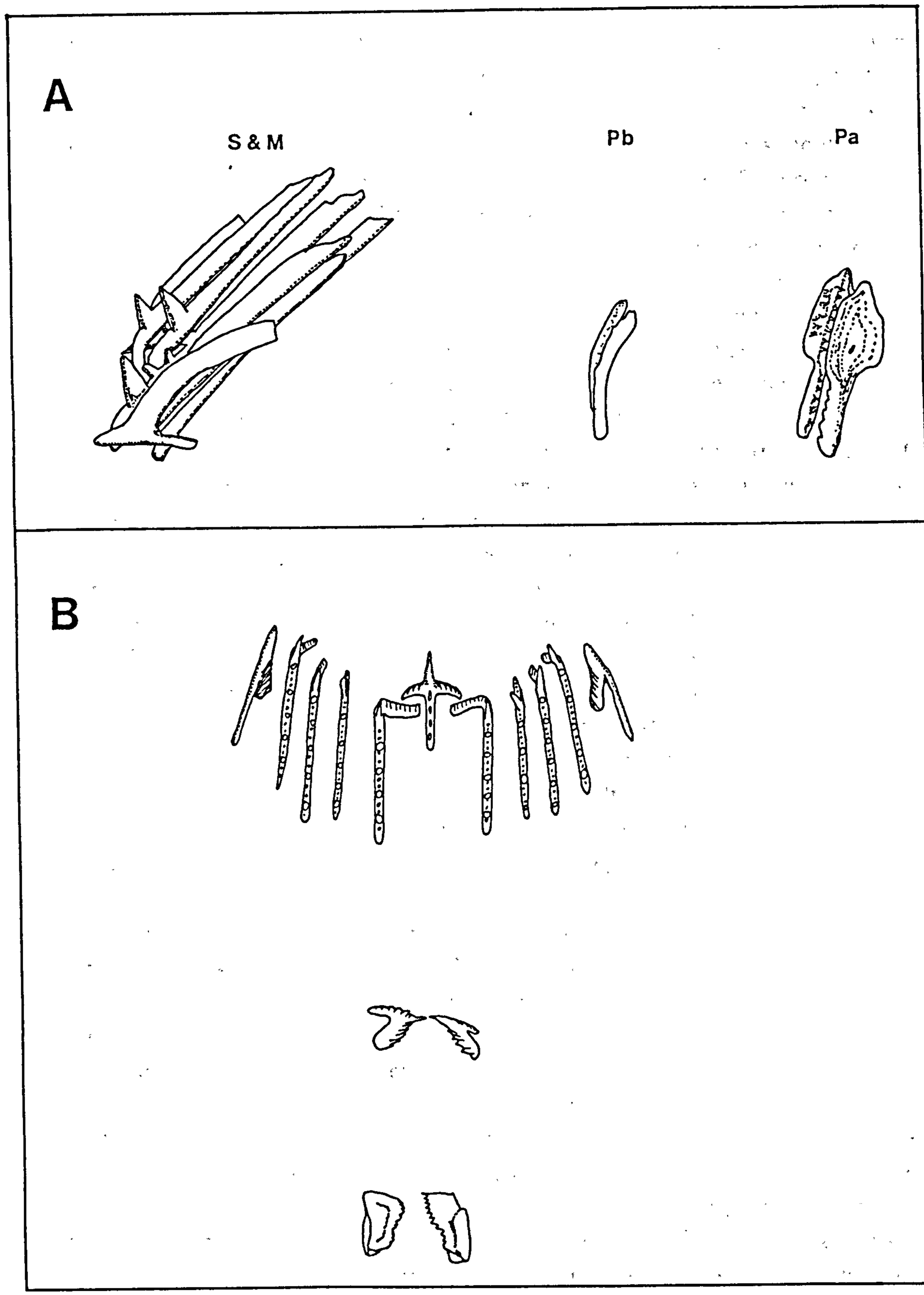
It seems reasonable to suppose that if a function can be deduced for one apparatus, it will be applicable to all others. It is therefore an advantage to recognise functionally equivalent elements occuring in different types of apparatus. Sweet (In: Clark et al. 1981) was able to apply his Pa, Pb terminology (see section 1.2b) to the first three of the above categories, thus illustrating potential positional and functional homologies. He also suggests that in the apparatus of Icriodella superba s.f. there are equivalents to Pa, Pb, M, Sa and Sb elements, implying that Type 4 apparatuses may also be based on the same essential plan. In general however it is agreed that the Pa, Pb notational scheme does not fully account for apparatuses which include cone elements (Nicoll 1982).

iii) Three dimensional structure.

It has long been accepted that most conodont apparatuses were bilaterally symmetrical (Schmidt 1934), and that the elements were laterally opposed as right and left forms rather than as upper and lower jaw-like structures (Rhodes In: Moore 1962). The discovery of the conodont animal specimens (Briggs et al. 1983, Aldridge et al. 1986) has shown that the apparatus was orientated with the paired platform elements toward the posterior of the apparatus and the ramiform basket toward the anterior (see fig. 1.2.4). The vast majority of known bedding-plane assemblages are of polygnathacean (Type 1) apparatuses. Aldridge et al. (1987) re-investigated many of these and added information from the conodont animals. They were able to assign each assemblage to one of four patterns depending on the relative orientation of the three sets of elements (Pa, Pb and ramiform). In a remarkable piece of "palaeo-pathology" they showed how each of these patterns could be produced by collapsing a single three dimensional structure in different orientations, as would be the case when dead conodont animals came to rest at varying angles. The deduced structure is shown in figure 1.2.4, the paired platform elements are transversely orientated to the long axis of the animal and the ramiform elements are oblique. The death assemblage orientations could just as easily be produced by ventrally or dorsally facing denticles, however analysis of the conodont animal specimens leads Aldridge et al. (1987) to favour the latter.

The exact position of the M elements is difficult to ascertain and in a study of fused element clusters, Nicoll (1985, 1987) and Nicoll and Rexroad (1987) suggest they were not lateral but situated to the anterior of the S elements. Nicoll suggests all the elements could have been situated in a food groove, and positioned with the cusps and denticles of the ramiforms pointing ventrally, and with the pectiniform elements in the horizontal plane (cf. fig. 1.2.4). Nicoll (1987) compared fused clusters of Ozarkodina and Polygnathus elements, and deduced that the Sd elements were aligned with the other S elements in the former but totally posterior to them in the latter. The suggested controlling-factor for this difference is the presence or absence of a posterior process on the Sa element. Aldridge et al. (1987) based many of their conclusions on bedding-plane assemblages of Gnathodus bilineatus, the Sa element of which does have a posterior process, yet they aligned the Sd elements with the other S elements. The present evidence is inconclusive with regard to the detailed architecture of the ramiform elements, although the data from bedding-plane material should provide more reliable conclusions than fused-cluster analyses.

figure 1.2.4 Schematic representation of the structure and life-position of components in the Type 1 apparatus, as deduced by Aldridge et al. (1987): A-lateral view.
B-upper view.



iv) Function.

Early thoughts on the operation of conodont elements were not constrained by the need for an integrated multielement function. Accordingly suggestions have ranged far and wide. Pander (1856) thought conodonts were fish teeth and this view has consistently been invoked ever since (e.g. Ulrich and Bassler 1926, Branson and Mehl 1933, Schmidt 1934, Ellison 1944). Murchison (1854), to whom Pander showed his specimens prior to publication, at first thought conodont elements to be part of a trilobite, and then revised his view to concur with Owen (In: Murchison 1867) that they were the "spines, hooklets or denticles of naked Mollusks or Annelides". Zittel and Rohon (1886) considered a function as annelid jaws and this view has been supported by among others Scott (1934) and Du Bois (1943). Other suggestions have included: the radular teeth of gastropods (James 1884, Loomis 1936 and Pilsbry 1937); tubuli from the carapace of a crustacean (Harley 1861); copulatory spicules of an extinct group related to the Nematoda and Turbellaria (Denham 1944); elasmobranch gill-rakers (Eichenberg 1930); and equivalents of the mandibles, hyal basket and gill basket of jawed fish (Schmidt 1934, Schmidt and Müller 1964).

The modern debate takes into account the need for any postulated function to be applicable to the entire apparatus as defined above. Also the discovery of the soft parts associated with the conodont elements has meant that the affinity of the conodont animal (see section 1.2d) is no longer a prime control on considerations of apparatus function. It is accepted that the apparatus was situated in the cephalic region of a vermiform marine animal, probably related to the primitive vertebrates or higher invertebrates. Due to their "concentric envelope" growth mode (Müller In: Clark et al. 1981), the elements must have been covered by soft tissue, at least during their formation. Current opinion is divided on whether or not the elements were covered by soft tissue during their operation. If not, a simple tooth function can be envisaged, otherwise some form of lophophore support function could be implied. Lophophores occur in filter feeding organisms (e.g. brachiopods) and comprise a set of ciliated tentacles which ring the mouth.

The suggestion that the conodont apparatus acted as a support for some form of soft tissue has been made by a number of researchers. Hass (1941) argued that due to the mode of growth, signs of ontogenetic repair and lack of worn surfaces the elements must have acted as internal skeletal supports and could not have been naked teeth. Lindström (1964, 1973, 1974) accepted this premise and suggested the apparatus could have acted as a lophophore support. Conway Morris (1976) added weight to the argument when he described a unique specimen of Odontogriphus omalus as a conodont-bearing lophophorate. Two years later, following some scepticism about Odontogriphus being a true conodont-bearing animal (only moulds of small "spikes" were preserved), Hitchings and Ramsay (1978) proposed a slightly different soft tissue support

function. Basing their model on Rhodes' (1952) interpretation of Scottognathus (Du Bois 1943), Hitchings and Ramsay saw the apparatus as part of an integrated filter feeding system and respiratory organ. The S elements acting as a sieve and support for ciliated tissue, with the M and Pb elements anterior to them as preliminary sieve units. The Pa elements were positioned anterior-most and acted as "lock-gates" opening and closing the system. However the fact that the finer ramiform elements occur anterior to the pectiniform elements in the Granton animals negates all these proposals. Recently Nicoll (1985, 1987) has put forward a theory in which the elements are covered in ciliated soft tissue, and the ramiform elements are anterior to the pectiniforms. The apparatus is situated in a "food grove" which is open to the water ventrally (Nicoll 1985, fig. 10). The ramiform elements act as a passive filtering mechanism, and the pectiniforms as "crushers and bruisers" of planktonic particles allowed through by the ramiform filter. A grasping function for the ramiform elements is rejected on the grounds that they are never found with their denticles opposed to each other. The main cusps of the M elements are seen as bars to stop the entry of any large particles into the food grove, while the posterior processes, with their associated ciliary currents deflect small particles towards the S element filter system. Similarly the cusps of the S elements deflect the larger particles, while the denticles filter and channel food matter. Nicoll (1987) sees the animal as microphageous in habit; and has looked at the way in which opposed pectiniform elements could have interacted. In many cases the oral surfaces intermesh, and due to space considerations he suggests it is more likely that the elements rocked or rasped over each other rather than moving apart and together like vertebrate teeth.

Priddle (1974) resurrected Schmidt and Müller's (1964) proposal that the elements were covered with a horny cusp, and in addition drew parallels between them and the "teeth" of modern myxinoids which are borne on an eversible lingual structure. The contention that the elements were uncovered during their operation and acted like vertebrate teeth has been argued most strongly by Jeppsson (1979) and is supported by Briggs et al. (1983) and Aldridge et al. (1987). The major drawback with this argument has been the addition of successive outer lamellae during growth (Conway Morris 1980); but as pointed out by Bengtson (1976, 1980) and Jeppsson (1979) this could be explained if the elements were folded into a soft-tissue covering during rest and growth periods and then everted during use. Jeppsson (1979) noted a number of structural similarities between various vertebrate teeth and conodonts (e.g. general shape, surface striations and barbs) and considered them to be analagous structures. Jeppsson was also able to draw parallels between occluding teeth and platform elements, shearing teeth and ozarkodinan elements, and non-converging teeth and ramiform elements. Similarly Briggs et al. (1983) suggest the most credible integrated function to involve the ramiform

elements grasping prey for processing by the pectiniform elements. Aldridge et al. (1987) further propose a cutting function for ozarkodinan elements and a grinding function for platform elements. The grasping action could have been facilitated by muscular rotation of the elements during active use.

In reviewing the proposed apparatus functions none of the suggestions ring true in every detail. It seems reasonable to accept that the apparatus was part of an ingestive mechanism, and that each was highly specialised for dealing with a particular type of prey. It must be remembered that associated with each element was the often unfossilised basal funnel (Sweet In: Clark et al. 1981) which would have drastically altered the shape of many elements. The elongate shape of the conodont animal, its asymmetrical tail fins and myotomic musculature all suggest an active raptorial habit; this is easier to reconcile with a tooth function than a filtering function. It seems that the ramiform and pectiniform elements performed slightly different functions as borne out by the occurrence of apparatuses without platform elements (e.g. Idioprioniodus), the possibility of some apparatuses losing their ramiform elements in high-stress environments (Horowitz and Rexroad 1982), and the fact that platform and ramiform elements commonly evolved at different rates (presumably in response to evolution of prey or competitors). In polygnathacean apparatuses the ramiform elements are most easily reconciled with a capturing or grasping function - followed by the ozarkodinan elements "slicing" bits off to be "mashed" by the platforms. However if this were the whole story the elements are seemingly over elaborate and it is likely that there are integral parts of the whole ingestive system which are not fossilised.

1.2f Conodont classification.

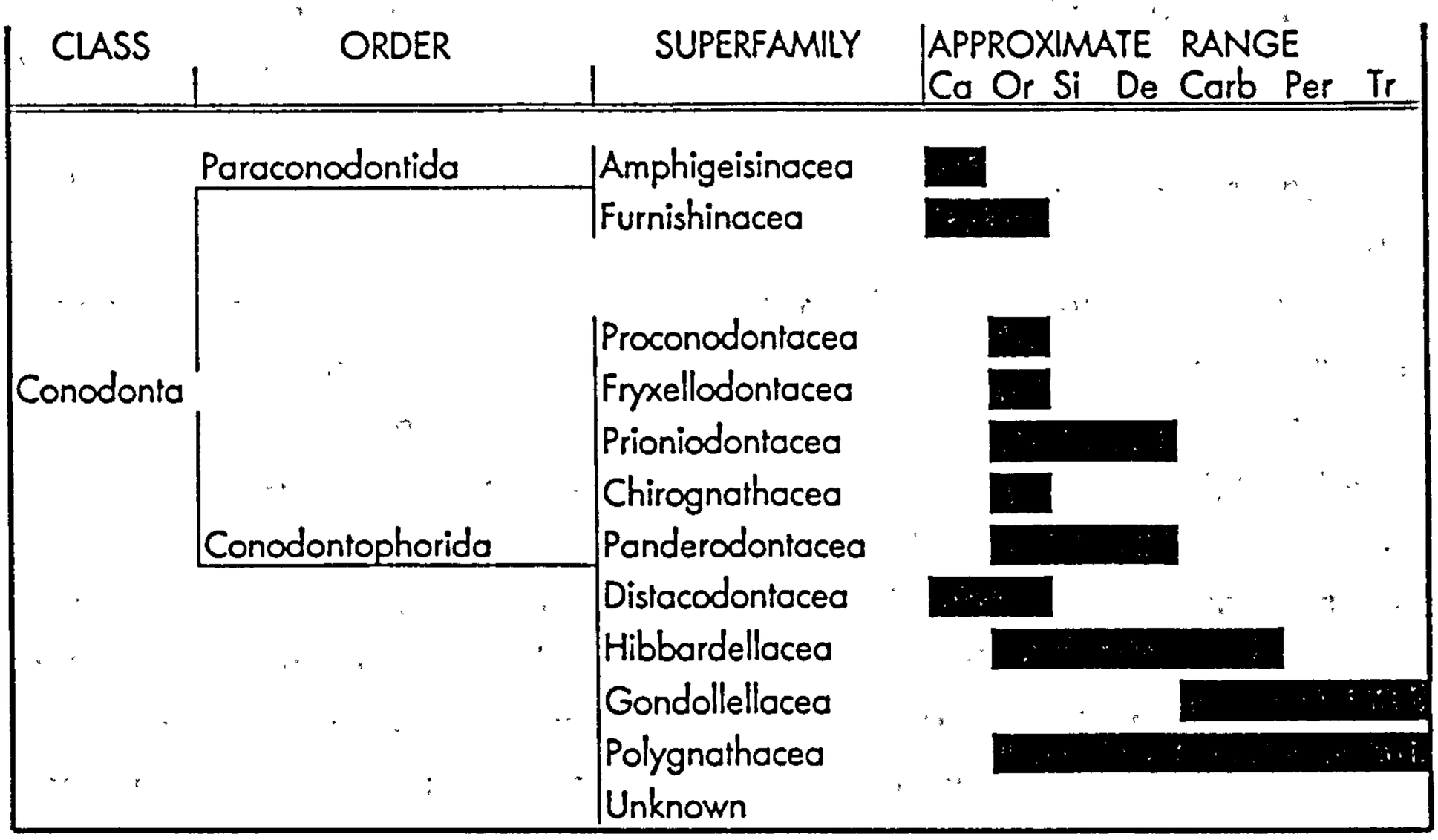
Lindström (1970) was the first to employ a multielement approach in erecting a full-scale conodont classification system. His scheme replaced several single-element systems (Ulrich and Bassler 1926, Branson and Mehl 1944, Hass In: Moore 1962). Lindström used several criteria to delineate his taxa, including: knowledge of natural assemblages, geological occurrence, presumed phylogeny, gross morphology, internal structure, chemical composition and nature of the basal filling. The scheme comprised two orders: the Westergaardodinida ("primitive" forms comparatively rich in organic matter and lacking white matter), and the Conodontophorida (conodonts proper). The latter contained eight superfamilies including the Distacodontacea (a simple group comprising only coniform elements or those with a single row of denticles), the Panderodontacea (mainly simple cones) and several groups with platform-based apparatuses. Within the Conodontophorida Lindström established twenty one families and four subfamilies.

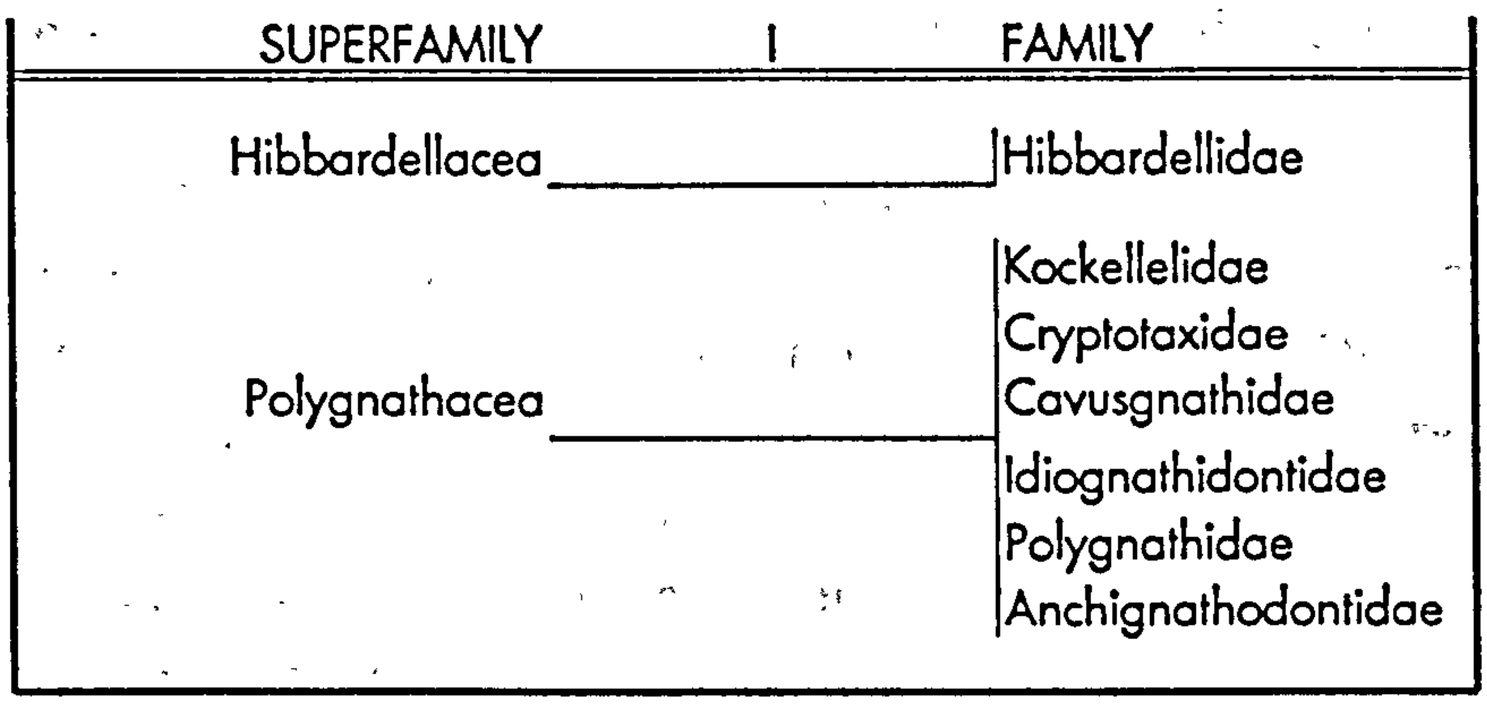
Clark et al. (1981) expanded Lindström's classification to include: two orders, differentiated on structural and chemical differences; eleven superfamilies, based on grouping of similar apparatus types and forty-seven families, each with distinctive apparatuses. Additionally forty-eight genera were listed under "family unknown".

The scheme of Clark et al. (1981) was regarded by its authors as "provisional" and was criticised by Fårhæus (1983, 1984) who highlighted various shortcomings including: a series of violations of the international code of zoological nomenclature (ICZN), looseness of wording of the diagnoses, and inconsistent application of the stated criteria for establishing assignments. Fårhæus' fundamental criticism was however the lack of a rigidly-applied scientific philosophical framework in the designations of rank and affinity.

Whilst being mindful of the shortcomings outlined above, for want of a suitably established alternative the Clark et al. (1981) conodont classification system is adopted in this study (fig 1.2.5).

figure 1.2.5 Suprageneric conodont classification scheme of Clark et al. (1981)





1.2g Facies control on mid-Viséan conodont distribution.

Until the mid-1960's conodont research was essentially orientated towards stratigraphy and the establishment of biozonational schemes (Seddon and Sweet 1971). More recently studies of the life habit and palaeoecology of the conodont animal have become common, and have gained impetus from the discovery of the exceptionally preserved specimens from Granton and Wisconsin (Briggs et al. 1983, Mikulic et al. 1985, Aldridge et al. 1986). Before the advent of ecological studies it was thought that conodont distribution was not facies related. The prevalent opinion of the earlier workers was summed up by Müller (In: Moore 1962): "conodonts commonly are not confined to sedimentary facies, since the same species is found to occur in different lithologies (e.g. limestone, shale, sandstone)".

As opinions began to change, Merrill (1962, 1965) reported "facies control" in his studies of Pennsylvanian conodonts. Varker (1967) was amongst the first to suggest Viséan faunas were affected by facies control. He noted that in the Brigantian and Pendleian rocks of northern England Apatognathus s.f. is found in the coral-brachiopod biofacies (shallow), but is absent from the goniatite biofacies (deep). In an attempt to explain the presence of such conodont-biofacies several broadscale ecological models were put forward. Seddon (1970), Seddon and Sweet (1971), and Druce (1973) suggested an active pelagic existence for the conodont animal with different species occupying various horizontal, depth-stratified zones; such that death assemblages become progressively more diverse in deeper water. However, further work illustrated that many shallow-water conodont species do not co-occur with deep-water forms. Druce (1970), Barnes et al. (1973a) and Barnes and Fåhræus (1975) invoked a nektobenthic or benthic life habit, such that changes in lithofacies would have provided a direct distributional control, and Barnes and Fåhræus also thought that certain conodonts may have been pelagic. Although this model was able to account for many recorded distributions, Klapper and Barrick (1978) showed that no conclusive explanation of the life habit can be achieved by a study of death assemblage distribution patterns. They conducted a comparative study of the distribution of modern benthic and pelagic marine organisms (chaetognaths, forams and isopods), and concluded that some pelagic (planktic) organisms show death assemblage patterns commonly associated with benthic organisms and vice versa.

As more data became available the early models were seen to have been somewhat simplistic, particularly with respect to the complex distribution patterns of coeval conodonts across Upper Palaeozoic shelf environments. In a study of Upper Palaeozoic faunas from Europe, America and Australia, Druce (1973) concluded that three broad biofacies could be seen throughout:

I Very shallow depths: characterised by simple cone forms at first then after the Famennian Stage by species with asymmetrical Pa elements, such as the cavusgnathoid genera.

II Intermediate depths, up to 50 m: characterised by species with "simple" Pa elements e.g. Lochriea commutata.

III Depths greater than 50 m: characterised by species with more elaborately ornamented Pa elements e.g. Gnathodus girtyi.

Subsequent data has largely corroborated these findings, although no palaeoecological justification was offered. A given genus is not confined to any one of the biofacies, but individual species probably are. Druce proposed that biofacies II contains the less elaborate "root stock" platform elements, and any subsequent evolutionary complexity was associated with a move from biofacies II to III. In general, the important zone species with a worldwide distribution occur in biofacies III.

Austin (1976), in a study of British Dinantian conodonts, related the distribution of upper Viséan conodont elements to a generalised carbonate platform model. A major division was made between coeval faunas recovered from shallow and deep water environments. Gnathodus and Ligonodina s.f. (e.g. Idioprioniodus and Kladognathus) were seen as distal-shelf genera occupying back-reef and reef areas. 'Apatognathus' s.f. and Spathognathodus cristulus s.f. (= Hindeodus) occupied the mid-shelf area and occur in back-reef, lagoon and neritic oolite sediments. Cavusgnathus and Mestognathus were viewed as proximal shelf genera occuring in littoral dolomites and neritic oolites. From his model Austin illustrated links between element morphology and environment. Asymmetrical Pa elements with an anterior blade offset to one margin are found in supratidal sediments (e.g. Cavusgnathus). Pa elements with large basal cavities (e.g. Gnathodus) are commonly recovered from more distal shallow water sediments; and those with small, narrow, restricted basal cavities (e.g. Polygnathus) typify deeper water environments. Austin suggested environmental energy levels and distance from shore as possible controls on distribution. Subsequent findings have supported the latter; but the sedimentological model on which Austin based his biozones (Austin 1976, figs. 3 and 6) is highly generalised and the implied energy levels do not relate to the present day sedimentological understanding of the upper Viséan shelf seas of South Wales (see section 2.1d).

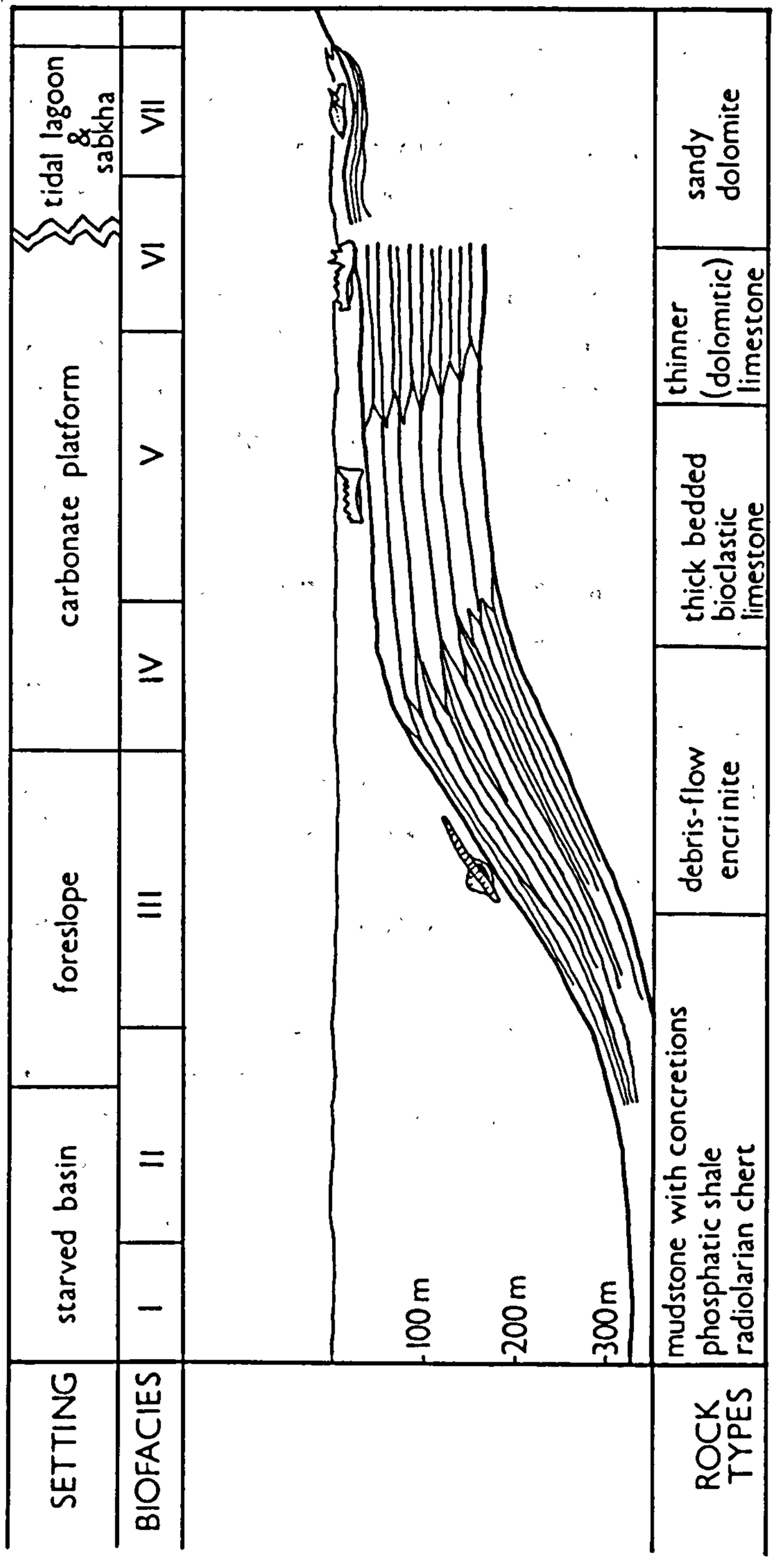
von Bitter (1976) compared coeval faunas from Ireland and North Wales described by Aldridge et al. (1968): the former is basinal and dominated by Gnathodus and the latter is a shelf fauna dominated by Mestognathus, 'Apatognathus' s.f. and Spathognathodus s.f. These faunas were used as a control against which to compare a fauna from the Windsor Group of Nova Scotia (Viséan-?early Namurian). By comparison with the North Wales fauna, von Bitter was able to deduce that the dominance of Cavusgnathus windsorensis

(normally uncommon) in parts of the Windsor Group occurred due to a very high-stress nearshore environment (shallow water, high energy and fluctuating salinity), in which few other species could flourish. C. regularis and C. unicornis were also interpreted as shallow water species but typical of slightly less extreme conditions, which they shared with other shelf genera such as Mestognathus, Taphrognathus and 'Apatognathus' s.f. von Bitter also noted that Mestognathus was of limited geographical occurrence, and in Windsor Group sediments flourished in high energy inter-tidal/reef conditions supporting algal mats and oolitic shoals. In concurrence with previous authors Gnathodus was seen as inhabiting more basinward deeper water environments.

Austin and Davies (1984) studied the distribution of Dinantian conodonts in Great Britain with respect to facies, and drew up separate basinal and shelf zonations (fig. 1.4.1). However they were only able to recognise relatively few coeval biofacies and some of their sedimentological information is open to question (e.g. the Pen-y-holt limestones of Stackpole Quay are interpreted as high energy sediments deposited in a water depth of a few metres: cf. section 2.1d), hence some of the inferred conodont life habits may be inaccurate. An important point resulting from their review of the available data was that shallow-shelf faunas should be recognised as such and not be used for correlation purposes.

From studies in the Western U.S.A. (Utah and Nevada), Sandberg and Gutschick (1984) revised and updated their earlier conodont biofacies models (Sandberg 1976, Sandberg and Ziegler 1979, Sandberg and Gutschik 1979, Sandberg and Dreesen 1983, 1984 and Gutschik and Sandberg 1983), and proposed seven coeval conodont biofacies for Viséan times (fig. 1.2.6). These biofacies are based on a number of cross-shelf profiles which were related to detailed facies analyses. The authors note that studies of the more restricted near shore platform environments of Britain and Belgium may lead to the discovery of additional biofacies. Environmental factors considered in the establishment of the biofacies are: salinity, bottom sediment, aeration and light intensity; these become increasingly influential in shallow shelf seas where many specialised ecological niches may co-exist (Dreesen et al. 1986). Further to their general model Sandberg and Gutschik attempted to infer detailed habitat preferences for several conodonts, some of which are slightly at variance with previous suggestions. Gnathodus is interpreted as a nektobenthic slope dweller whose habitat bottomed out seaward against the dysaerobic zone, Hindeodus as an outer platform genus and Mestognathus as a dweller in hypersaline lagoons. Dreesen et al. (1986) draw attention to the sedimentological processes which may cause apparent mixing of conodont biofacies, these include storm surges, tidal currents, debris flows (fluxoturbidites) and transgressive pulses.

figure 1.2.6 Cross-shelf conodont biofacies scheme for Lower Carboniferous times (after Sandberg and Gutschick 1984).
I = Bispathodid biofacies (low conodont abundance).
II = Scaliognathid/Doliognathid biofacies (low to high).
III = Gnathodid/Pseudopolygnathid biofacies (low to very high).
IV = Eotaphrid biofacies (low to high).
V = Hindeodid biofacies (low).
VI = Pandorinellinid biofacies (low).
VII = Mestognathid biofacies (?).



They also highlight the probability that some of the shelf-conodont biostratigraphical zones of the Dinantian sequence in Belgium (fig. 1.4.4) represent successive biofacies rather than conodont chronozones, hence great care should be taken in using conodont-zone boundaries as time lines.

1.2h Applications of conodont studies.

Apart from being studied, as may any fossil group, for purely academic reasons, the study of conodonts also has a number of practical justifications. Microfossils are invaluable in modern biostratigraphy because the traditionally used macrofossils tend to be broken during recovery from hydrocabon wells. Ulrich and Bassler (1926) were the first to illustrate the great biostratigraphical potential of conodont elements, and since their work conodonts have become an integral part of most Lower Palaeozoic, Devonian and Tournaisian micro-palaeontological zonations. The advent of palaeoecological studies has also allowed conodont-based palaeoenvironmental interpretations to be made. As conodont elements are heated they change colour and this colour alteration index (CAI) is used in studies of the host-rock thermal history (Epstein et al. 1977, Rejebian et al. 1987).

The nature of the calcium phosphate crystal lattice is such that it is comparatively stable through time and can be used for trace element and isotope geochemical studies. The organic matrix upon which the crystals are secreted has produced the oldest stainable cells known (Fåhræus and Fåhræus-van Ree 1987), and is therefore important for evolutionary studies of metazoan cells in general and early vertebrates in particular (whatever the ultimate affinity of the conodont animal, see section 1.2d). Conway Morris and Harper (1988) have endeavoured to use conodonts in an investigation into the reasons why eukaryote cells contain far more DNA than is needed to encode the cells genetic information. Conodont-cell genome size has been inferred from cell-size in conodonts through time. The lack of detailed data on conodont species transitions and mode of life has caused problems in linking trends in genome size with aspects of conodont evolution, however this promises to be a rewarding line of research in the future.

1.3 THE ARUNDIAN STAGE AND ITS CORRELATION.

1.3a Recent advances in British Dinantian stratigraphy.

The term Dinantian was first proposed in 1893 by Minier-Chalmas and de Lapparent as the lower of two divisions of the Carboniferous; and its status as a subsystem was formally ratified in 1971 by the I.U.G.S. Subcommission on Carboniferous Stratigraphy (George and Wagner 1972). The terminology and standards for the Lower Carboniferous in Britain have been reappraised by George et al. (1976). The term Avonian, as proposed by Vaughan (1905) to be synonymous with Lower Carboniferous, is no longer accepted. The associated zonal scheme based on corals and brachiopods is thought to reflect a series of local biotopes rather than a strictly evolutionary sequence, and this has led to problems in the application of the "Avonian" faunal zones in other parts of the United Kingdom (U.K.), and even in the Bristol area (George 1972).

George et al. (1976) have erected a scheme which comprises six Stages within the Dinantian Subsystem, based on major transgression/ regression cycles and their associated lithological and faunal changes (fig. 1.3.1 column 6). At the time of its definition the base of the Courceyan Stage did not correlate with the base of the Tournaisian Series; however the latter was redefined by Conil et al. (1977) such that both now agree and occur at the old Tn1b horizon. In light of this Ramsbottom and Mitchell (1980) suggested reinstating the Tournaisian and Viséan Series in the U.K. and subdividing the former into the Hastarian and Ivorian Stages. This proposal has not met with much support (Fewtrell and Smith 1981, Clayton and Sevastopulo 1981) and this thesis follows the original scheme of George et al. (1976).

figure 1.3.1 (explanation)

The information for this figure comes from George *et al.* (1976), Harland *et al.* (1981), and Waters and Lawrence (1987). The precise definition and correlation of stratigraphical divisions and their boundaries is a much debated subject, and the information presented here is solely intended as a guide to allow comparisons between the reports of conodont workers using different notational schemes.

Correlation of the base of the Viséan Series is particularly problematical. George *et al.* (1976) placed the boundary below the base of the Chadian Stage, but the present figure equates the two boundaries - following the work of Conil *et al.* 1977, and Waters and Lawrence (1987 fig 8).

Local zonational schemes following the work of Vaughan (1905), and not detailed here, include those of: Reynolds and Vaughan (1911, Burrington Coombe), Dixon and Vaughan (1912, Gower Peninsula), Garwood (1913, Ravonstonedale) and Reynolds (1921, Avon Gorge).

Key to columns.

1. American Subsystem
2. European Subsystem
3. American Series
4. European Series
5. American Stages
6. British Stages
7. Avon Gorge Zones of Vaughan (1905), with non-sequences (horizontal hatching) from George *et al.* (1976):
   Modiola Zone = M
   Lower Caninia Zone = C_1 & C_2 (Syringothyris Zone)
   Upper Caninia Zone = S_1
   Main Seminula Zone = S_2
   θ ϕ Subzone = D_1
   Lonsdaleia Subzone = D_2
   (Horizon δ occurs at top of C_2)
8. Revised Vaughan Zones of Dixey and Sibley (1918), Vale of Glamorgan: Lower Caninia Zone = C_1
   Upper Caninia Zone = C_2S_1
9. Green and Welch (1965), Wells; and Smith *et al.* (1967), Chesterfield: Seminula Zone = S_2
   Lower Dibunophyllum Zone = D_1
   Upper Dibunophyllum Zone = D_2
   Upper Posidonia Zone = P_2
10. German notation.
11. Belgian notation, **Note**: the slightly different correlation of Paproth *et al.* 1983 (see fig 1.4.4) is preferred in this thesis.
12. Stratigraphy of the Gower Peninsula:
    PBL = Penmaen Burrows Limestone
    CBM = Caswell Bay Mudstone
13. Stratigraphy of the Pembroke area.
    LHB = Linney Head Beds
    HBL = Hobbyhorse Bay Limestone
14. Major transgression/regression cycles of Ramsbottom (1973).

figure 1.3.1 Stratigraphical correlation scheme used in this study.
(but see note for column 11).

| | | |

1.3b Correlation of the Arundian Stage.

The Arundian is a stage in the Viséan Series, roughly equivalent to the C_2S_1 Zone of Dixon and Vaughan (1912), and was first defined by George et al. in 1976. It corresponds to the third of Ramsbottom's (1973) major transgression/regression cycles of the British Dinantian (fig. 1.3.1 column 14). The Arundian stratotype section is in the cliffs of south Dyfed, on the east side of Hobbyhorse Bay (see appendix D), hence the derivation of the stage name from the latin arundo - meaning hobbyhorse. The stages erected by George et al. (1976) are based on precisely defined stratotype sections, but are recognised by their characteristic faunas. The boundaries are placed at convenient lithological changes, and the classification is neither a true lithostratigraphy nor a true biostratigraphy (Simpson 1985). In the case of the Arundian stratotype this has created problems. The base of the Arundian is taken at the first lithological change occurring below the entry of the typical Arundian fossils, forams of the family Archaediscidae. Consequently the faunal boundary is 16 m above the lithological boundary (Simpson and Kalvoda 1987).

Few macrofaunal species are truly characteristic of the Arundian, as many occur in the underlying Chadian as well, and the old "C zone" macrofaunal assemblage covers both the Chadian and lower Arundian. Amongst the microfossils forams are the most widely used biostratigraphically although, because their distribution is thought to be facies related (Simpson and Kalvoda 1987), they are not completely satisfactory. Conodonts have not been much used, and Mitchell et al. (1982) state that "conodonts are relatively rare in the Arundian and are of limited stratigraphical value". The results of the present study (section 2.3c) show that, in suitable environments, conodonts were abundant during Arundian times, and in such areas they may be of biostratigraphical use.

The variety of stratigraphical terminology which has been used in the description of Carboniferous rocks in conodont studies throughout the world is a major hindrance in attempting to construct an overall synthesis of Carboniferous conodont occurrence. In this study, figure 1.3.1 can be used to translate reported stratigraphical ranges to the scheme proposed by George et al. (1976).

1.4 MID-VISÉAN CONODONTS.

1.4a Introduction.

Conodont species-diversity reached a peak in the mid-Famennian, following rapid diversification amongst the Polygnathacea (Sweet, in Clark et al. 1981; Aldridge 1988). Following this, although there were numerous minor diversity cycles, the overall picture was one of continual decline until complete extinction occurred in the uppermost Triassic. The Courceyan Stage was however a time of relatively high diversity, and is represented by up to nine conodont zones, with an average duration of approximately 0.9 million years. Faunas were dominated by Siphonodella and Pseudopolygnathus in offshore environments, and by Polygnathus and Hindeodus in shallower water. Ziegler and Lane (1987) report a major conodont extinction event at the end of the Tournaisian Series (end-Courceyan), after which conodont diversity and rate of evolution were greatly reduced. The entire Viséan Series is represented by just four (deep water) or five (shallow water) conodont zones (Varker and Sevastopulo 1985), with an average duration of approximately 4 million years.

In Viséan times the genus Gnathodus became the dominant form in distal shelf settings, where it co-occurred with the genera Lochriea, Hindeodus, Idioprioniodus, Kladognathus and Vogelgnathus. The more proximal-shelf environment was dominated by cavusgnathoid conodonts including Mestognathus, Patrognathus and Cavusgnathus (see section 1.4j). The multielement relationship of some species of the form genus 'Apatognathus' remains equivocal (see section 1.4i); they have been recovered from all parts of the Viséan shelf environment.

1.4b The genus Gnathodus

SUPERFAMILY: Polygnathacea
FAMILY: Idiognathodontidae

i) Introduction.

Over 80 species of Gnathodus s.f. have been described in the literature. Examples of the genus have been recovered from all continents except Antarctica, from rocks of mid-Tournaisian to mid-Namurian age (mid-Courceyan to topmost Kinderscoutian, or topmost Kinderhookian to early Morrowan in the U.S.A.). For most of its range Gnathodus is of biostratigraphical importance, and is the dominant form recovered from outer shelf environments. Over 84% of the Pa elements recovered in this study belong to the genus. Sandberg (In: Lane et al. 1980) suggests Gnathodus lived

in the lower part of the aerobic zone, concentrated at the foreslope of the shelf edge (see fig. 1.2.6), and although absent from hemipelagic sediments, may extend landwards onto carbonate platforms.

Norby (1976) studied complete apparatuses preserved on shale bedding planes of the Tyler Formation of central Montana, and was able to reconstruct the apparatus in which Gnathodus bilineatus s.f. occurred in the Pa position. Comparison of the G. bilineatus apparatus with those known from later idiognathodontids (e.g. Idiognathoides, Idiognathodus) indicates that while the Pa elements show marked morphological changes, the other elements remain remarkably similar; and at least at the present level of recognition, many of the non-Pa elements would appear to be vicarious. Indeed, Norby (1976) suggests that, awaiting further work, it would be realistic to assume that, apart from the Pa elements, the apparatuses of different Gnathodus species were essentially alike. Given this premise the non-Pa apparatus of the gnathodid elements recovered in this study is based on the apparatus of G. bilineatus. The Gnathodus apparatus belongs to the Type 1 category of Klapper and Philip (1971). Norby (1976) and Aldridge et al. (1987) conclude from their studies of preserved apparatuses that it was septimembrate (contrary to Austin and Rhodes, In: Clark et al. 1981, who suggested it was probably seximembrate):

Pa scaphate	(gnathodontan)	x2
Pb angulate	(ozarkodinan)	x2
M dolabrate	(synprioniodan)	x2
Sa alate	(hibbardellan)	x1
Sb, Sc and Sd bipennate	(hindeodellan)	x8

For an explanation of the terminology see section 1.2b. The diagnostic element after which the genus is named is the Pa element. In general when reference is made to "Gnathodus" in past literature, it is the Pa element which is being discussed.

ii) Diagnosis and recognition.

The Gnathodus Pa element (e.g. interpretive sketches 2.2.4 and 2.2.5) displays class II symmetry (sensu Lane 1968). It has an anterior denticulate free blade and, as redefined by Lane et al. (1980), an asymmetrical posterior platform over a large, deep and flared basal cavity (or cup). The inner side of the platform is narrower, bears a parapet, and meets the blade further anteriorly than the more expanded outer platform. The free blade is medial and in upper view may appear either straight or slightly curved; it is usually at least half the length of the whole element. Upper-surface ornamentation of the platform is extremely variable and may be absent, or may consist of a single or scattered nodes, parapets, transverse ridges or a combination of these. Where the blade continues posteriorly on to the platform a distinct nodose carina is formed, and the posterior carina denticles may be simple or laterally expanded. Speciation is

largely based on the ornamentation and shape of the platform, and the nature of the posterior carina denticles. Recognition of Gnathodus species is complicated by the presence of many transitional specimens, which are particularly common in the Mississippian (Thompson and Fellows 1970). It often appears that certain trends within Gnathodus species occur as a plexus of continuous variation within which a number of marker species have been defined (e.g. G. semiglaber - G. antetexanus - G. texanus).

iii) Type species.

The genus Gnathodus was originally established by Pander in 1856 when G. mosquensis was cited as the type species. Recently, controversy has arisen over whether this is valid. No holotype was ever designated and the three specimens illustrated by Pander have been lost, despite a search by Sergeeva, Khalymbadzha, Barskov, Alekseev and Goreva in the cities where Pander lived (Leningrad, Kazan and Moscow). Pander (1856) only illustrated one view of each of the specimens and Lane and Ziegler (1979) suggest that they were probably not studied in three dimensions, but embedded in the host rock, and this may have led to misidentification. To recognise Gnathodus an upper view is needed to avoid confusion with Streptognathodus, Idiognathodus, Idiognathoides, Neognathodus and Declinognathodus. Similarly a lower view is needed to avoid confusion with many of the polygnathids.

At least since the work of Roundy (1926), it has become accepted that the genus Gnathodus is essentially of Lower Carboniferous age. This situation probably arose because Pander stated that his specimens came from the Bergkalk or "Mountain Limestone" - synonymous with the Lower Carboniferous Limestone in the U.K. Subsequent resampling of the original localities by Barskov et al. (1977) indicates that "G. mosquensis" came from late Upper Carboniferous rocks (the Dorogomilaer Horizon of Kasimovian age). Consequently Barskov et al. suggest "G. mosquensis" is probably a representative of Streptognathodus or Idiognathodus and is therefore invalid as a type species for the accepted concept of the genus Gnathodus. Following the International Code of Zoological Nomenclature to the letter, Barskov et al. (1977) suggested dropping the name Gnathodus altogether except in the unlikely event of synonymising Streptonathodus and Idiognathodus. The next oldest synononymised reference to Gnathodus is Dryphenotus Cooper, 1939, which Barskov et al. (1977) were in favour of adopting. In view of the confusion this would cause, both in systematics and biostratigraphy, due to the long established conception of Gnathodus as a Lower Carboniferous genus, Lane and Ziegler (1979) proposed that the name should remain as it is. They originally put forward Gnathodus texanus Roundy 1926 as a possible type species, but this has not been defined in terms of multielement taxonomy. The earliest reference to a Gnathodus Pa element which has been included in a multielement

reconstruction is Polygnathus bilineatus Roundy 1926; and this has been designated as the type species by The International Commission on Zoological Nomenclature (Tubbs 1986).

iv) Phylogeny.

Lindström (1964) suggested that in the Upper Devonian Gnathodus evolved from Spathognathodus (=Bispathodus) stabilis s.f., a form with increased basal expansion, and tubercles or denticles on the upper surface. It must be remembered that Lindström included the forms later assigned to Lochriea (see below) in his concept of Gnathodus. He noted two main trends, one toward simplicity: G. commutatus and relatives; and a second which had an asymmetrical cup and increased ornamentation:
G. kockeli -> G. delicatus -> G. bilineatus.

Following Lindström's work the concept of the genus Gnathodus was altered by the removal of his "simplistic" group to a separate genus (see Lochriea below). Thompson (1979) cites Protognathodus kockeli as the progenitor of the Gnathodus stock, and suggests it gave rise in turn to G. cf. kockeli, G. delicatus and G. punctatus in Kinderhookian times. In lowest Osagean times, G. punctatus led simultaneously to G. cf. bilineatus and G. semiglaber. Essentially this lineage mirrors Lindström's second group (above). Thompson was unable to resolve the G. semiglaber lineage clearly, but thought it probable that two lines emerged:

(i) G. semiglaber -> G. bulbosus -> G. pseudosemiglaber
(ii) G. semiglaber -> G. antetexanus -> G. texanus

Subsequent attempts to refine Gnathodus' phylogeny have been complicated by the common occurrence of specimens which are transitional between recognised species, the isolated nature of many of the published studies and "differences in philosophy of taxonomic identification" (Thompson, 1979). There is general agreement that Bispathodus is ancestral to Gnathodus, although the proximity of the relationship depends on the range of confines established for the latter.

Lane et al. (1980), like Thompson (above) cite Protognathodus kockeli as the starting point for Gnathodus evolution, and propose that it gave rise to an intermediate species, Pr. praedelicatus near the top of the Lower crenulata Zone (mid-Courceyan). They only recognise forms with an asymmetrical cup as belonging to Gnathodus although the earliest Gnathodus' and Protognathodus' do appear to intergrade. Pr. praedelicatus has an oval shaped cup and a range of ornamentation which could illustrate the potential range of future evolutionary trends. In "an explosive genetic outburst" at the base of the isosticha - Upper crenulata Zone, Pr. praedelicatus gave rise to G. delicatus, G. typicus and G. punctatus more or less simultaneously. Unlike Thompson (above) Lane et al. (1980) consider the nature of the posterior carina denticles

(see interpretive sketch 2.2.5) to be as important a taxonomic indicator as the nature of the parapets, and on this basis designate the last three named species as markers for three separate evolutionary lineages within the genus Gnathodus.

1. G. delicatus group.
   includes G. cuneiformis, although this may have arisen separately from Pr. praedelicatus. Typified by development of long rows of nodes paralleling the blade on both sides.
2. G. typicus group.
   Shows development of a narrower cup and reduction of outer-cup nodes.
3. G. punctatus group.
   G. punctatus evolved to G. semiglaber through a reduction in the size of the inner parapet and a reduction in ornamentation of the outer cup. In turn G. semiglaber gave rise to G. pseudosemiglaber by narrowing of the cup and development of a pseudoparapet on the outer side. Eventually G. pseudosemiglaber gave rise to G. texanus by extreme narrowing of the cup and reduction or loss of the pseudoparapet.

Lane et al. (1981) suggest the "bilineatus group" to have emerged later, indicative of a fourth evolutionary lineage in which parapets are well developed and the posterior blade denticles are expanded. G. girtyi is problematical and may either be included with group 3, or may represent a separate fifth group.

To summarise; general phylogenetic trends based on successive first appearances can be elucidated, but even though Gnathodus species form an integral part of many Lower Carboniferous biozonations, their detailed phylogeny is equivocal. Even that which is agreed upon may yet change as more and more first appearances are found to be facies controlled rather than evolutionary. The scheme outlined by Lane et al. (above) may appear to answer all the problems, but the actual situation is not that simple. Intermediate forms abound and show a continuous range of posterior tip development. An example involving Arundian faunas from South Wales is highlighted in Austin and Davies (1984) in which essentially similar, co-occurring forms are diagnosed as either G. texanus or G. pseudosemiglaber due to minute differences in the degree of expansion of posterior tip denticles. In Austin (1987), these same forms are redesignated as G. typicus. Adherence to the phylogeny outlined by Lane et al. would imply that this represents a completely different lineage from those above. The high number of similar examples in the literature suggests that the expansion of the posterior tip may not be a genetically significant factor, but just part of a continuous morphological variation. Biostratigraphical correlation is further complicated by the differences of opinion on identification between different workers. To fully clarify the problem, a monographic study involving re- examination of existing collections and extensive re-collection is needed, and the resulting faunas must be examined using multielement criteria.

1.4c The genus Hindeodus.

SUPERFAMILY: Polygnathacea

FAMILY: Anchignathodontidae

i) Introduction.

All the elements of the Hindeodus apparatus were described together, in single element terms, by Rexroad and Furnish (1964). Hindeodus was first described in multielement terms by Baesemann (1973), although he assigned the apparatus to the genus Ozarkodina. Sweet (In: Ziegler 1977) suggested this assignment to be false and recommended grouping the apparatus with his more recent form Anchignathodus to create the multielement genus Hindeodus The genus has a long stratigraphic range: from mid-Courceyan to earliest Triassic times; and has been recovered from Europe, N. and S. America, Asia, Australia and the Middle East. Hindeodus is commonly reported as typifying the shallow mid-shelf environments (Austin 1976). Sandberg and Gutschick (1984) propose an outer shelf Hindeodid biofacies and in this study Hindeodus is recovered throughout the shelf. The apparatus broadly conforms to the Type 1 plan of Klapper and Philip (1971), and is thought to have been seximembrate (Sweet and Clark In: Clark et al. 1981):

Pa	scaphate	(spathognathodontan)	x2
Pb	angulate	(ozarkodinan)	x2
M	dolabrate	(neoprioniodontan)	x2
Sa	alate	(trichonodellan)	x1
Sb	digyrate	(plectospathodontan)	x?
Sc	bipennate	(hindeodellan)	x?

The trichonodellan Sa element is without a posterior process, and in some species the M element may be apatognathan and digyrate rather than dolabrate. For an explanation of the terminology see section 1.2b.

ii) Diagnosis and recognition.

Hindeodus is unusual in that the Pa elements are relatively stable components of the apparatus, whilst the M element, and probably the S elements also, change quite markedly through time (Mapes and Rexroad 1986). The Hindeodus Pa element displays class II symmetry (sensu Lane 1968). The unit is short, crest-like, and often slightly arched in lateral view. The cusp is anteriormost and in lateral view is 2 or 3 times wider than the other denticles. The cup takes the form of a lachrymate flaring-out of the base of the unit.

iii) Phylogeny.

The phylogenetic derivation of Hindeodus is poorly understood. The distinctive Sa element, which lacks a posterior process, might suggest a link with Ozarkodina (Ziegler 1977); however the Pa, Pb and Sb elements are distinctly different. The earliest species to occur is H. cristulus in which Spathognathodus cristulus s.f. occupies the Pa position. Ziegler (1977) suggests that an uninterrupted evolutionary sequence links H. cristulus with H. typicalis of the uppermost Permian, although this phylogeny is largely based on Pa elements only (Spathognathodus s.f. or Anchignathodus s.f.). The earliest recorded occurrence of Hindeodus is a report (unillustrated) of Spathognathodus cristulus s.f. from the early Courceyan of the Avon Gorge (Rhodes et al. 1969). The oldest known Pb elements (Ozarkodina curvata s.f.) are reported by Rexroad and Collinson (1963) from the St. Louis Limestone (Holkerian/Asbian). Both of these occurrences are somewhat later than the youngest known example of Ozarkodina.

1.4d The genus Idioprioniodus.

SUPERFAMILY: Hibbardellacea

FAMILY: Hibbardellidae

i) Introduction.

This apparatus lacks Pa elements, and conforms to the Type III plan of Klapper and Philip (1971). It was first investigated by Rhodes (1952) who, in a study of late Westphalian black shales, described the multielement genus Duboisella typica. It is now apparent that Rhodes included two species of Idioprioniodus in his apparatus (Norby 1976). Subsequently, von Bitter (1972) suggested an association which included four of the five elements described by Rhodes, together with two others ("Neoprioniodus"). Idioprioniodus was established as the senior synonym for the genus by Baesemann (1973). Merrill and Merrill (1974) statistically analysed ten faunas in which elements referable to Idioprioniodus had been recovered. Their results indicated that two species occur: I. typus is an upper Pennsylvanian (Stephanian) species which lacks Pb elements, and "I. conjunctus" (= I. healdi) has Pb elements and is entirely pre-Missourian (pre-lower Stephanian). It is thought that the loss of the Pb element occurred gradually such that at one time both species co-occurred, and then I. typus became increasingly dominant until it was the only species. Nicoll and Rexroad (1975) extended the range of "I. conjunctus" down into the Mississippian; and Norby (1976) corroborated this and established I. healdi as the senior synonym for "I. conjunctus".

The stratigraphical range of Idioprioniodus is difficult to ascertain, but it is certainly present from mid-Mississippian to latest Pennsylvanian times (early

Viséan to Stephanian). At least during Pennsylvanian times (Silesian) the genus is thought to have lived in markedly low-energy environments, and may also have tolerated low pH conditions (Merrill and von Bitter 1976). The apparatus is septimembrate (in the Mississippian):

Pa	(absent)		
Pb	angulate	(metalonchodinan)	x2
M	dolabrate	(neoprioniodontan)	x2
Sa	alate	(hibbardellan)	x1
Sb	digyrate	(lonchodinan)	x2
Sc	digyrate	(lonchodinan - 2 morphotypes)	x4
Sd	bipennate	(ligonodinan)	x4 (?)

For an explanation of the terminology see section 1.2b.

ii) Diagnosis and recognition.

The very fact that the genus can not be recognised from Pa elements may help to account for the scarcity of reports in the literature. This also highlights a general reluctance amongst some Carboniferous workers to fully adopt multielement taxonomy and illustrates the advantages inherent in using a multielement system.

iii) Phylogeny.

The apparatus is very similar to that of Hibbardella as defined by Klapper and Philip (1972), and Norby (1976) suggests that Idioprioniodus may have evolved from Hibbardella during the Devonian or early Mississippian (Courceyan).

1.4e The genus Kladognathus.

SUPERFAMILY: unknown

FAMILY: unknown

i) Introduction.

Kladognathus was first described in multielement terms by Rexroad (1981) following a study of the low-diversity, shallow water (euryhaline ?) fauna of the Vienna Limestone Member in Southern Indiana (Chesterian / Brigantian - Chokierian). Although not yet fully elucidated for each species, the apparatus is known to lack P elements. Norby (1976) tentatively suggested an association of three of the included discrete elements, and Rexroad (1981) ratified this suggestion but cited a different M element (Neoprioniodus scitulus s.f. rather than Neoprioniodus peracutus s.f.).

Rexroad (1981) erected four species of Kladognathus: K. tenuis, K. primus, K. mehli and K. spp. The M and Sa elements are entirely vicarious, the Sb

element is relatively stable and the Sc elements evolve rapidly. Horowitz and Rexroad (1982) proposed a further possible species: K. levis, and this can be included in an evolutionary lineage based on changes in the animal's Sc component, as follows:

K. levis -> K. tenuis -> K. primus -> K. mehli.

In this sequence the first species has only Ligonodina levis s.f. as an Sc element; the second has L. levis s.f. with L. tenuis s.f.; the third has K. primus s.f. with one of the Ligonodina forms and the fourth has K. mehli s.f. with one of the Ligonodina forms (Rexroad 1981, Horowitz and Rexroad 1982). The fifth Kladognathus species, K. sp. of Rexroad (1981), is not fully established but is thought to include Magnilaterella complectens s.f. as an Sb element.

The discrete element Lambdagnathus s.f. may be a component of the Kladognathus apparatus. Norby (1976) noted that the micro-ornamentation of Lambdagnathus fragilidens s.f. is similar to that of some of the Kladognathus Sb and Sc elements, and all occur in the same shallow water biofacies. However the Lambdagnathus s.f. elements are under-represented compared with the Kladognathus elements (Rexroad 1981), and do not closely group statistically with them (Horowitz and Rexroad 1982). If in the future Lambdagnathus s.f. is found to occur in the Kladognathus apparatus, the delicate nature of the element may explain the statistical discrepancies (Rexroad 1981).

The stratigraphical range of Kladognathus has not been fully established; although Aldridge (1988), in his provisional range chart, implies a range from Chadian to Pendleian times. The evidence available suggests that Kladognathus preferred shallow water, proximal shelf conditions, and may have been able to live under considerable environmental stress. The genus is typically recovered from rocks of the Cavusgnathus biofacies and can form an appreciable component of restricted Cavusgnathus-dominated faunas (Rexroad 1981, Horowitz and Rexroad 1982, Rexroad and Merrill 1985).

Further studies are required before the exact nature of the Kladognathus apparatus can be established, but Rexroad (1981) suggests it to be as follows:

Pa	absent		
Pb	absent		
M	dolabrate	(neoprioniodontan)	x2?
Sa	alate	(hibbardellan)	x1?
Sb	bipennate	(magnilaterellan)	x2?
Sc	bipennate	(ligonodinan or kladognathodontan)	x?

For an explanation of the terminology see section 1.2b.

ii) Diagnosis and recognition.

The ligonodinan Sc elements are thought to have been vicariously shared with another genus, and thus to have longer stratigraphical ranges than Kladognathus per se (Rexroad 1981). Consequently Kladognathus must be

recognised on the basis of its conservative M and Sa elements (Neoprioniodus scitulus s.f. and Hibbardella milleri s.f.), or its distinctive kladognathan or magnilaterellan elements. Species recognition is largely based on the Sc elements (see above).

iii) Phylogeny.

The supposed evolutionary sequence within the genus is outlined above, but there has been little discussion in the literature on the phylogeny of the group as a whole.

1.4f The genus Lochriea.

SUPERFAMILY: Polygnathacea
FAMILY: Uncertain

i) Introduction.

Up until about twenty years ago Lochriea Pa elements were classified as species of Gnathodus s.f. In a review of the genus Gnathodus they were seen as a discrete "simple" group by Lindström (1964), and six years later Meischner (1970) raised them to the status of a separate genus: Paragnathodus, but did not present any description, definition or designation of type species. This new genus included the "simple" species commutatus, nodosus and homopunctatus, and later symmutatus, mononodosus, multinodosus and cruciformis were added to the group. All these species probably evolved from the same or a similar ancestor, and appear to have a separate phylogenetic lineage from Gnathodus (Norby 1976, Belka 1985). Higgins (1975) described and defined Paragnathodus as a genus, and excluded symmutatus and homopunctatus due to a supposed difference in phylogeny (Rhodes and Austin 1971). Norby (1976) re-examined the bedding-plane assemblage illustrated by Scott (1942) as Lochriea montanaensis, and determined the Pa elements to be Paragnathodus commutatus s.f. "Paragnathodus" was therefore designated as a junior synonym of Lochriea which Norby (1976) defined as a multielement apparatus. Norby was unable to examine any assemblages containing nodosus or monodosus Pa elements but thought it likely that they too belonged to the genus Lochriea on account of the similarity in form; he further suggested that future studies may result in homopunctatus and symmutatus being similarly designated. In this study, awaiting further work, the latter two species are retained as species of Gnathodus.

It is thought that in the basinal Culm facies of S.W. England, the range of Lochriea may extend down into late Courceyan rocks (Varker and Sevastopulo 1985), elsewhere in Europe the lower limit of its range is thought to be late Chadian/early Arundian. Lochriea is known to range upwards into late

Arnsbergian times, and has been reported from Europe, and North America. L. commutata consistently has an earlier first occurrence than other species of the genus, but L. nodosa and L. mononodosa often continue slightly later (Meischner 1970, Higgins 1975), although Varker and Sevastopulo (1985, p253) indicate a common extinction date for all forms. Druce (1973) suggested that they lived in intermediate water-depths (e.g. 50 m), and in this study L. commutata has been recovered from outer ramp and proximal mid-ramp sites.

The Lochriea apparatus belongs to the type 1 category of Klapper and Philip (1971), and Norby (1976) proposes it to be seximembrate:

Pa	scaphate	(gnathodontan)	x2
Pb	angulate	(ozarkodinan)	x2
M	dolabrate	(neoprioniodontan)	x2
Sa	alate	(hibbardellan)	x1
Sc and Sd	bipennate	(hindeodellan)	x8

For an explanation of the terminology see section 1.2b.

ii) Diagnosis and recognition.

The Lochriea Pa element (interpretive sketch 2.2.33) may display Class Ib or Class II symmetry (sensu Lane 1968). The anterior free blade is approximately half the total length of the unit and has a distinctively subrectangular lateral profile. The posterior cup is subcircular to subquadrate in upper view and may be unornamented or bears one or several large nodes. The denticulation of the free blade is similar to that of the carina in lateral view and in upper view the width of the denticles increases posteriorly. The cup is widely flared (scaphate) as in Gnathodus.

iii) Phylogeny.

According to Higgins (1975) Lochriea is derived from, and closely related to, the genus Spathognathodus s.f. Meischner (1970, fig 2) implies, in his Carboniferous range chart, that during late Tournaisian times (late Courceyan) Lochriea evolved from Spathognathodus stabilis s.f. (= Bispathodus) or a similar short bladed form. The fact that Gnathodus had already developed highly ornamented platforms by this time provides additional justification for separating the simplistic Lochriea from the genus Gnathodus. Norby (1976) proposes that Gnathodus symmutatus and Lochriea commutata evolved from a similar ancestor at about the same time, and both subsequently gave rise to more ornamented forms. G. symmutatus gave rise to G. homopunctatus, while L. commutata gave rise to L. mononodosa and then L. nodosa. G. symmutatus and G. homopunctatus differ morphologically from Lochriea in having blade denticles of differing sizes but, apart from that, they are essentially similar. It is likely that future analysis of the non-platform elements of homopunctatus will

result in them being assigned to Lochriea (Norby 1976). Belka (1985) proposes a new species: Lochriea cracoviensis as the immediate forbear of L. commutata, and concurs with Meischner (1970) in his proposal of Bispathodus stabilis as the root stock for Lochriea, rather than a species of Gnathodus.

1.4g The genus Polygnathus

SUPERFAMILY: **Polygnathacea**

FAMILY: **Polygnathidae**

i) Introduction.

For much of Devonian and early Carboniferous time, Polygnathus was an appreciable component of shallow/mid-shelf conodont faunas. The genus has a stratigraphical range from the Siegenian Stage of the Lower Devonian (P. dehiscens), to the Arundian Stage (P. bischoffi); and has been recovered from all inhabited continents. Polygnathus is widely used in biozonations throughout its range (Weddige and Ziegler 1979, Higgins and Austin 1985).

The apparatus was at first thought to be seximembrate (Klapper and Philip 1971, 1972); but in common with most Ordovician - Carboniferous apparatuses is now known to be septimembrate (Nicoll 1985). Polygnathus was used by Klapper and Philip (1971) to illustrate the Type 1 apparatus plan; in Carboniferous genera the apparatus is:

Pa	carminiplanate	(polygnathodontan)	x2
Pb	angulate	(ozarkodinan)	x2
M	dolabrate	(neoprioniodontan)	x2
Sa	alate	(hibbardellan)	x1
Sb and Sc	bipennate	(hindeodellan)	x6
Sd	bipennate	(angulodontan or hindeodellan)	x2

ii) Diagnosis and recognition.

The Polygnathus Pa element displays Class II symmetry (sensu Lane 1968). The platform can vary in shape from ovate to lanceolate and bears a nodose medial carina and some manifestation of transverse ridges. The platform edges tend to be upturned and thickened. The anterior blade is commonly the same length as the platform and bears from 10 to 16 laterally compressed fused denticles (Rhodes et al. 1969). The basal cavity is restricted and commonly surrounded by a zone of recessive margin. Species recognition is based on a combination of platform outline and ornamentation.

iii) Phylogeny.

The genus is thought to have originated in the middle part of the Lower Devonian from a genus with spathognathodontan Pa elements (Weddige and

Ziegler 1979); possibly Ozarkodina. This is evidenced by the large spathognathodontan basal cavity in the Pa elements of P. dehiscens - the earliest form. Further evolution involved reduction of the basal cavity to a small basal pit and the development of a great variety of platform outlines and ornamentation. Weddige and Ziegler (1979) were able to discern three main evolutionary branches within Polygnathus (the linguiformis, costatus and robusticostatus groups), and noted that forms recovered from deep water environments tend to be more robust than those from neritic waters. P. bischoffi appears to have developed from the linguiformis stem.

1.4h The genus Vogelgnathus.

SUPERFAMILY: Polygnathacea

FAMILY: uncertain

i) Introduction.

The Vogelgnathus apparatus was first described in multielement terms as Pandorinellina campbelli by Norby (1976), following study of an almost complete bedding-plane apparatus. Horowitz and Rexroad (1982) suggested that the apparatus differed sufficiently from the Devonian examples of Pandorinellina to justify erection of a new genus; and Norby and Rexroad (1985) designated the new genus as Vogelgnathus. Norby and Rexroad (1985) describe two species of Vogelgnathus: V. campbelli and V. n. sp., in which the Pa elements differ but the remaining elements are presumed to be vicariously shared. Gnathodus akiyoshiensis s.f. Igo 1973 and Spathognathodus postcampbelli s.f. Husri 1974 are also thought to be referable to Vogelgnathus. Armstrong and Purnell (1987) illustrate elements of a Vogelgnathus apparatus which they also term n. sp.

The stratigraphical range of Vogelgnathus has not been fully established. Vogelgnathus was recovered from rocks of late Chesterian age by Norby and Rexroad (1985), who suggested it originated at about the same time as Hindeodus and Lochriea in early St. Genevieve times. This correlates with the Brigantian Stage in the U.K. (Harland et al. 1981). However in the U.K. Hindeodus and Lochriea are known from rocks of Courceyan and Arundian age respectively (Varker and Sevastopulo 1985); and the Pa element of V. campbelli is found in rocks at least of Arundian age and possibly as old as Chadian (Metcalfe 1981). The simplest explanation for this anomaly is that these genera did not migrate into what is now the U.S.A. until much later than their first occurrence in Europe, and that their first occurrences were simultaneous in the U.S.A. because of ecological rather than phylogenetic reasons. Alternatively the stratigraphical correlation between the U.S.A. and U.K. reports of Vogelgnathus may be inaccurate. Vogelgnathus n. sp. of Armstrong and Purnell (1987) was

recovered from rocks of Chadian age, and is the oldest reported species of Vogelgnathus. Vogelgnathus therefore is known to range from mid-Chadian times (Keokuk in the U.S.A.) to Chokierian times (Elvirian in the U.S.A.). The environmental tolerance and preference of the genus has not been discussed in the literature, although Armstrong and Purnell report their V. n. sp. from shallow (nearshore ?) conditions intermediate between a highly restricted Cloghergnathus/Taphrognathus biofacies and a less restricted Patrognathus/Mestognathus biofacies (Purnell pers. comm. 1987). Norby and Rexroad (1985) recovered complete bedding-plane assemblages of V. campbelli in association with assemblages of Gnathodus bilineatus, Lochriea commutata and Idioprioniodus healdi; all of which are known to occur in offshore mid-shelf to distal shelf environments. It is probable that the genus Vogelgnathus was not restricted to any specific biofacies.

The apparatus is seximembrate and of the Type 1 plan of Klapper and Philip (1971). Although distinctive it is similar to Ozarkodina, Pandorinellina, Gnathodus, Hindeodus, Lochriea and Diplognathodus (Norby and Rexroad 1985):

Pa	scaphate	(spathognathodontan)	x2
Pb	angulate	(ozarkodinan)	x2
M	dolabrate	(angulodontan)	x2
Sa	alate	(diplododellan)	x1
Sb	bipennate	(angulodontan)	x?
Sc	bipennate	(hindeodellan)	x?

For an explanation of the terminology see section 1.2b.

ii) Diagnosis and recognition.

The apparatus has a spathognathodontan Pa element. This is blade-like and has numerous small sub-equal denticles, fused nearly to their tips along its upper edge. The basal cavity extends to the posterior tip and is between one third and one half the total length of the unit; the nature of the basal cavity is thought to be of primary taxonomic significance (Norby and Rexroad 1985).

The Pb element is typically rather small and is often markedly under-represented in recovered faunas (Horowitz and Rexroad 1982). The element has a strong, sharp-edged and somewhat bowed cusp; and short anterior and posterior processes. The S elements are generally small, but are often distinctive as they bear a large, angled distal denticle which itself bears fine denticles along its margin.

iii) Phylogeny.

Horowitz and Rexroad (1982) disagreed with Norby's (1976) tentative assignment of this genus to Pandorinellina, because of the uniqueness of some elements and the lack of continuity between this form and established

(Devonian) Pandorinellina species. Instead Horowitz and Rexroad (1982) suggested the genus may have arisen from Lochriea rather than Pandorinellina. Norby and Rexroad (1985) proposed that both Vogelgnathus and Lochriea were derived directly from Gnathodus, and that the evolution of Vogelgnathus may be an example of neotony.

1.4i Taxonomic problems with the genus Apatognathus.

SUPERFAMILY: unknown
FAMILY: unknown

i) Introduction.

Apatognathus was defined in multielement terms by Nicoll (1980), and the genus was specifically designated as being restricted to the Late Devonian. This has resulted in a taxonomic quandary with regard to the status of the nine Carboniferous species previously referred to the form genus Apatognathus s.f. The Devonian Apatognathus has a septimembrate apparatus in which apatognathan elements fill the M, Sa and Sc positions (Nicoll 1980). The validity of Nicoll's claim that Apatognathus per se is stratigraphically separated from the Carboniferous apatognathan elements may be open to question. The apparatus includes the form genus Apatognathus varians s.f., which has been reported from Carboniferous rocks by Bischoff (1956), Conil (1959) and Rhodes et al. (1969). Nicoll assumes that A. varians s.f. was incorrectly identified by all these workers. If Nicoll's work is accepted, the Carboniferous apatognathan elements (Clarke 1960, Varker 1967, Rhodes et al. 1969) cannot be referred to Apatognathus. However, no apparatus in which they occur has yet been fully, formally described (but see ?Hindeodus scitulus section 2.2e). Pending further work, Varker and Sevastopulo (1985) continue to use form taxonomy but place the generic name in inverted commas to imply doubt over the exact taxonomic status: 'Apatognathus' s.f., and this procedure is adopted here where necessary.

The possible nature of the multielement apparatus to which 'Apatognathus' s.f. belongs, has been alluded to by several authors. Austin and Rhodes (1969) described a fused cluster from Late Carboniferous rocks of the Avon Gorge, comprising four specimens of 'Apatognathus' s.f. and one of Spathognathodus scitulus s.f. These authors also suggest that 'Apatognathus's.f. and S. scitulus s.f. have similar stratigraphical ranges, commonly occur in the same sample and are both relatively rare. Nicoll (1980) adds that studies of the Viséan Yindagindy Formation of Western Australia suggest a multielement association between 'A.' porcata s.f., 'A.' gemina s.f., Spathognathodus scitulus s.f. and Ozarkodina laevipostica s.f. For further discussion of this multielement association see section 2.2e ?Hindeodus scitulus.

'Apatognathus' s.f. is generally considered to be typical of shallow or near-

shore conditions (Varker 1967). von Bitter (1976) placed 'Apatognathus' s.f. in his Biofacies II association - from inner shelf and reef environments. Higgins and Varker (1982) grouped 'Apatognathus' s.f. with the cavusgnathoid genera on the basis of their illustrating a high degree of facies control. This group was typically recovered from littoral and lagoonal facies, but can range further offshore. In the present study 'Apatognathus' s.f. is recovered from every part of the shelf environment.

ii) Diagnosis and recognition.

'Apatognathus' s.f. elements are essentially tuning-fork shaped with denticulate processes and an apical cusp. The apical cusp is large and commonly curves toward one process. The processes may be markedly asymmetrical in size, orientation and denticulation. The denticles of the processes are discrete and point outwards and also curve upwards in the same orientation as the apical cusp.

1.4j The cavusgnathoid genera.

SUPERFAMILY: Polygnathacea

FAMILY: Cavusgnathidae (Mestognathidae for Mestognathus)

i) Introduction.

The cavusgnathoid genera possess asymmetrically paired Pa elements (Class III sensu Lane 1968); and typically lived in near-shore, shallow water, high stress environments. Taphrognathus, Cavusgnathus and Adetognathus form a continuum of morphologically similar forms (Mapes and Rexroad 1986), of which Taphrognathus and Cavusgnathus have been reported from the Arundian of the U.K. (Austin and Davies 1984, Varker and Sevastopulo 1985). Other cavusgnathoid genera have been reported from the Arundian Stage by various workers including: Cloghergnathus (Armstrong and Purnell 1987), Patrognathus (Metcalfe 1981) and Mestognathus (numerous authors). Mestognathus was placed in its own family Mestognathidae by Austin and Rhodes (In: Clark et al. 1981) but has been included informally amongst the cavusgnathoid genera by von Bitter et al. (1986). These genera exhibit a high degree of facies control on their distribution (Higgins and Varker 1982). Cavusgnathoid conodonts have been recovered from all continents except Antarctica.

It is not known whether the Mestognathus apparatus included non-platform elements, as no natural assemblages have been found, and disjunct elements are comparatively rare. From the faunas reported to include Mestognathus it seems most likely that the genus only bore one or more pairs of Pa elements (von Bitter et al. 1986). Given the presence of ramiform elements

in coeval cavusgnathoids, it is possible that under optimum conditions ramiforms were present in Mestognathus and that their loss was a reaction to environmental stress (Merrill and von Bitter 1984, von Bitter et al. 1986). The multielement composition of Cavusgnathus and Clydagnathus have been elucidated from bedding-plane apparatuses (Scott 1934, 1942; Norby 1976; Briggs et al. 1983); and Baesemann (1973) reconstructed Adetognathus from Missourian shale and limestone residues. The apparatus is quinquimembrate and broadly conforms to the Type 1 plan of Klapper and Philip (1971), except that an extra pair of Sc elements substitutes for the Sb elements:

Pa	scaphate	(cavusgnathan)	x2
Pb	angulate	(ozarkodinan)	x2
M	digyrate	(neoprioniodontan)	x2
Sa	alate	(hibbardellan)	x1
Sc	bipennate	(hindeodellan)	x8

For an explanation of the terminology see section 1.2b. Pending further work, it is reasonable to assume a general similarity between the apparatuses of different cavusgnathoid genera (Rexroad and Merrill 1985).

ii) Diagnosis and recognition.

The cavusgnathoid Pa elements all have a posterior platform with some manifestation of a central groove and marginal nodes or thickening. There is an anterior free blade of not more than four large denticles or nodes, which may be toward one side of the element or sub-central. The cusp is the posterior-most of the blade denticles or nodes, and is often markedly larger than the others. The basal cavity is usually elongate and small compared with Gnathodus.

Although numerous form species of the Cavusgnathus Pa element have been described, Rexroad (1981) only recognised four multielement species and suggested the other forms to be variations or dimorphs within the Pa pairs. In the Cavusgnathus Pa element the blade is always on the right side of the element, and right and left elements of the same pair must be defined on curvature. In some species the left and right Pa elements are of the same form (e.g. C. naviculus), while in others the Pa elements are dimorphic (e.g. C. unicornis). The non-platform elements are easily recognised as belonging to one of the cavusgnathoid genera, but relating them to individual species can be difficult (Norby 1976, Rexroad 1981).

Rexroad and Merrill (1985) suggest that several problems have clouded the taxonomy of the cavusgnathoid group, particularly the difficulty in separation of ecophenotypic variations from genetic variations. Several morphological features, which are of taxonomic importance, are seen to recur iteratively throughout the Carboniferous e.g. shifting of position of the blade, proportion of free and fixed blade, length of free tips of blade denticles and the development of a posterior "crest".

iii) Phylogeny.

The Cavusgnathidae are believed to have originated in the Middle Famennian phase of explosive polygnathid diversification (Sweet and Bergström In: Clark et al. 1981). Clydagnathus and Patrognathus are the oldest of the cavusgnathoid genera. Clydagnathus is tentatively suggested to have developed from Scaphignathus (Beinert et al. 1971), and to have given rise to Mestognathus late in the Courceyan Stage (von Bitter et al. 1986). Patrognathus was thought by Austin and Mitchell (1975) to have given rise to Windsorgnathus which in turn was the progenitor for Cavusgnathus.

1.4k Lower Carboniferous conodont biozonational schemes.

In the Lower Carboniferous, conodonts are one of the most useful and biostratigraphically sensitive fossil groups, particularly in the Tournaisian Series. The first Lower Carboniferous conodont zonation was erected in Germany in the late 1950's (Bischoff 1957, Voges 1959), and this was soon followed by a zonation of the Mississippian in the U.S.A. by Collinson, Scott and Rexroad (1962). In general, however, conodonts do not hold such a pre-eminent position in the biostratigraphical schemes of the U.K. as they do in those of many other countries.

i) Britain.

In the ninety years following publication of the first work on British Dinantian conodonts (Moore 1863), only five more papers on the subject were forthcoming; all of which described Scottish faunas (Varker and Sevastopulo 1985). It was not until the late 1960's that studies of British Dinantian conodonts began to gain momentum, and in 1969 Rhodes, Austin and Druce published their study of the conodont succession of the Avon Gorge at Bristol, and the north-crop of the South Wales coalfield. This was particularly important as the stratigraphy of the British Dinantian (Avonian) was essentially based on Vaughan's 1905 coral/brachiopod zonation of the Avon Gorge succession (fig. 1.3.1 column 7). Following criticism (Ziegler 1971b, Matthews and Naylor 1973) and newly available data, Austin (1973) reduced the suggested conodont stratigraphy from fourteen zones to eleven, and established the Avon Gorge zonation as a basis for correlation (fig. 1.4.1).

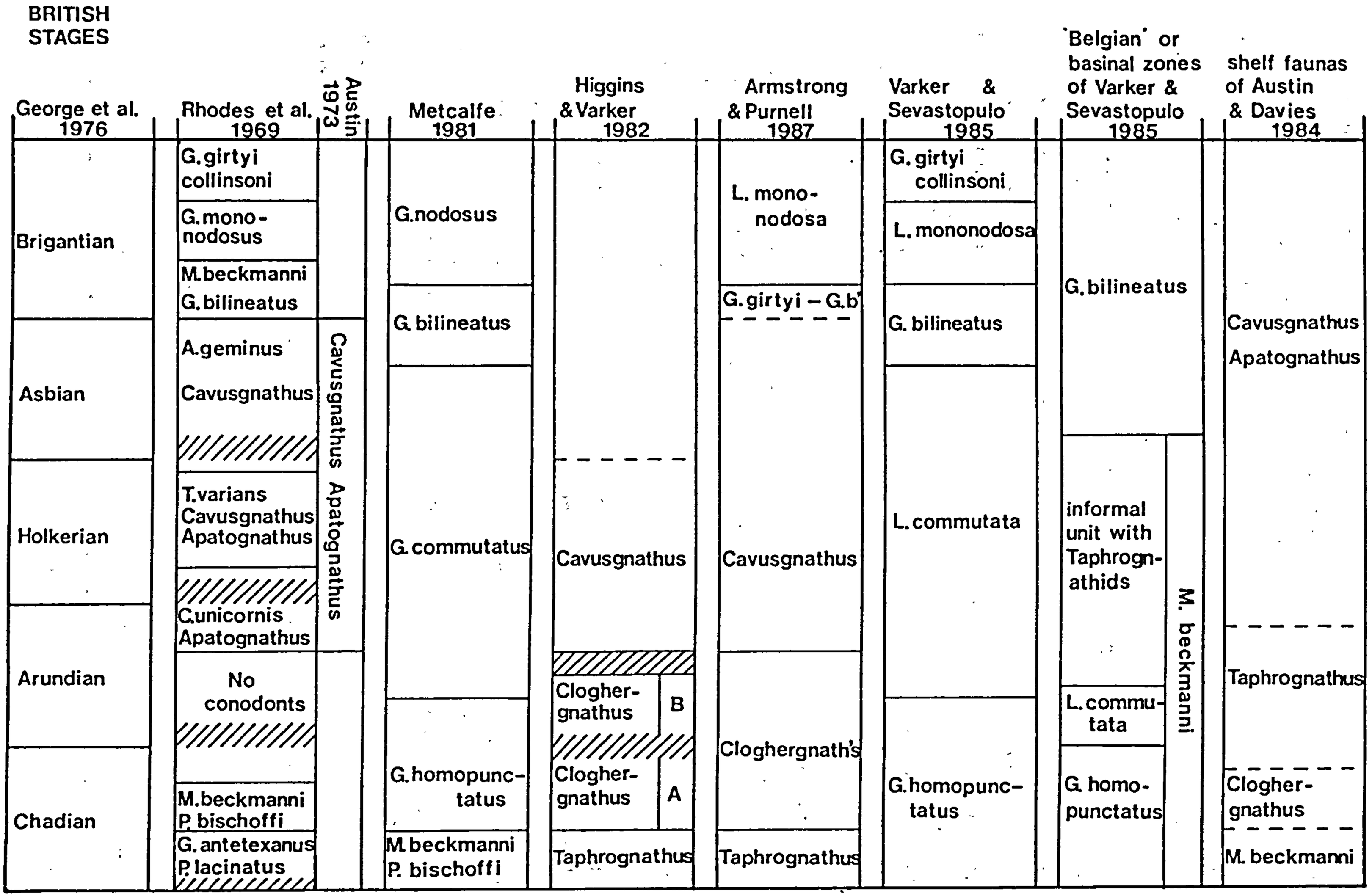
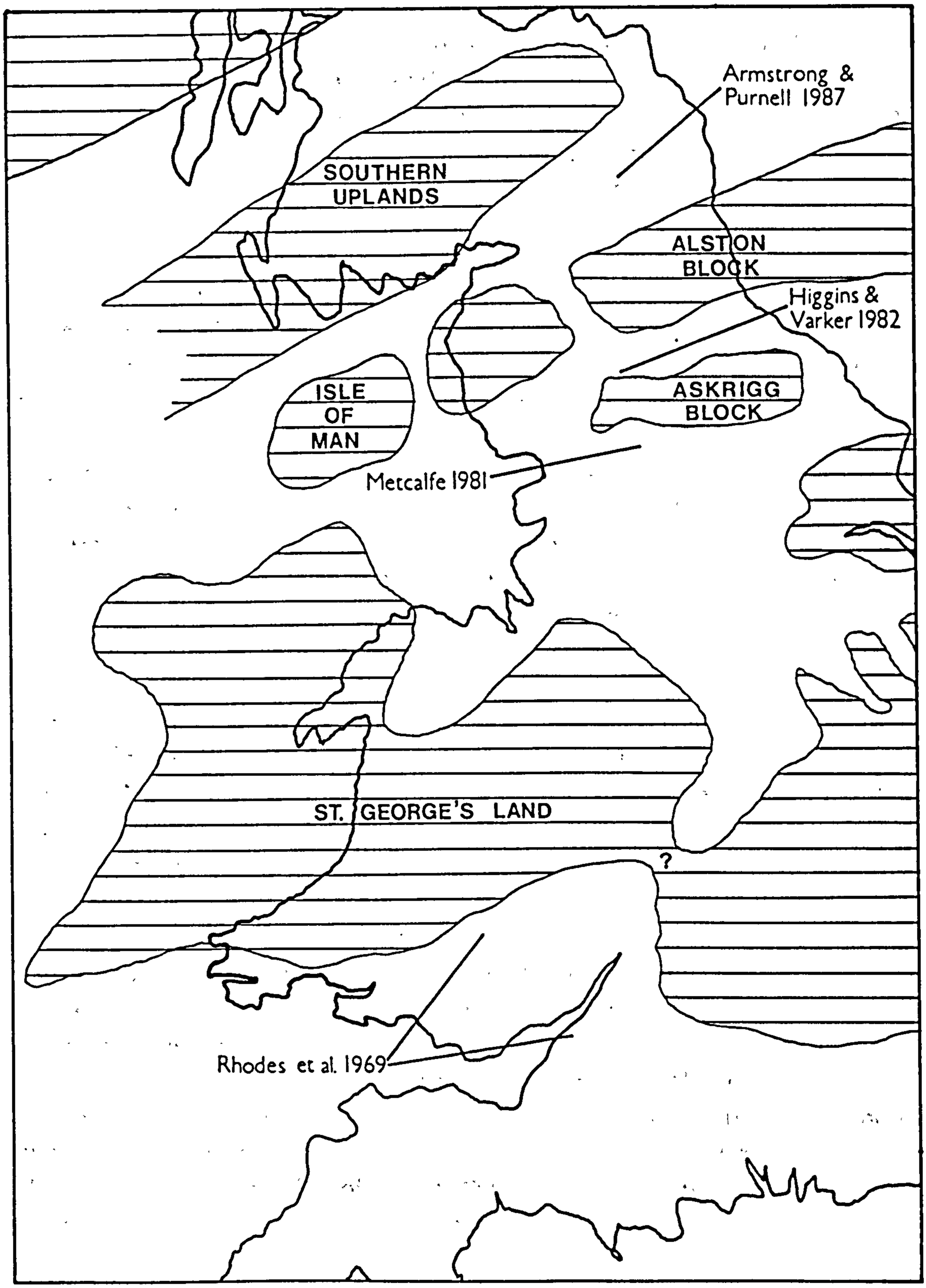


figure 1.4.1 British conodont zonation schemes for the Viséan Series.

A problem with the zonation is that the Avon Gorge section is now known to contain a number of non-sequences (George et al. 1976), and a zone of "no conodonts" in which conodonts are present in other areas. Correlation of the zonation with subsequent U.K. studies has been problematical (Matthews and Naylor 1973, Metcalfe 1981). This has led to the establishment of several localised conodont zonation schemes (Metcalfe 1981, Johnston and Higgins 1981, Higgins and Varker 1982, Armstrong and Purnell 1987). The need for numerous localised zonations suggests that Dinantian conodont distribution was, to an extent, facies controlled. The palaeogeography of the time comprised a variety of environments from the "basinal" culm measures of South-West England to shallow carbonate shelves with a variety of isolated subenvironments to the north (fig. 1.4.2). Recently Varker and Sevastopulo (1985) have attempted to produce a generalised Dinantian conodont zonation for Great Britain and Ireland by combining different parts of the published zonations (fig. 1.4.1). A twofold division is suggested with the Belgian zonation of Paproth et al. (1983) applicable to the basinal areas of South-West England and Ireland; and the conflated British scheme being used further north on the carbonate shelf areas.

Apart from that of Johnston and Higgins (1981), all of the conodont zonations listed above cover at least part of the Arundian time interval. In the Rhodes et al. (1969) zonation, conodonts were only recovered from rocks equivalent in age to the uppermost Arundian. Subsequent zonations which have attempted to fill in the gaps for the Arundian Stage of the U.K. are summarised in figure 1.4.1. Metcalfe (1981) studied conodonts from the upper Courceyan to Pendleian (early Namurian) stages of "The Craven Lowlands" (fig. 1.4.2) and erected six local-range biozones of which only three were correlatable with the Avon Gorge scheme. In Metcalfe's scheme (fig. 1.4.1) the Arundian interval spans the boundary between the Gnathodus homopunctatus Zone, and the long-ranging Gnathodus commutatus Zone (N.B. the latter eponymous species is now termed Lochriea commutata, see section 1.4f). Higgins and Varker (1982) listed some of the limitations of the Avon Gorge zonation, particularly with respect to the paucity of information covering the middle part of the Dinantian interval. Austin (1973) has three zones for the Brigantian Stage and six for the Courceyan, but non-sequences, an interval of "no-conodonts" and just one zone (Cavusgnathus-Apatognathus) cover the entire succession from middle Chadian to Asbian times. Consequently Higgins and Varker studied the Ravenstonedale area (fig. 1.4.2) which is a standard for the North of England (Garwood 1913), and is thought to be a more complete succession for the interval outlined above than occurs in the Avon Gorge. Within the middle Chadian to late Holkerian interval two zones and two sub- zones were erected. An upper Cavusgnathus Zone correlates with part of the Avon Gorge Cavusgnathus-Apatognathus Zone, and a subdivided Cloghergnathus Zone fills in the gap below.

figure 1.4.2 Palaeogeographical reconstruction for Arundian times (after Moore pers. comm. 1987), showing the location of British conodont zonations cited in figure 1.4.1.



Armstrong and Purnell (1987) investigated the conodont succession of the Northumberland Trough (fig. 1.4.2). For the Chadian through Holkerian interval their findings correlate closely with those of Higgins and Varker (1982). In the Northumberland Trough the Arundian Stage is represented by the top of a Cloghergnathus Zone with an impoverished fauna containing no diagnostic forms; a barren interval and the base of a long ranging Cavusgnathus Zone.

Rhodes et al. (1969), Austin (1973) and Metcalfe (1981) do not discuss in detail the environment of deposition pertaining to their zonations. Consequently it is difficult to relate non-correlations between the zonations with contrasting environmental constraints. However most of the Avon Gorge faunas are probably shallow water inner-shelf in character, and the Craven Lowlands faunas more deep-water, shelf edge. Higgins and Varker (1982) consider environmental factors in detail and propose their zonation to comprise an "extremely shallow water fauna", in contrast to the basinal faunas of the same age, described by Voges (1959), in which Siphonodella and Gnathodus are dominant. Sub-zone B of Higgins and Varker, in the upper Arundian, was a time of comparatively deeper conditions, but the fauna is still dominantly shallow water. The fauna of the Cloghergnathus Zone is not seen as being distinctive but simply as "an interregnum between the disappearance of Taphrognathus and the appearance of Cavusgnathus". Higgins and Varker (1982) note that both Magnilaterella robusta s.f. (a kladognathan element) and Neoprioniodus singularis s.f. (the Lochriea M element), which are indicative of sub-zone B, are known to have longer ranges elsewhere and their occurrence here is seen to reflect the onset of deeper water conditions. The authors conclude that their zonation is fundamentally facies controlled - but is of biostratigraphical use within the shallow water environment. Armstrong and Purnell (1987) state the Northumberland Trough faunas to be entirely marginal marine and shallow water in nature, and assume them to be euryhaline. Evidence for the latter comes from the presence of algal laminites and gypsum pseudomorphs in Arundian rocks of the Cambeck Formation. Also many of the recovered elements are exceedingly small, particularly species of Vogelgnathus and Taphrognathus, and euryhaline conditions are proffered as a possible explanation. The Northumberland Trough is seen as a distinct depositional basin, but environmental conditions are thought to have been very similar to those of the Ravonstonedale shelf sequence (Higgins and Varker 1982).

In addition to the zonational schemes discussed above, Arundian conodont faunas have been reported from South Wales by Austin and Davies (1984) and Austin (1987); from the Isle of Man by Swift (In: Dickson et al. 1987), and from Eire by Austin et al. (1970) and Austin and Husri (1974).

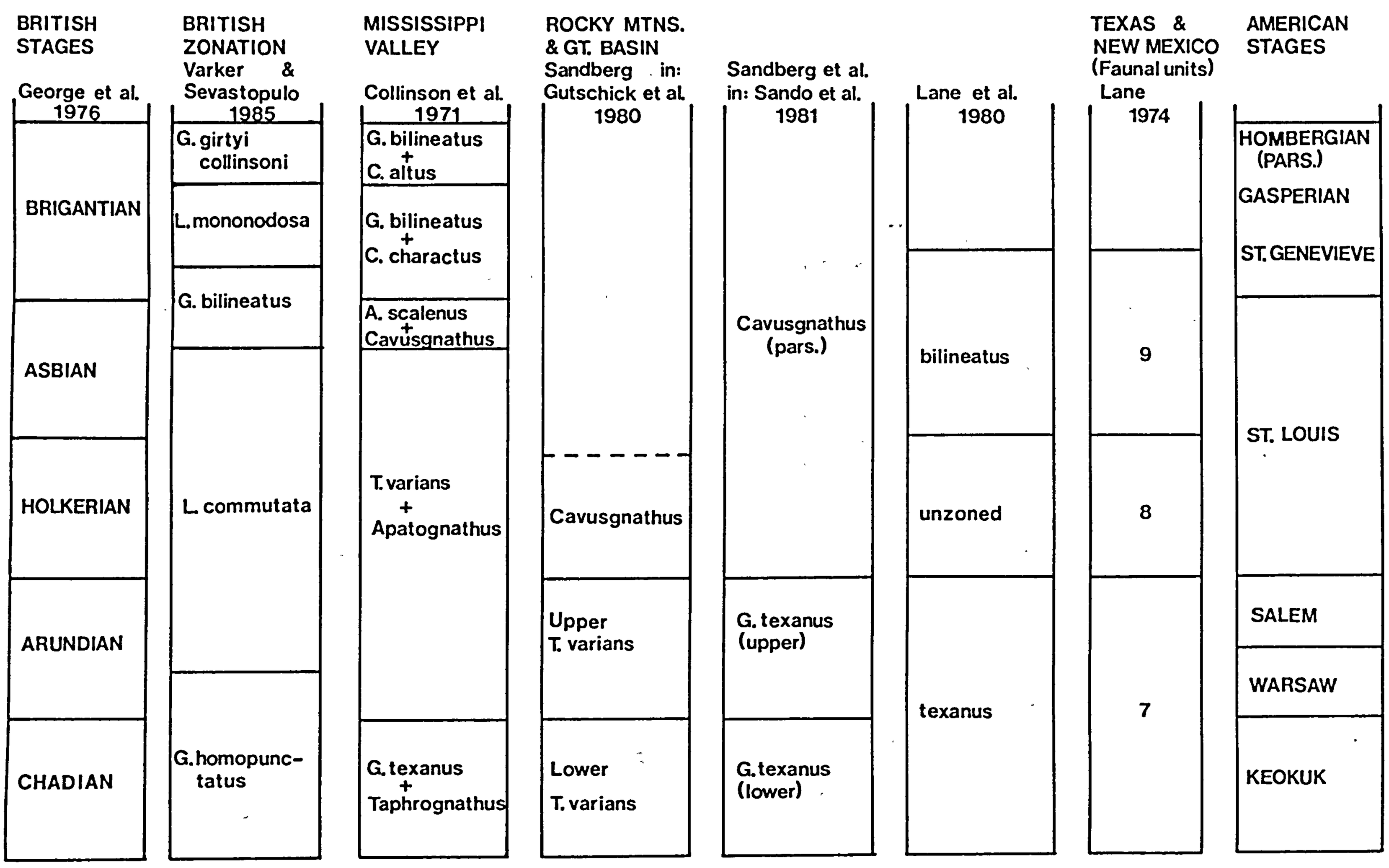


figure 1.4.3 American conodont zonation schemes for mid-Mississippian times. (the correlations are best approximations from the cited papers).

ii) North America.

The main pioneering studies of Lower Carboniferous conodonts were made in the U.S.A. in the 1920's and 1930's (Ulrich and Bassler 1926, Huddle 1934, and Branson and Mehl 1933-4, 1938a, 1940, 1941). The first American Carboniferous conodont zonation by Collinson et al. (1962) was based on faunas recovered from the Mississippi Valley. This was reviewed and updated, to include subsequent American studies, by Collinson et al. (1971); and five conodont zones represent the Chadian to Brigantian interval, with the Arundian interval being covered by the lower part of a long-ranging T. varians and Apatognathus Zone (fig. 1.4.3). Lane (1974) recovered conodonts from continuous sequences in Texas and New Mexico, and was able to define a series of nine faunal units, the last three of which covered the Chadian to mid-Brigantian interval (fig. 1.4.3). Subsequently Sandberg and various colleagues carried out a series of conodont studies in the Rocky Mountain and Great Basin areas (Sandberg et al. 1970, 1978; Gutschick et al. 1980; Sandberg and Gutschick 1980), and were able to correlate their findings with those of Lane (1974). This resulted in the conflated North American zonation of Sandberg et al. shown in figure 1.4.3, in which the Arundian correlates to the upper part of a G. texanus Zone. Lane et al. (1980) endeavoured to combine the established American zonation with reported conodont occurrences from Europe (essentially Germany and Belgium); and thus produced a preliminary global standard post-Siphonodella zonation (fig. 1.4.3). In this scheme a texanus Zone covers the entire Chadian-Arundian interval (and extends upwards to the inception of G. bilineatus in Europe or Cavusgnathus in America).

iii) Europe.

In Germany the studies of Bischoff (1957), Voges (1959, 1960) and Meischner (1970) resulted in a conodont zonation consisting of ten zones within the Lower Carboniferous, in which the entire early-Chadian to late-Asbian interval, is represented by a single zone: the "anchoralis-bilineatus interregnum" (fig. 1.4.4). Meischner (1970) states that the German zonation is derived from studies of complete sections in a pelagic geosynclinal environment.

A series of studies by Conil et al. (1964, 1976, 1977), Groessens (1974) and Paproth et al. (1983) has resulted in a Belgian conodont zonation scheme for the Lower Carboniferous which comprises thirteen subzones in the Tournaisian, and just four subzones in the Viséan (fig. 1.4.4). The early and middle parts of the Arundian Stage are correlated with a G. commutatus subzone by Paproth et al. (1983), and the subsequent interval up to early Asbian times is covered by an informal 'Taphrognathodides' subzone. These authors report that conodonts are very rare in the Arundian to Asbian rocks of Belgium, but comparatively abundant in Brigantian (V_3c) rocks.

Ebner (1977) studied the 23.8 m thick Sanzenkogel Formation of Graz in Austria (which represents a timespan equivalent to the Chadian-Arnsbergian interval), and was able to define ten conodont zones (fig. 1.4.4). The Chadian to mid-Asbian interval is covered by a G. typicus Zone and a G. sp. A Zone. G. typicus of Ebner (1977) would probably be considered as part of the G. texanus plexus herein, although Ebner's illustrations and description are insufficient for definitive synonymy.

Marks and Wensink (1970) erected a conodont zonation for Spain, in which the entire Chadian to Asbian interval is represented by a G. typicus Zone, (see Perret 1974 for conodonts from the French Pyrenees).

In a study of the Lower Carboniferous rocks of southern Poland, Belka (1985) distinguished three consecutive Viséan conodont zones - based on first occurrences of species of Gnathodus, namely: texanus, austini and bilineatus. Belka preliminarily correlated his texanus and austini Zones with the lower and upper parts of the texanus Zone of Lane et al. (1980). In the present study G. austini is synonymised with G. texanus, and the Arundian conodont fauna of South Wales is correlated with the upper part of Belka's texanus Zone (and possibly with the lower part of his austini Zone).

In the Russian zonation presented by Nigmadzhanov (1987) the Arundian interval spans the boundary between a Gnathodus texanus - Paragnathodus symmutatus Zone and a Paragnathodus commutatus Zone.

iv) Australia.

Within the Viséan sequence of New South Wales, Jenkins (1974) recognised a Pseudopolygnathus cf. nodomarginatus Zone, followed by a Patrognathus? cf. capricornis Zone. Precise correlation of the upper limit of the latter Zone with established European zonations has not been possible, but Jenkins (1974) implies that this Zone may extend upwards into rocks of Arundian age.

v) China.

The conodont zonation presented by Zengji (1987) is difficult to correlate with any of the western schemes because of the large number of new species cited coupled with diagnoses written only in Chinese, and the lack of Plates. However, the Arundian interval appears to correlate with the upper part of a Mestognathus latilobatus - Gnathodus hunanensis Assemblage Zone.

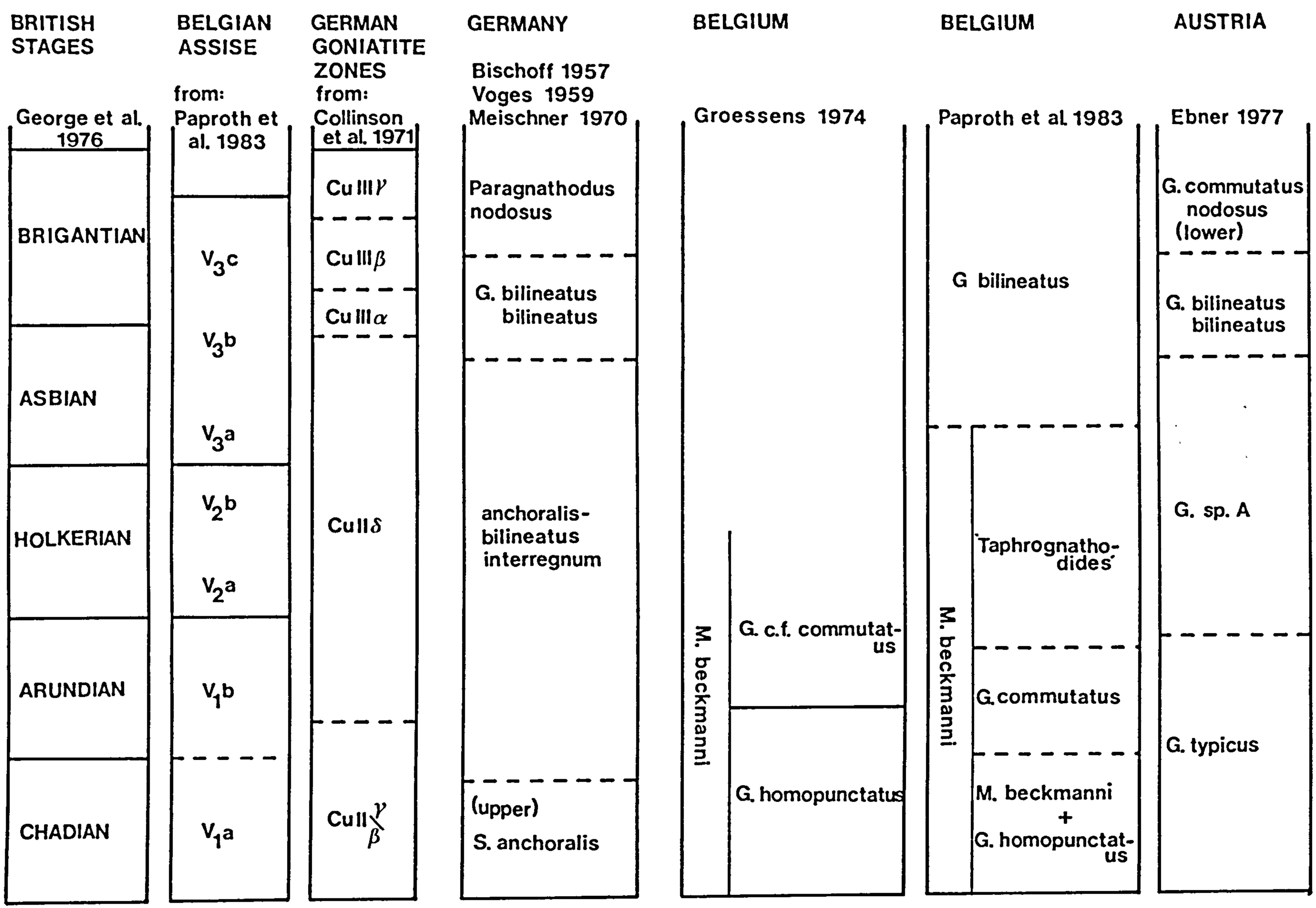


figure 1.4.4 European conodont zonation schemes for Viséan times.
(the correlations are best approximations from the cited papers).

2.1 INTRODUCTION TO THE FIELD STUDY.

2.1a The scope of the study.

Conodont faunas, from a variety of palaeoenvironmental settings in South Wales, have been recovered and examined. Five well-correlated Arundian sequences on the coast of south Dyfed have been sampled in detail, and reconnaisance samples have been taken from four localities on the Gower Peninsula, and one presumed Arundian sequence at Llanelly Quarry (fig 2.1.1). Sampling was carried out in liaison with Dr. John Simpson, formerly of Reading University and with Dr. John Scott formerly of Aberystwyth University, both of whom have completed major sedimentological studies of the area (Simpson 1985, Scott 1987). The aims of the study were various:

i) To investigate the Arundian conodont faunas of South Wales, using a multielement approach, and to correlate the findings with those reported from other areas.

ii) To discover whether Arundian conodonts are of biostratigraphical use in the carbonate shelf environments of South Wales (and other comparable areas).

iii) To achieve an understanding of the distribution of the conodonts with respect to ecological and taphonomical/sedimentological factors.

iv) To investigate the implications of the findings for conodont phylogeny.

Concentrating the investigation on the Arundian Stage in particular, has been of value for several reasons:

i) The Avon Gorge section, on which the conodont zonation of Rhodes et al. (1969) was based, contains a non-sequence and a zone of "no conodonts" in the Arundian interval (George et al. 1976).

ii) Subsequent British zonational schemes covering the Arundian interval (Metcalfe 1981, Higgins and Varker 1982, Armstrong and Purnell 1987) have not been fully intercorrelatable.

iii) The Arundian type-section is within the study area (George et al. 1976).

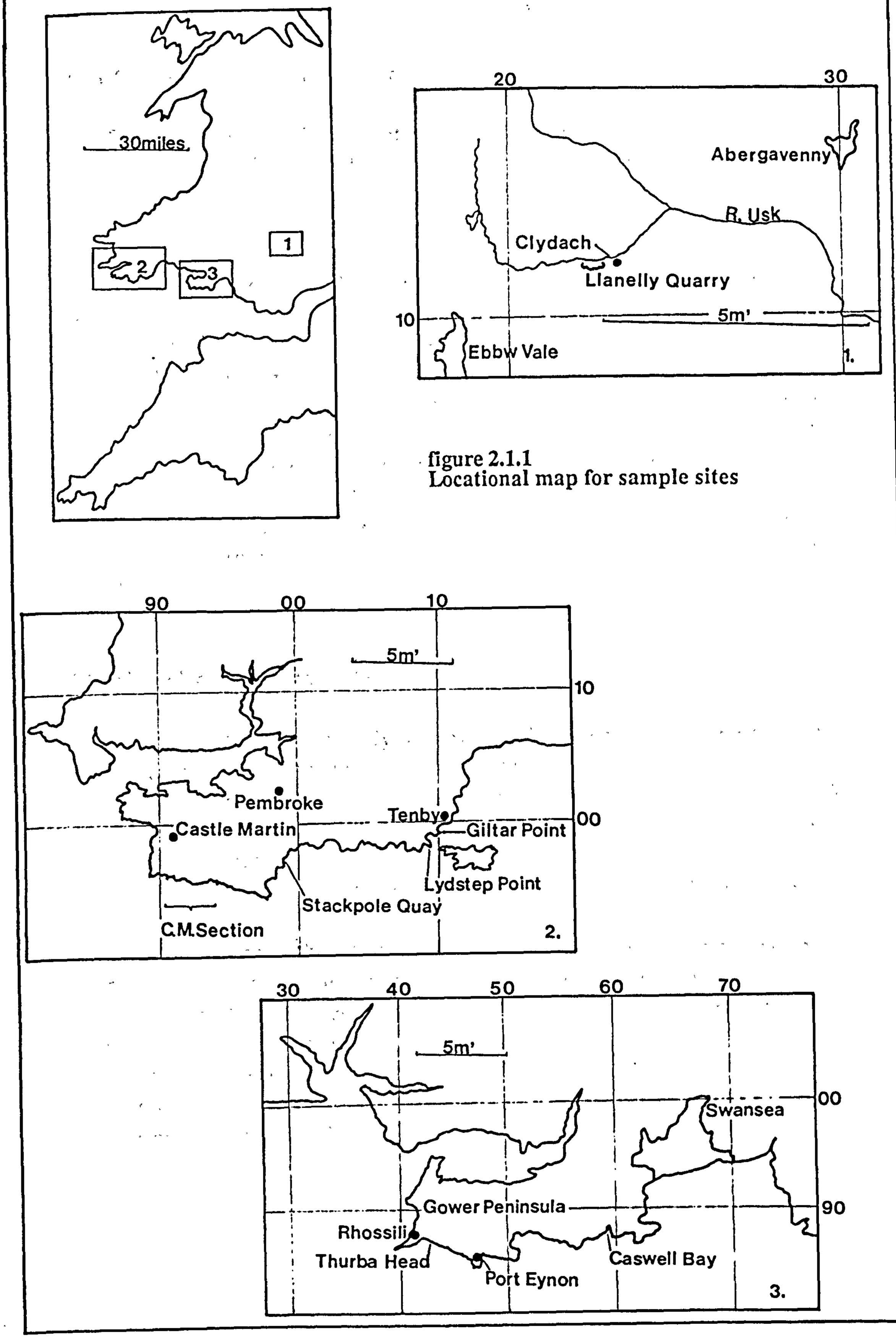


figure 2.1.1
Locational map for sample sites

2.1b The geographical and geological setting.

The study area (fig 2.1.1) stretches across South Wales from The Clydach Gorge in the east (Llanelly Quarry) to Castlemartin in the west; a distance of approximately 60 miles (100 km). Conodonts were recovered from nine representative Arundian profiles - covering the northcrop of the South Wales Coalfield (Llanelly Quarry), the Gower Peninsula (Burry Holms, Thurba Head, Port Eynon and Caswell Bay), and the Pembroke area of south Dyfed (Castlemartin M.O.D. Range, Stackpole Quay, Lydstep Point, Giltar Point and Tenby South Beach). All of these sites are coastal exposures except for Llanelly Quarry. Details of the sample localities are given in appendix D.

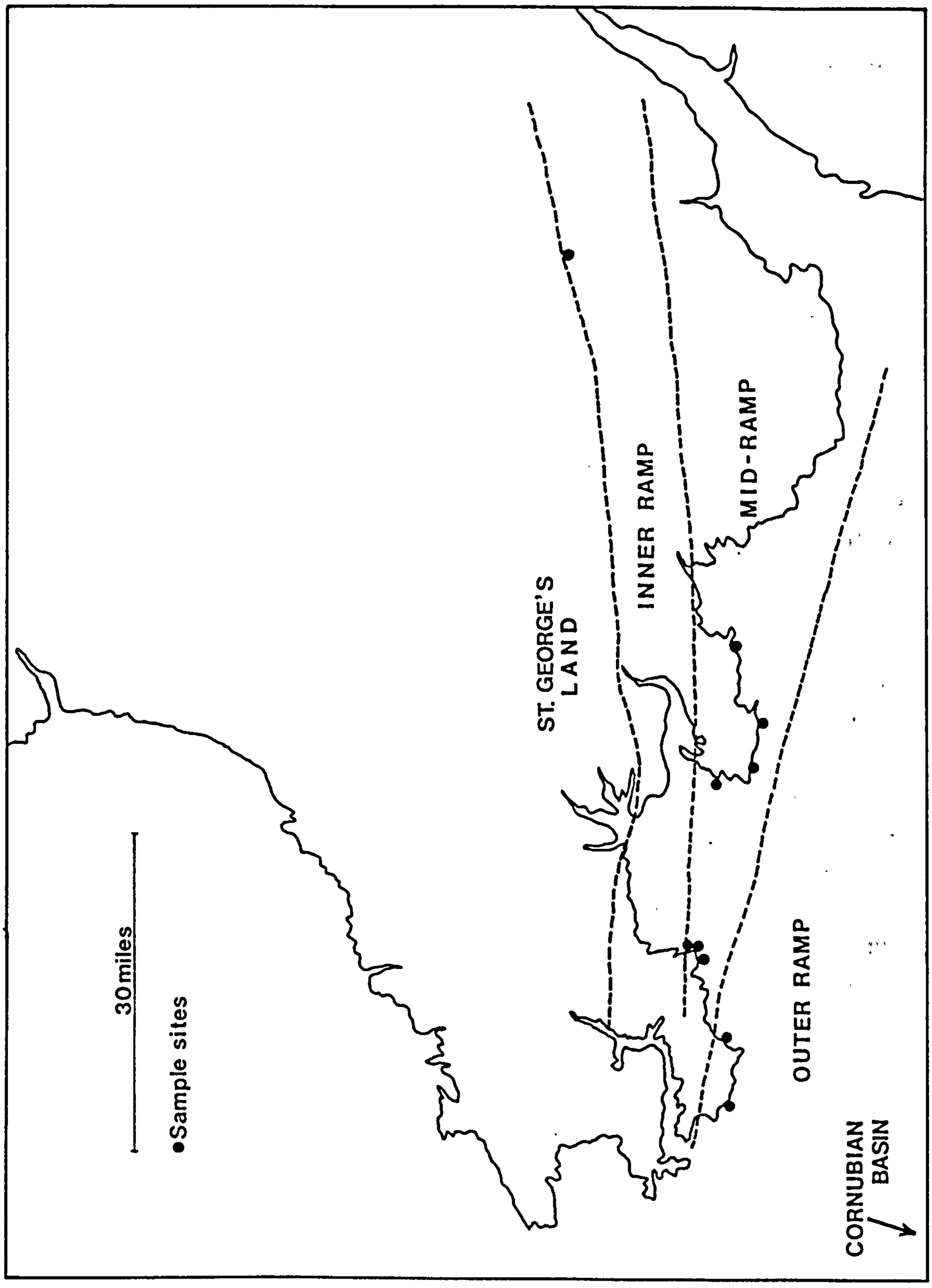
The Arundian sediments of South Wales are predominantly limestones, which were deposited across a broad carbonate ramp (Wright 1986). The palaeo-water-depth across the ramp probably ranged from approximately 200 m to less than 1 m (Simpson 1987); and sediments deposited include interbedded wackestone and lime-mudstone tempestites, oolites, laminated grainstones and micrites. The terminology of the local lithological units is shown in figures 1.3.1 and 2.3.6.

2.1c The palaeogeography of the study area.

In Arundian times the study area was probably situated just north of the equator, on the south-western edge of a major Caledonian continental area (Turner and Tarling 1975), and comprised a shelf sea some 100 km wide. To the immediate north was the low-lying Old Red landmass of St. George's Land (or the 'Wales-Brabant landmass' of Kent 1975), and to the south was the deep Culm or Cornubian Basin, (or 'Hercynian Ocean' of Leeder 1976), as illustrated in figure 2.1.2.

The study area is thought to have had a tectonic setting on the northern margin of a pre-Variscan extensional system, which extended from South Wales to the Bristol Channel Landmass (sensu Tunbridge 1986). Syndepositional subsidence to the south of the Ritec Fault is seen as a major control on sedimentation in south Dyfed (Powell 1989). The zone of transition, between the carbonate shelf of the study area and the Culm Basin deposits to the south, is not exposed (Leeder 1976).

figure 2.1.2 Palaeogeography of the study area during Arundian times (after Simpson), and the distribution of sample sites in the present study.



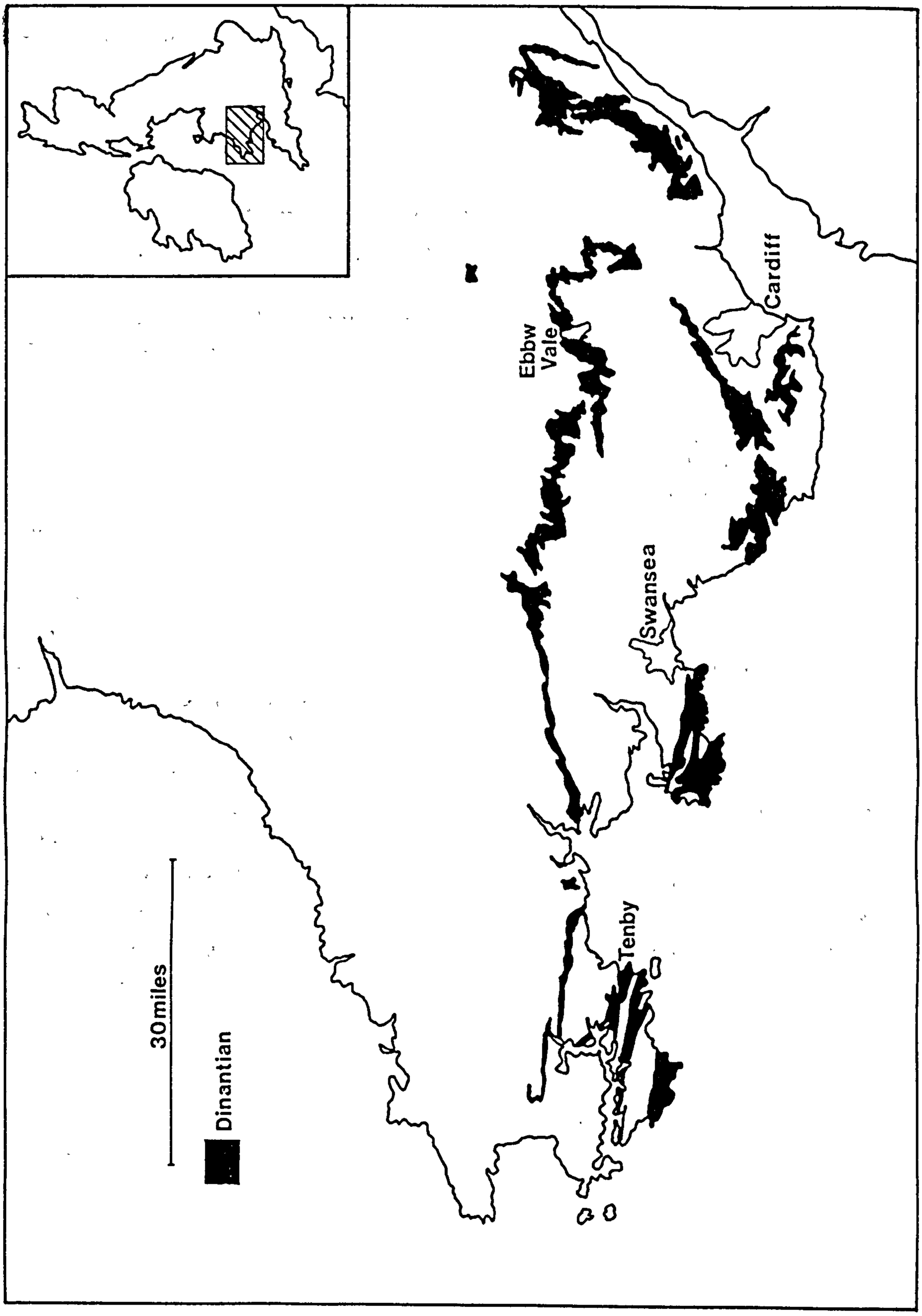
2.1d The Arundian palaeoenvironment.

The Dinantian sediments of South Wales (fig 2.1.3) comprise a 100 km wide wedge of shelf limestones and dolomites, thinning northwards from a total of 1000 m to less than 150 m. The base of the Arundian is marked by a major transgression, and during the subsequent 5-10 million years (George et al. 1976) up to 300 m of interbedded wackestones and lime-mudstones were deposited in the south, thinning to less than 30 m of dolomitic mudstones and conglomerates, with frequent emersion surfaces, in the north. Both Simpson (1985) and Wright (1986) suggest these deposits to be representative of a carbonate ramp environment similar to the modern day Arabian Gulf Trucial coastal region. Such ramps are thought to be typical features of the early stages of carbonate build-ups following the drowning of a continental area (Wright 1987). A carbonate ramp (Ahr 1973) has a gentle slope ($<3^{o}$) and passes gradually from nearshore shallow water facies out into basinal facies, usually with no break in slope between the shallow water and basinal areas. This is in contrast to the rimmed platform model, which is more usually cited in conodont studies of carbonate environments (e.g. Austin 1976, Sandberg and Gutschik 1984).

Wright (1986) suggests a general environmental model for the lower and middle parts of the Dinantian Subsystem in South Wales, in which the carbonate ramp is divided into three facies belts: inner, mid and outer-ramp. The differences between belts are governed by such physical factors as water depth, energy level (normal wave base), and distance from shore. The belts are thought to have had gradational boundaries with each other. Simpson (1985), in dealing specifically with the Arundian Stage, corroborates the above and presents a detailed study of the outer and mid-ramp belts.

Evidence for the Arundian Stage being a time of unusually shallow seas throughout most of the British Isles comes from numerous authors (Rhodes et al. 1969, George et al. 1976, Higgins and Varker 1982, Wright 1986, Armstrong and Purnell 1987). The South Wales area is therefore a good place to study Arundian conodonts as relatively deep-water faunas are recovered from the outer ramp belt; although even the distal shelf seas were probably shallower during the Arundian Stage than in the previous and subsequent Stages (Wright 1986).

figure 2.1.3 Dinantian rocks of South Wales.



i) outer ramp belt.

This belt is represented by limestones of the Pen-y-Holt Formation (George et al. 1976), which has been sampled at Castlemartin and Stackpole Quay (fig. 2.1.4), on the coast of south Dyfed (fig. 2.1.1). The Pen-y-Holt Formation comprises a 300 m thick succession of rhythmically interbedded bioclastic wackestones and lime mudstones. The beds are laterally pervasive and are of a constant thickness, which can range from cm's to a few m's. Dixon (1921) divides the Pen-y-Holt Formation into six lithological sub-units (his groups 4-9 inclusive).

9. Dark, thin bedded limestones, and thin mudstones. Gastropods abundant and often dolomitised, other fossils often chalcedonized. Occasional dolomites.
8. Thinly interbedded mudstones and impure limestones. Several dolomites.
7. Limestones with thin mudstones, similar to group 9.
6. Mudstone with a few thin impure limestones. Fossils abundant.
5. Dark limestones with mudstones and cherts.
4. Dark limestones with black nodular cherts, and interbedded mudstones.

The macrofauna contains many species which range upwards from the Chadian, although the incoming of Lithostrotion is distinctive. These beds are interpreted as having been deposited in a distal shelf environment below normal wave base, at a water depth of approximately 100 m to 200 m, and at a distance of some 20 km to 30 km from the shoreline (Simpson 1987). The bioclastic wackestones are seen as tempestite, event deposits, settling out from clouds of suspended material stirred up by unusually violent storms. The lime mudstones are interpreted as the background pelagic sedimentation slowly accumulating between each major event. The lime mudstones have a very similar lithological and faunal composition to the wackestones but contain more mud, fewer bioclasts and more whole fossils. The tops of both units often show colonisation surfaces, and signs of burrowing. The succession at Castlemartin contains some 530 wackestone units, suggesting an event cyclicity of the order of one per 9,000 or 18,000 years depending on whether the figure of 5 million years or 10 million years is taken for the duration of the stage.

ii) mid-ramp belt.

This belt is represented by the Caswell Bay Mudstone (and its lateral equivalents) and the High Tor Limestone Formation (Wright 1986). These have been sampled at Lydstep Haven, Giltar Point and Tenby South Beach in south Dyfed, and at Burry Holms, Thurba Head, Port Eynon and Caswell Bay in the Gower Peninsula (figs. 2.1.1, 2.1.5 and 2.1.6). The environment of deposition is more varied than that of the outer ramp, and has resulted in 150 m of unstratified crinoidal packstones, cross stratified peloidal and ooidal grainstones, dolomitised lime mudstones and interbedded shales and bioclastic limestones. Relative changes in sea level are viewed as having a strong influence on sedimentation patterns in this belt (Wright 1986). Although each section is different there is a generalised cycle of five facies units through Arundian times (Dixon 1921):

5. Interbedded dolomites and mudstones ("shales"), with gastropods. Generally 12 m to 18 m thick.
4. Crinoidal packstones, often finely laminated. Bioturbation, few fossils. Generally 36 m to 45 m thick.
3. Thin-bedded dolomitized limestones and lime mudstones, with crinoid and brachiopod debris, may have gastropods. Generally impersistent; 3 m to 9 m thick.
2. Evenly bedded crinoidal packstones, often with laminations. Some oolites, generally very fossiliferous and 30 m to 36 m thick.
1. Dolomite with mudstones, may have gastropods. Generally 0.5 m to 12 m thick.

Dixon's group 1 equates with the Caswell Bay Mudstone (Simpson 1985), which has been interpreted further east as a peritidal back-barrier deposit which formed during the basal Arundian transgression (Wright 1986). The overlying High Tor Limestone (groups 2-5) is interpreted as resulting from a shoreward migration of the bioclastic sands which formed the barrier during earliest Arundian times. Simpson (1985) notes that the beds of groups 2 and 4 at Giltar and Tenby differ slightly from the above as they comprise cross-stratified peloidal and ooidal limestones, and are interpreted as being slightly more onshore deposits.

The High Tor limestone is interpreted as having been deposited some 8 km to 10 km north of the Pen-y-Holt limestones in a higher energy, mid to inner ramp setting - above storm wave base (Simpson 1985). Water-depths are thought to have been in the range from some m's to some tens of m's. At any one time the High Tor depositional régime may have included a range of sub-environments from crinoidal sands below mean wave base, toward the distal part of the mid-ramp, through ooid shoals to poorly sorted ooidal and peloidal sands (Simpson 1985).

The fauna of the crinoidal sands is seen as essentially autochthonous

(Simpson 1985), and this implies the same for the more shoreward parts of the mid-ramp. Evidence for the proximal provenance of the fauna comes from localised piles of crinoid cup plates, abundant long crinoid stems, the presence of crinoid holdfasts and the lack of current or wave-derived sediment stratification.

There are signs of a mid-Arundian regression (or shallowing event) prior to group 3 times (Scott pers. comm. 1986), which cannot be detected further out on the shelf.

iii) inner ramp belt.

Until recently the Arundian inner shelf belt was not thought to be exposed. Wright et al. (1981) suggest that it is represented by a 30 m (or thinner) sequence of euryhaline shallow water lagoon, intertidal, evaporite and soil deposits - which are exposed in the northcrop of the South Wales Coalfield as the Llanelly Formation. A reconnaissance sampling programme has been completed in the Llanelly Quarry sequence (fig 2.3.6), and a limited fauna has been recovered. Recently the corals, on which assignment to the Arundian Stage was based, have been re-examined (Sevastopulo pers. comm. 1988) and once again it has been proposed that the Llanelly Formation is pre-Arundian. The age of the Llanelly Formation and its fauna is discussed in section 2.3e.

2.1e Sampling and processing procedures employed in this study.

i) Introduction.

The vagaries of the techniques used to isolate conodont elements impose limitations on the accuracy and interpretation of results. As wide a variety as possible of the lithologies within a sampled section must be fully explored to gain a representative overall picture. Consequently a study has been made of techniques used by conodont workers, and the limitations of these techniques (see section 3.1).

ii) Procedure followed in this study.

Following the general principles outlined in section 3.1, samples of approximately 2 kg were taken from representative individual beds at each section. Locational and geological notes for each sampled horizon were made in a field note-book, and where possible the position of the sampled units was plotted on a sedimentary log. At each section the aim was to obtain a representative sample profile, particularly with respect to the cycle of sedimentological groups defined by Dixon (1921).

The majority of samples were dissolved in 10 l plastic buckets containing a solution of acetic acid, calcium acetate soup and water in the proportions

suggested by Jeppsson et al. (1985). Dolomitic samples were dissolved in formic acid buffered with bone-meal, and particularly mud-rich samples were broken down with Quaternary O and freeze-thaw techniques.

After being wet-sieved according to the procedure outlined in section 3.1c, the insoluble residues were separated using bromoform as explained in section 3.1d (ii). Each heavy fraction was examined under a binocular microscope, and the conodont elements were picked out using a fine, moistened paint brush. The faunas were mounted on cavity slides using gum tragacanth, and are stored at the University of Southampton, under the curatorship of Dr. R.L. Austin.

Plates were produced by gold-coating representative specimens and photographing them using an I.S.I. Model 60A scanning electron microscope.

iii) conodont sampling experiment.

Initial reconnaissance sampling of the Pen-y-Holt Limestone Formation at Castle Martin established the presence of a comparatively abundant conodont fauna. Following this, an experiment was carried out to investigate the way in which conodonts are distributed within the individual limestone units. It was anticipated that this would both facilitate efficient sampling and help to investigate the taphonomic factors involved with the Pen-y-Holt conodont faunas.

Early sampling of three limestone beds on the western edge of Pen- y-Holt Bay revealed that they each contained a representative and varied conodont fauna (samples CM 11, 15 and 19 of figure 2.1.4). Further samples were taken from the base, middle and top of each of these units (samples CM 12-14, 16-18 and 20-21). The conodont faunas recovered from each of these samples were then assessed and the results were compared with regard to the relative nature and abundance of the elements recovered.

Westrop (1986) illustrates that in the deposition of tempestites there is a high degree of sediment sorting which can produce considerable vertical variation in faunal composition throughout individual beds. Work by McGoff (pers. comm. 1988) indicates that in tempestite deposits it could reasonably be assumed that, due to the comparatively high specific gravity of conodont elements, there would be a concentration near the base of each event deposit. Further there should also be a concentration of the slightly larger, and more dense, pectiniform elements nearer the base.

The results of the experiment show that the distribution of conodont elements in beds of the Pen-y-Holt Limestone Formation does not accord with the predictive model of Westrop (1986). For example in the bed originally sampled as CM 11 the bottom of the bed is the most productive, but in the bed originally sampled as CM 15 the bottom is the least productive. Similarly the frequency of pectiniform and ramiform elements does not show any relative vertical sorting, but simply mimics the overall abundances.

For full quantification of the frequencies of occurrence, a much larger data base is required; however the results from the three beds sampled do illustrate the complexity of the situation in the beds of the Pen-y-Holt Formation, and show that to obtain a representative sample from any individual bed, it should be comprehensively channel sampled.

There are several possible reasons for the discrepancies between the predictions of Westrop's model and the actual Pen-y-Holt situation:

1. These may not be tempestite deposits, although the detailed discussion presented by Simpson (1985) leaves little doubt that this is the most likely mode of deposition.
2. The Westrop model may not be representative of tempestites in general, however this seems unlikely as it has been applied to a variety of situations and does sound empirically correct.
3. The storm events causing the deposition of the Pen-y-Holt beds may have been of an intensity such that there was no quiescent "fall- out" phase after the main storm allowing an orderly settling out of suspended particles.
4. Reworking by storms, tidal currents or bioturbation, prior to lithification, may have mixed the contained fossils.
5. Each "bed" seen today may be the result of a number of storm events, in which case the coarseness of the sample intervals would probably preclude recognition of vertical sorting patterns.

It is probable that a combination of the last three factors (3-5) is responsible for the conodont element distribution pattern which is seen in the Pen-y-Holt Limestone.

The results of the experiment show that resampling of the same beds can produce different faunal abundance figures; this may result from uneven channel sampling throughout the bed or may simply reflect the comparatively random way in which the fossils are distributed in the rock. The limitations on conodont/kg figures are highlighted, and although they may show general trends they should not be used as accurate indicators.

The figures for relative frequency of ramiform and pectiniform elements show that the latter are always over represented. This is a common feature of Carboniferous conodont faunas (e.g. Metcalfe 1981) and is probably a reflection of the comparative robustness of the pectiniforms, at both the preservation and sample-processing stage.

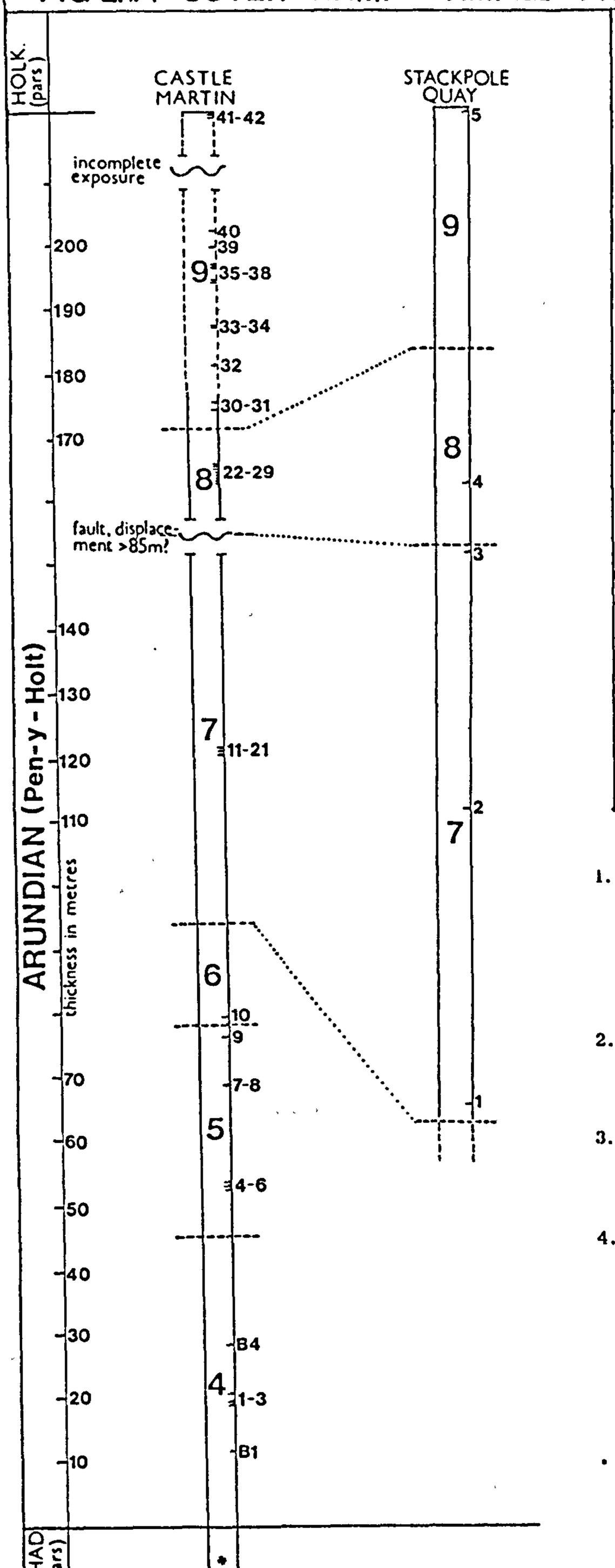
The provenance of faunas contained within tempestite deposits is thought to be highly localised (Westrop 1986). In the Pen-y-Holt Limestone the same macrofauna is seen in the lime-mudstones and the wackestones (although the fossils are typically more broken-up in the latter), and this is used by Simpson (1985) as corroborative evidence that the fauna of the event deposits is essentially autochthonous. The findings of the present study concur with this,

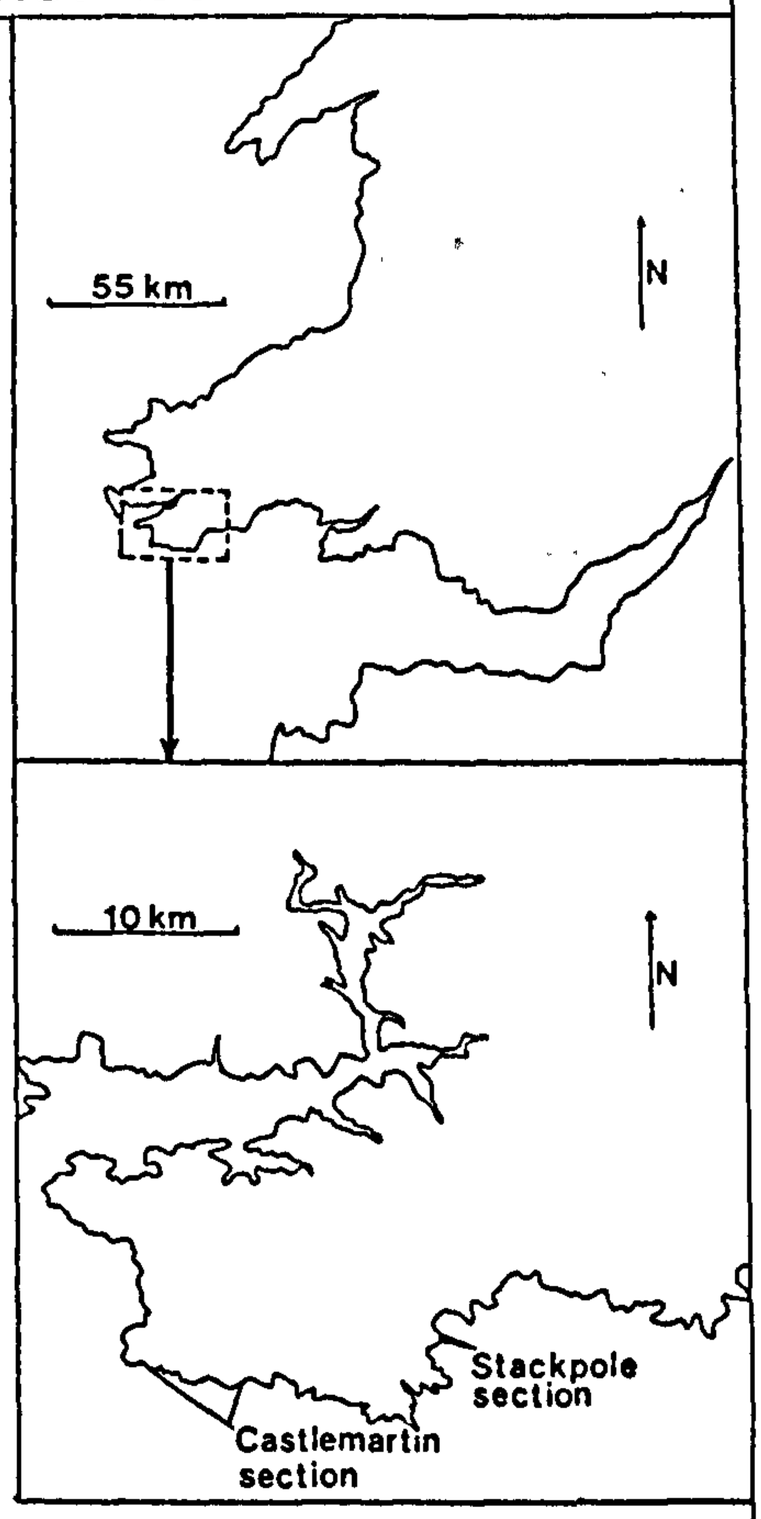
but there does appear to have been a comprehensive winnowing of the conodont elements between death and deposition.

2.1f Detailed sampling profiles.

The distribution of the sample points, at the various sites, is shown in figures 2.1.4, 2.1.5, 2.1.6 and 2.3.6 (the latter covers the Llanelly Quarry samples, and is included in section 2.3e for ease of discussion). The south Dyfed sections (2.1.4 and 2.1.5) are drawn to scale, and each is divided into a series of sedimentological units, based on those of Dixon (1921) - indicated by the large numbers in the centre of the columns. There is no direct correlation between the sedimentological units of the outer and mid-ramp sites (see section 2.1.d above for an explanation). The sample numbers are shown to the right of each column, and the letter-codes which precede the sample numbers at each site are listed.

FIG 2.1.4 OUTER RAMP SAMPLE PROFILE



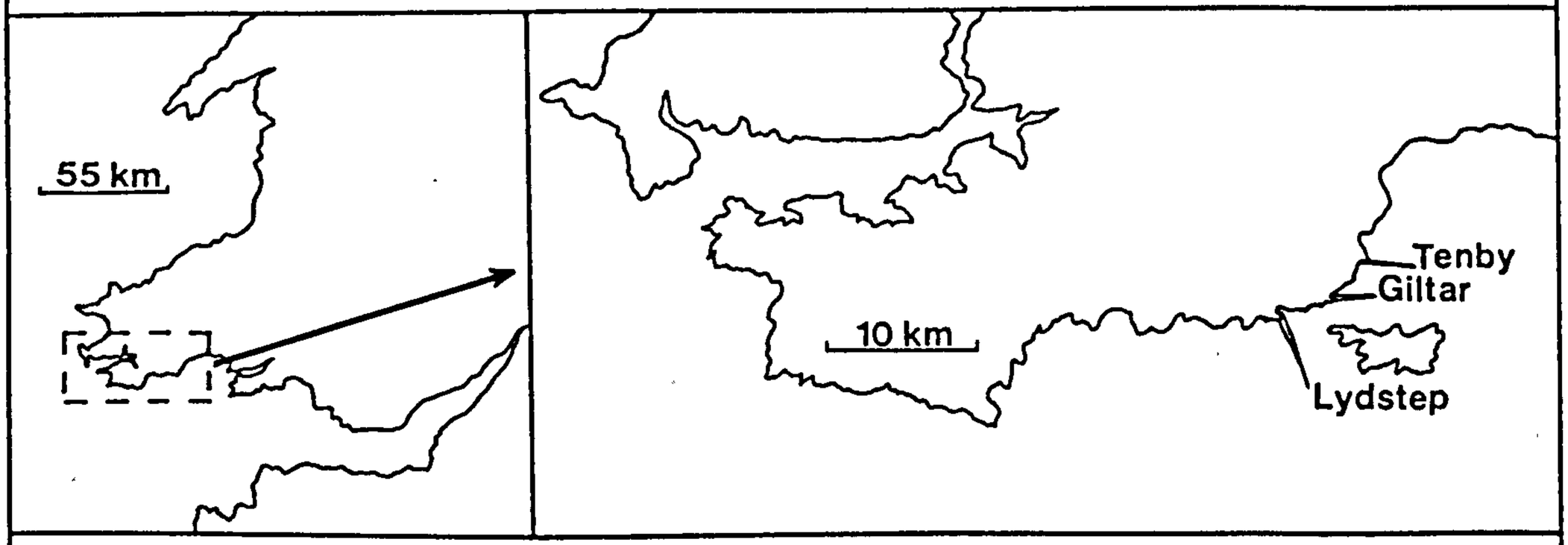


NOTES

1. Thicknesses for the Castlemartin section are based on Simpson (pers. comm.), and those for Stackpole Quay are based on Dixon (1921).
2. Sample numbers for the Castlemartin section are preceded by the letters CM.
3. Sample numbers from the Stackpole Quay section are preceeded by the letters SQ.
4. Dixon (1921) correlates the S_1 subzone (see fig 1.3.1) with his lithological group 9 plus the upper part of his group 8, and the C_2 subzone with his groups 1-7 plus the lower part of group 8.

* See Austin (1987) for a report of the conodonts recovered from the upper Chadian part of the Castlemartin section.

FIG 2.1.5 MID-RAMP SAMPLE PROFILE



(cbm= Caswell Bay Mudstone)

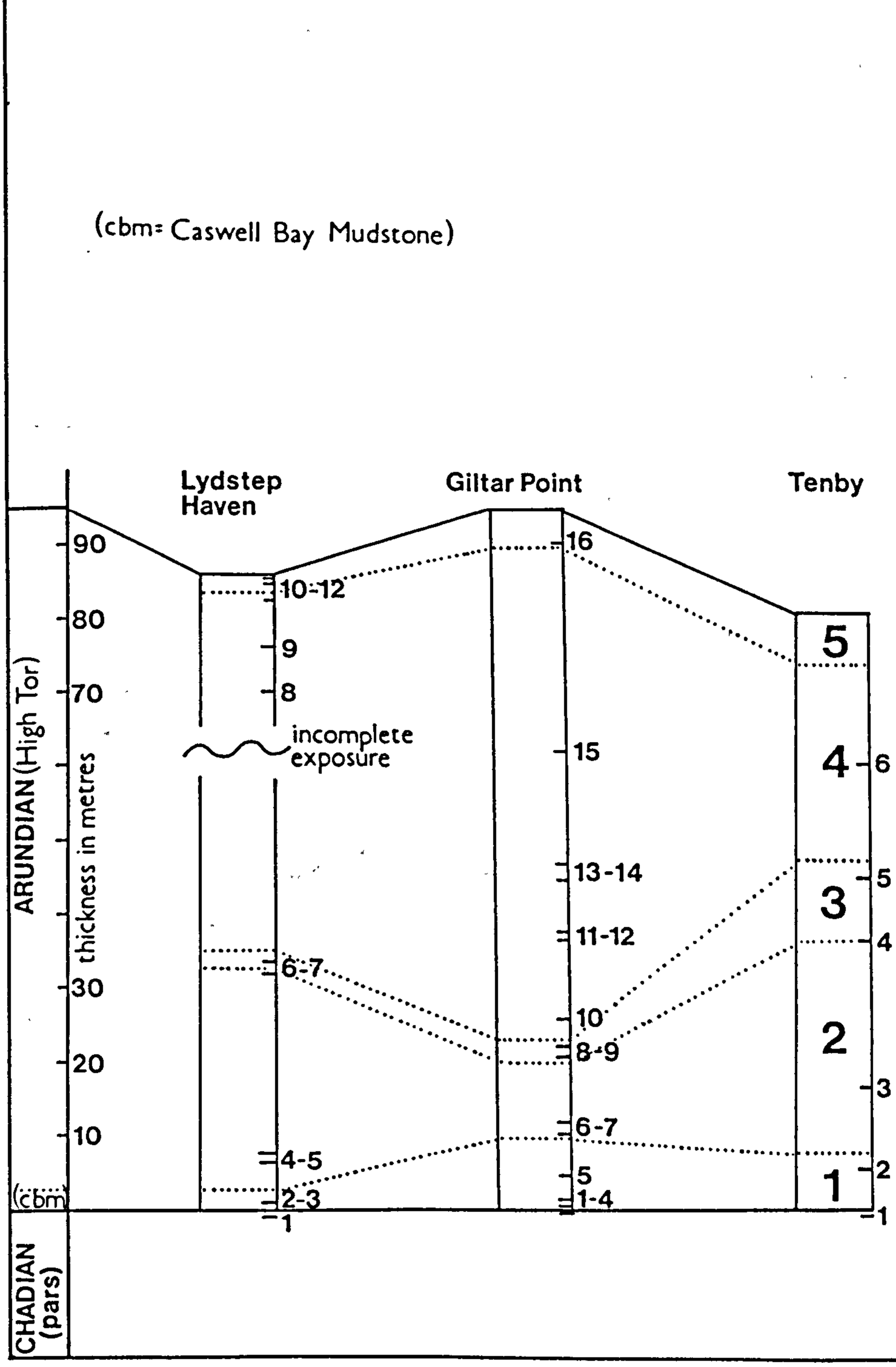
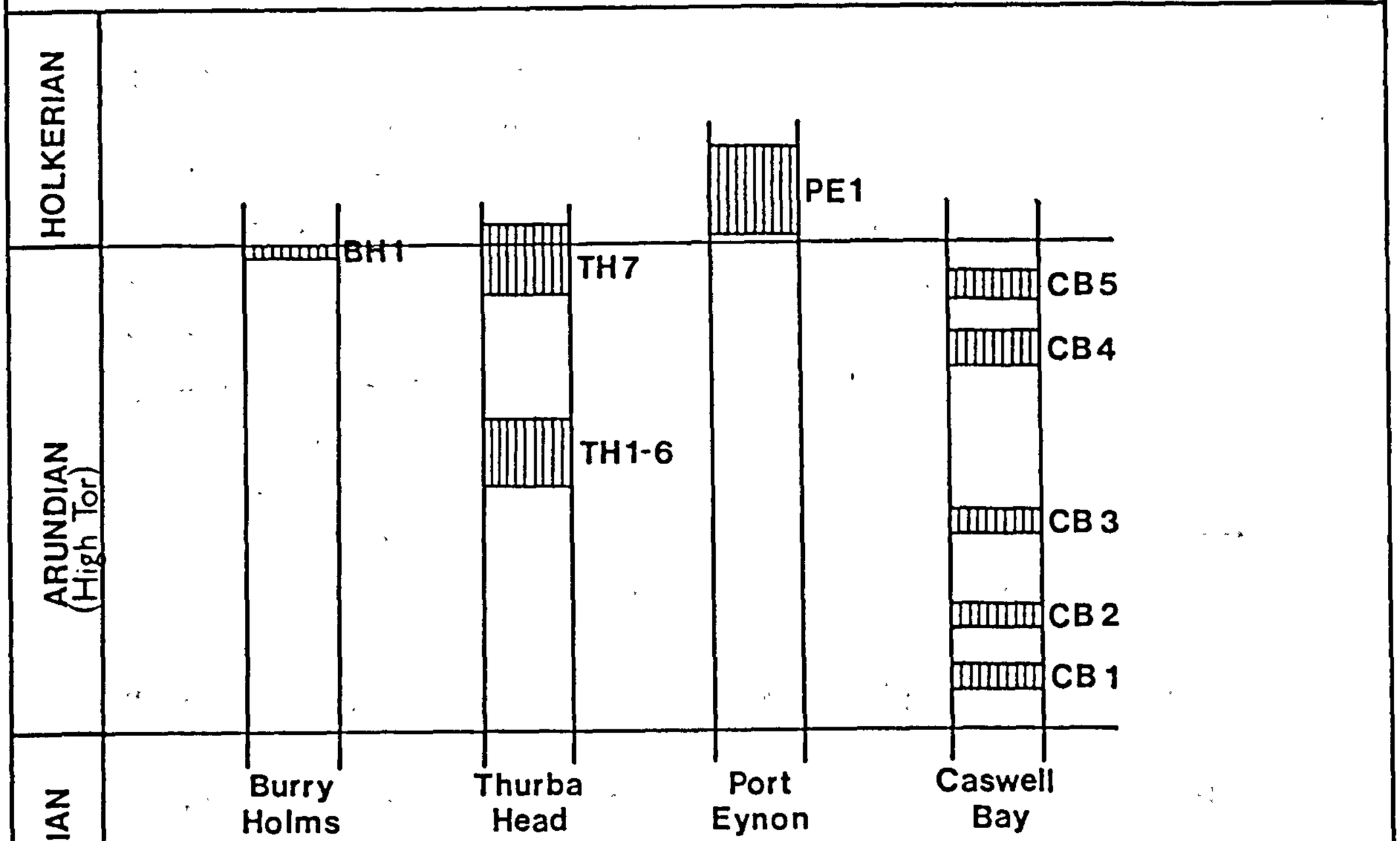
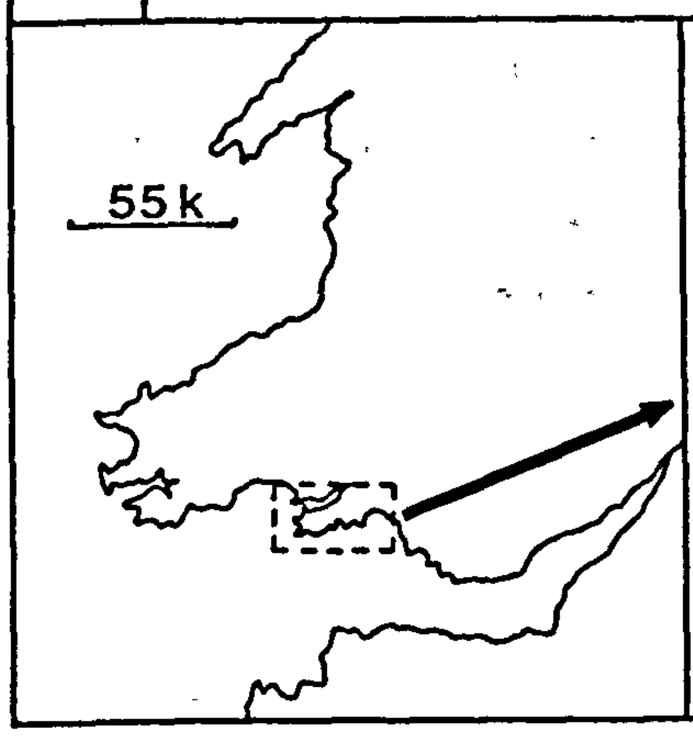
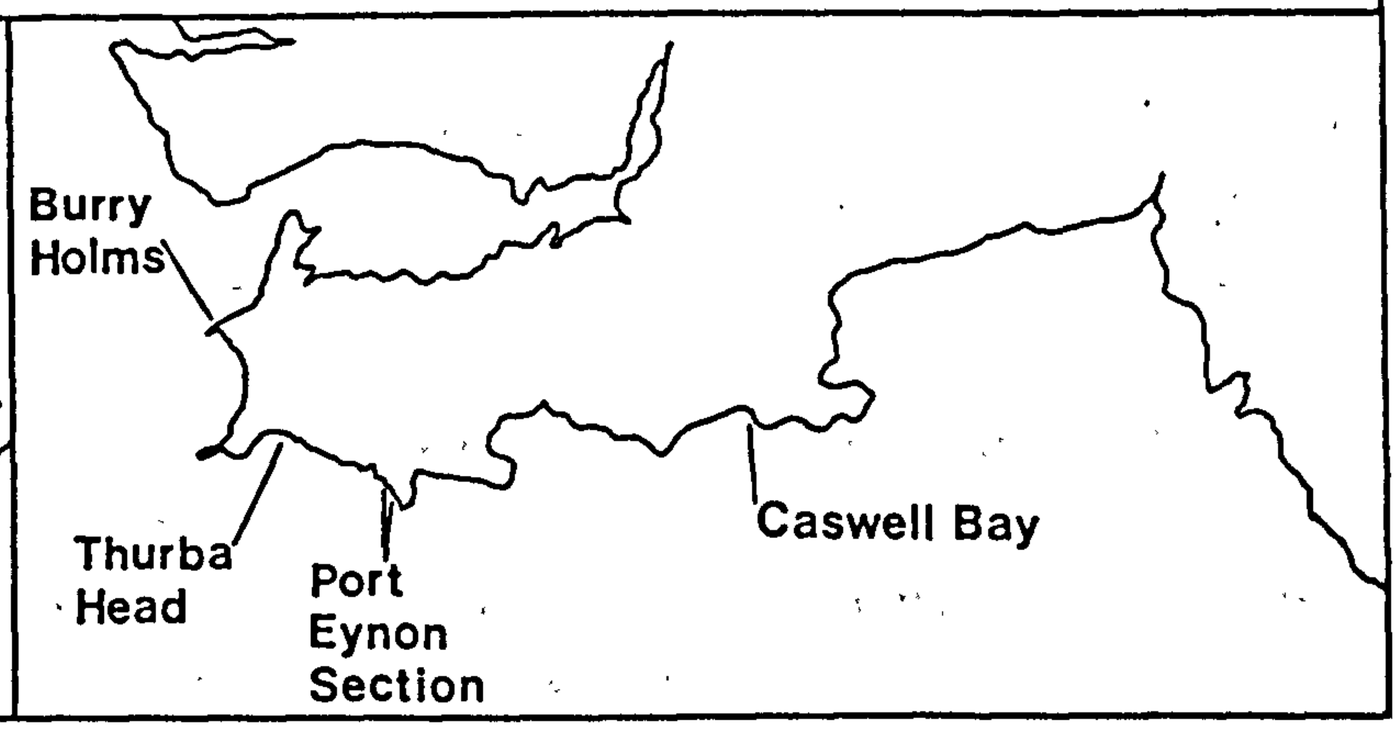


FIG 2.1.6 POSITION OF GOWER PENINSULA RECONNAISSANCE SAMPLES







2.2 SYSTEMATIC CLASSIFICATION OF CONODONT ELEMENTS RECOVERED IN THIS STUDY.

2.2a Introduction.

Where possible, the conodont elements recovered have been classified using multielement criteria (see section 1.2f). Those conodont elements not yet referable to a multielement apparatus are listed in single element terms, following the multielement section. The synonymy lists for each species include the first diagnostic description, alterations to the name or species-concept, and recent relevant references to the species in question. Non-nomenclatural signs have been attached to entries in the synonymy lists based on the suggestions of Richter (1948) and Matthews (1973):

.1969 . in front of the year. Responsibility is accepted for adding this reference to the species under discussion.

1969 No sign in front of the year. Responsibility is not accepted for this reference being included, but there is no reason to doubt its validity.

?1969 ? in front of the year. This reference is included with some uncertainty.

p1969 p in front of the year. Only part of the reference refers to the species under discussion.

vic1969 vic in front of the year. Although this reference does not cite the element as the species in question, the author states the element to be shared vicariously between a number of species.

For the sake of completeness, a brief synonymy list is given for elements not recovered in this study, but known to occur in an apparatus which is represented. In this case the synonymy is based on the best available and most recent information.

The letters s.f. (sensu formo) after a name indicate use of single element taxonomy. The sample ranges given for each species refer to figures 2.1.4, 2.1.5, 2.1.6 and 2.3.6. An introduction to each of the major groups covered, including a general diagnosis is given in section 1.4 (where Cavusgnathus, Clydagnathus, Mestognathus and Patrognathus are grouped as the cavusgnathoid genera for ease of discussion).

2.2b Genus: Cavusgnathus Harris and Hollingsworth 1933
Type species: Cavusgnathus alta Harris and Hollingsworth 1933
Synonymy: 1942 Lewistownella Scott
1975 Windsorgnathus Austin and Mitchell

Remarks:

The multielement reconstruction of Cavusgnathus is based on bedding plane studies by Scott (1942) and Norby (1974, 1976); and on statistical analyses by von Bitter (1972) and Horowitz and Rexroad (1982). Species recognition is largely based on the Pa elements and, although several Pa element form-species are known (all of which are right sided), Rexroad (1981) formally recognised only four multielement taxa: C. charactus, C. unicornis, C. altus and C. naviculus. The Pa elements referable to C. convexus s.f. and C. regularis s.f. are considered to occur in C. unicornis as parts of a dimorphic pair.

The Pa elements of Cavusgnathus and Mestognathus are very similar, but can be distinguished by the nature of the basal cavity: that of Cavusgnathus is wide and flaring, while that of Mestognathus is small and narrow.

Cavusgnathus altus (Harris and Hollingsworth 1933)

Plate: 1 figs 1-2.

Pa element

Synonymy:

1933 Cavusgnathus alta Harris and Hollingsworth Plate 1 figs 10a-b, page 201.

1941 Cavusgnathus cristata Branson and Mehl Plate 5 figs 26-31, page 177.

p1942 Lewistownella agnewi Scott Plate 40 figs 1 and 20, page 300.

1953 Cavusgnathus cristata Branson and Mehl. Hass Plate 14 figs 12-14.

1961 Cavusgnathus cristata Branson and Mehl. Rexroad and Burton Plate 138 fig 16, page 1151.

1966 Cavusgnathus alta Harris and Hollingsworth. Rexroad and Lane, text-fig 1, page 1391, (re-examination of holotype specimen).

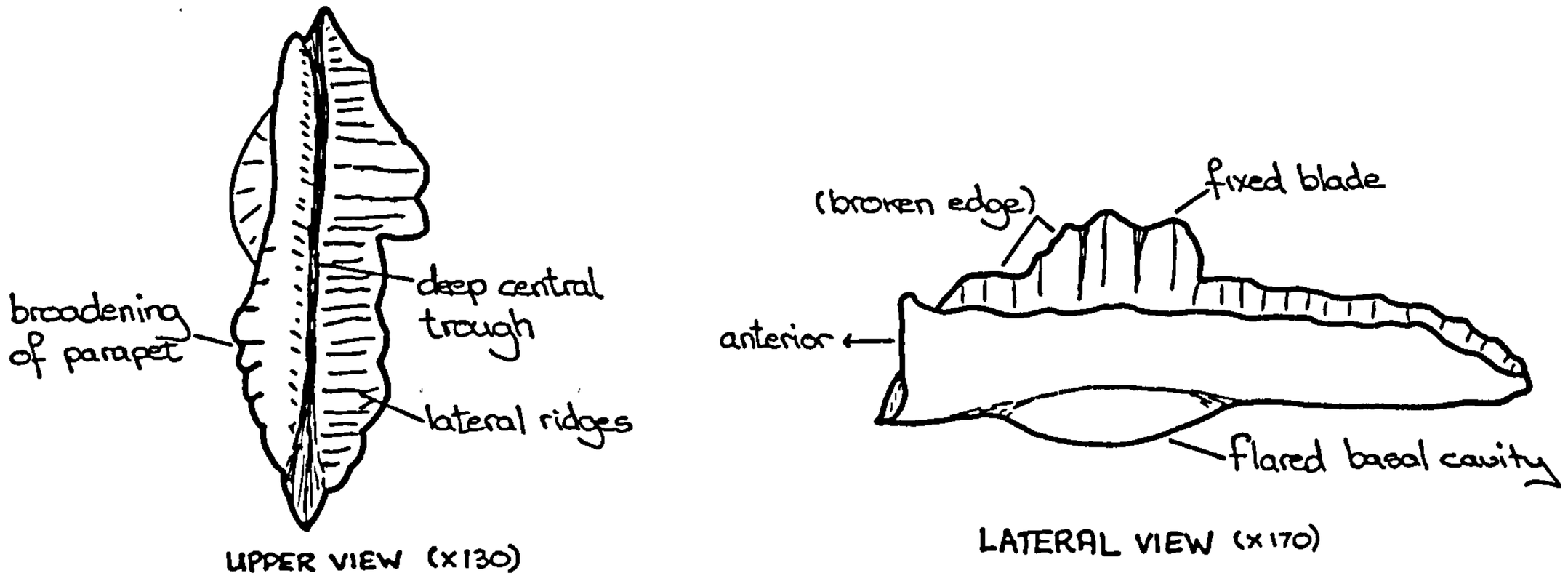
1969 Cavusgnathus cristatus Branson and Mehl. Rhodes et al. Plate 14 figs 3a-d, page 80.

?1969 Cavusgnathus altus (Harris and Hollingsworth). Webster Plate 4 fig 2, page 25.

1976 Cavusgnathus altus (Harris and Hollingsworth) Pd element; Norby Plate 1 figs 10-11, 13-14, page 77.

1981 Cavusgnathus altus (Harris and Hollingsworth) Pa element; Rexroad Plate 1 figs 28, 32-34, page 7.

Interpretive sketch 2.2.1 Cavusgnathus altus Pa element (sample GL 5).



Description:

Of the three specimens recovered, one is only poorly preserved and the other two are immature (one specimen may be a juvenile form of Mestognathus; see comments under "phylogeny" of von Bitter et al. 1986).

The unit has a deep central trough from which the sides of the platform rise up steeply at about 35° from vertical. The inner surfaces are ornamented with coarse lateral ridges, and where these terminate they produce a roundly crenulate upper margin to the platform in lateral view. The fixed part of the blade has three laterally flattened denticles, fused for the lower three quarters of their length. The tallest denticle is posterior-most (although the tip is missing in the example illustrated above), and is twice the height of the platform. The free portion of the blade is damaged in all specimens but has at least one denticle of similar dimensions to the denticles of the fixed blade, and probably at least one more (smaller) denticle. The height of all the blade denticles is roughly similar but decreases slightly toward the anterior.

There is a constriction below the left lateral platform margin, and beneath this a flaring-out of the basal cavity, which stretches for most of the length of the unit (but is incomplete in all specimens).

Discussion:

The poor state of preservation of these specimens precludes a more detailed analysis.

Sample range: GL 5 to GL 14.
Distribution: Middle mid-ramp.
Material: 3 specimens.

Non-platform elements:
Remarks:

There is an overall similarity between the non-platform components of different Cavusgnathus species and between Cavusgnathus and Adetognathus (Scott 1942; von Bitter 1972; Baesemann 1973; Norby 1974, 1976; Horowitz and Rexroad 1982; Rexroad 1981; Rexroad and Merrill 1985). In a detailed study of C. altus and C. unicornis, Rexroad (1981) concluded that their Pb and Sc elements were entirely vicarious, but the M elements were usually distinct. Multielement interpretation of the different Cavusgnathus species is further complicated by the possible loss of some elements in adults living in adverse ecological conditions; through lack of development or resorption (von Bitter and Merrill 1980, Rexroad 1981, von Bitter et al. 1986).

Pb element

(not recovered in this study, presumably due to the paucity of Cavusgnathus elements in general).
Synonymy:

1900 Polygnathus dubius Hinde Plate 9 fig 1, page 341.
1941 Ozarkodina mutabilis Branson and Mehl Plate 5 fig 16, page 177.
1957 Ozarkodina compressa Rexroad Plate 2 figs 1-2, page 36.
1969 Ozarkodina hindei Clarke. Rhodes et al. Plate 27 figs 16-17, 22, page 171.
vic1976 Cavusgnathus spp., O element; Norby Plate 2 figs 1a-12b, page 92.
1981 Cavusgnathus altus Harris and Hollingsworth Pb element; Rexroad Plate 1 figs 4-5, page 7.

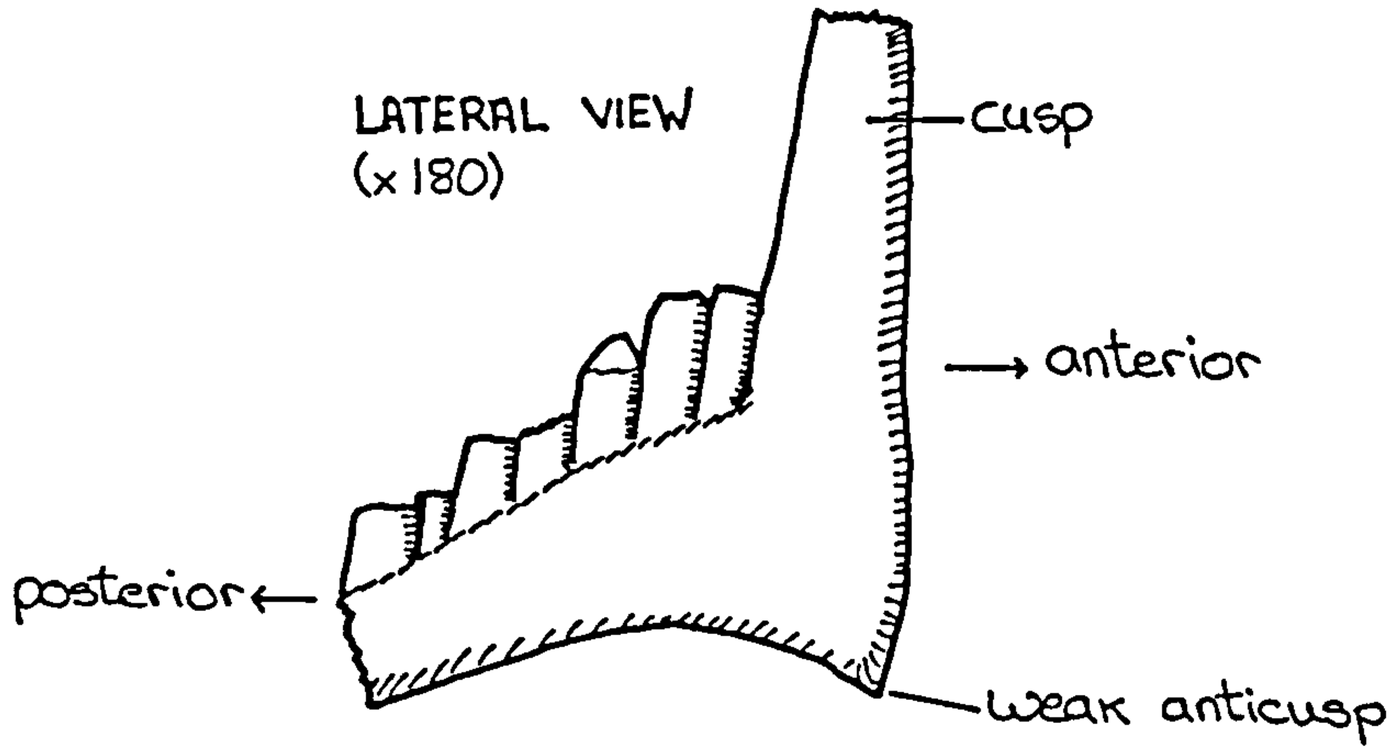
M element

Plate: 1 fig 3.
Synonymy:

1941 Prioniodus varians Branson and Mehl Plate 5 figs 7-8, page 174.
1960 Neoprioniodus brevis Clarke Plate 2 fig 7, page 13.
1969 Neoprioniodus varians (Branson and Mehl). Rhodes et al. Plate 21 figs 18a-b, page 165.
1974 Neoprioniodus varians (Branson and Mehl). Austin and Husri Plate 12 figs 21-22.
vic1976 Cavusgnathus spp., N_{1a} element; Norby Plate 3 figs 2-6c, page 94.
1981 Neoprioniodus varians (Branson and Mehl). Metcalfe Plate 18 fig 6.
1981 Cavusgnathus altus Harris and Hollingsworth M element; Rexroad

Plate 1 figs 29-31.

Interpretive sketch 2.2.2 Cavusgnathus altus M element (sample CM 5).



Description:

Comparatively small M unit with a deep, chunky and rounded posterior process which is slightly angled downwards away from the cusp. The cusp is four to five times larger than the other denticles, and there is a weakly formed anticusp and a slit-like basal cavity. The cusp is slightly twisted relative to the posterior process, and may be curved.

Discussion:

The one recovered specimen is broken (Plate 1 fig 3) and specific identification is tentative. For a fuller description of this form see Rhodes et al. (1969 page 165) under N. varians.

Sample range: CM 5.
Distribution: Outer ramp.
Material: 1 specimen.

Sa element

(not recovered in this study, presumably due to the paucity of Cavusgnathus elements in general).

Synonymy:

p1900 Prioniodus angulatus Hinde Plate 10 fig 18 (only), page 343.
1958 Hibbardella ortha Rexroad Plate 2 figs 9-12, page 18.
1969 Hibbardella (Hibbardella) ortha Rexroad. Rhodes et al. Plate 25 figs 22a-b, page 113.
vic1976 Cavusgnathus spp., A_3 element; Norby Plate 3 figs 1a-f, page 99.
?1981 Hibbardella ortha Rexroad. Metcalfe Plate 14 figs 3a-c.
1981 Cavusgnathus altus Harris and Hollingsworth. Rexroad Plate 1 fig 9, page 7.

Sc element

Plate 1 fig 4.

Synonymy:

p?1900 Ctenognathus obliquus Pander. Hinde Plate 10 fig 28 (only), page 344.
1953 Hindeodella ensis Hass Plate 16 figs 19-21, page 81.
1960 Hindeodella tenuis Clarke Plate 1 figs 10-11, page 8.
1969 Hindeodella tenuis Clarke. Rhodes et al. Plate 28 fig 27, page 126.
vic1976 Cavusgnathus spp., A_1 element; Norby Plate 2 fig 3, page 98.
vic1981 Cavusgnathus spp., Sc alpha-beta elements Rexroad; Plate 1 figs 1-3.

Description:

Hindeodellan ramiform element with a long, straight posterior process, the upper edge of which is slightly convex in lateral view. The shorter anterior process is deflected slightly downward. In comparison with most of the other hindeodellan elements recovered in this study, the bars of both processes are distinctively broad and blade-like and appear less elongate and delicate. The denticulation is typically hindeodellan with two or three smaller denticles separating a series of larger denticles.

Discussion:

The nearly-complete specimen recovered in this study is damaged and the anterior process has been bent round towards the cusp. Parts of hindeodellan bars commonly make up a sizeable proportion of the "unidentifiable-fragments" component of the sample residues, and although present, the Sc component is always under-represented in the study because of the difficulties of specific

identification.

Sample range: GL 9.
Distribution: Middle mid-ramp.
Material: 1 specimen.

2.2c Genus: Clydagnathus Rhodes Austin and Druce 1969
Type species: Clydagnathus cavusformis Rhodes Austin and Druce 1969
Remarks:

Clydagnathus Pa elements have a short anterior blade; an ornamented elongate platform with a central trough and an asymmetrical basal cavity. Although similar to Cavusgnathus, the Pa elements can be discerned by the anterior closure or constriction of the medial trough, the merging of the marginal ornament with the blade and the lateral rather than longitudinal expansion of the cavity. Scaphignathus Pa elements differ in having a carina which runs for the entire length of the upper surface of the platform.

Clydagnathus gilwernensis Rhodes Austin and Druce 1969
Plate: 1 figs 5a-5c.

Pa element

Synonymy:

1969 Clydagnathus gilwernensis Rhodes et al. Plate 2 fig 1, page 87.
1969 Clydagnathus gilwernensis Rhodes et al. Druce Plate 4 figs 2a-4
Plate 30 fig 8, page 51.

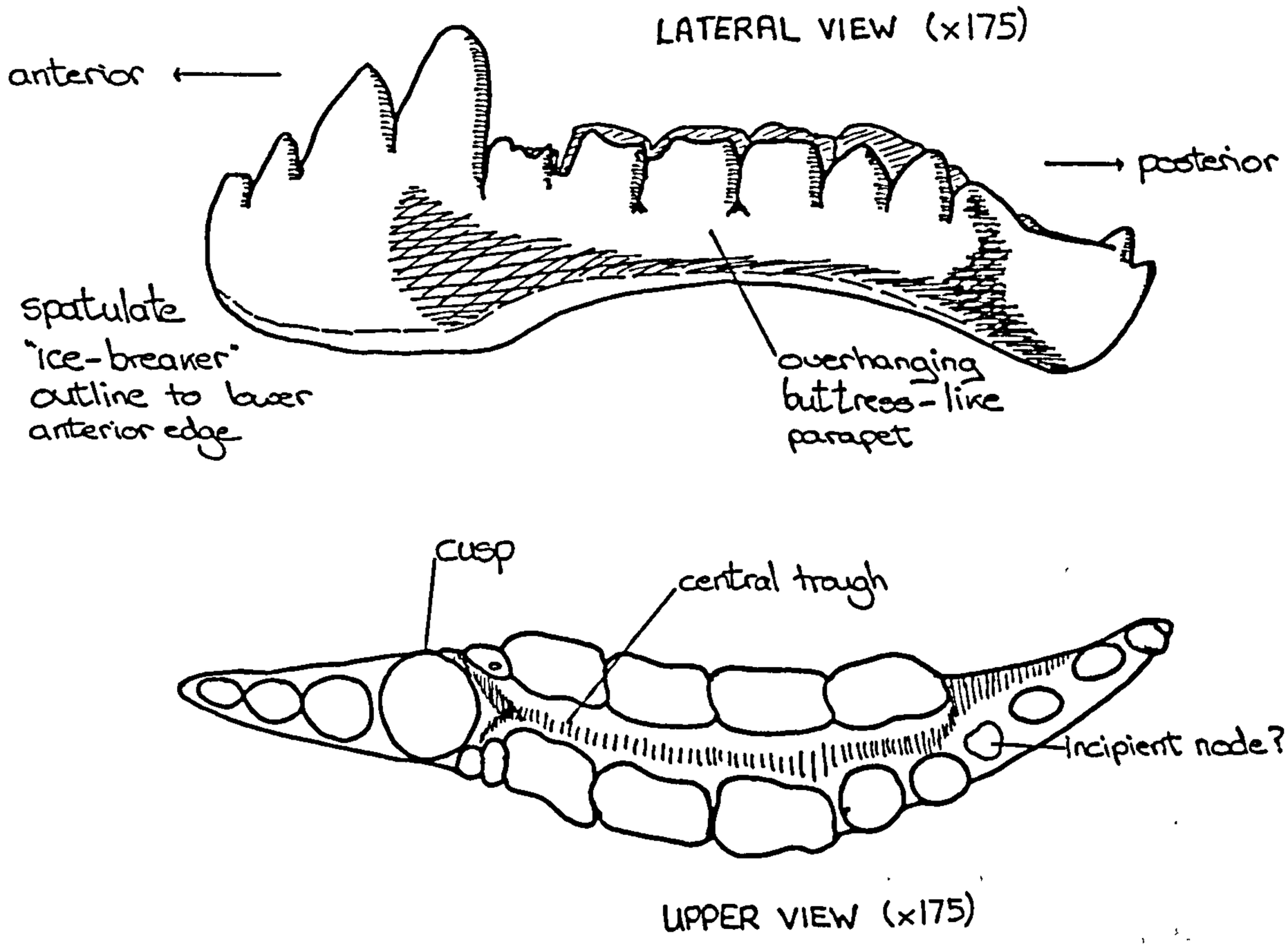
Description:

In upper view the Pa element is lanceolate and comprises a short anterior blade which is medially situated (in contrast to other Clydagnathus species), and a curved platform with a shallow central trough - which gives way to a weak carina of three separate nodes at the posterior. The platform margins are ornamented with robust, blocky nodes.

In lateral profile, the anterior blade bears four blunt or chevron-tipped denticles which decrease markedly in size toward the anterior. The lower and anterior margin meet to form a distinctively clydagnathid bluntly spatulate "ice breaker" outline (see interpretive sketch 2.2.3). The platform is arched about the cavity in mature specimens.

The basal cavity is elongate and asymmetrical and occurs in the anterior third of the platform. The lips are thickened and continue anteriorly and posteriorly from the cavity.

Interpretive sketch 2.2.3 Clydagnathus gilwernensis Pa element (sample LL 1).



Discussion:

The two specimens recovered are comparatively small; one is well preserved, and the other is extremely etched. The descriptive details above are based on the well preserved specimen, and agree closely with the original description (Rhodes et al. 1969). These authors note that an arched platform in lateral view (as above) is indicative of a mature specimen.

Sample range: LL 1
Distribution: Inner ramp.
Material: 2 specimens.

Non-platform elements:

Remarks:

No full apparatus reconstruction has been made for Clydagnathus, but it is likely to have had similar non-platform elements to those of the other cavusgnathoid genera (see Cavusgnathus above).

Corroborative evidence for this assumption comes from the apparatus of the conodont animal assigned to Clydagnathus ? c.f. cavusformis by Briggs et al. (1983). Unfortunately the elements were not preserved in a manner which

allowed a complete systematic description, but the ramiform elements illustrated (Briggs et al. 1983 figures 2B and 2C) appear similar to those of Cavusgnathus.

2.2d Genus: Gnathodus Pander 1856
Type species: Polygnathus bilineatus Roundy 1926
Synonymy: 1939 Dryphenotus Cooper.
1957 Westfalicus Schmidt. Moore and Sylvester-Bradley.

Remarks:

The paucity of complete ramiform elements has meant that, in common with the findings of Norby (1976), it has not been possible to discriminate between the non-platform elements of different Gnathodus species. This does not necessarily imply that no distinction exists. The non-platform elements of the apparatus are described just once, following the descriptions of the Pa elements.

The speciation of Gnathodus has been based entirely on studies of its Pa elements, and the criteria used include platform outline (in upper view), nature of parapets or ornamentation and degree of lateral expansion of the posterior tip of the carina (e.g. Lane et al. 1980). Problems arise because of the continuous nature of the variations in these parameters. Intermediate forms abound and the situation with regard to specific designation is confused and inexact. For example the specimen illustrated in Plate 3 figure 2 as an intermediate form within the G. texanus plexus has been variously identified as G. typicus, G. semiglaber, G. pseudosemiglaber, G. austini and G. texanus/ pseudosemiglaber by five contemporary Carboniferous-conodont workers. Efforts to clarify the situation fall into two categories: taxonomic "splitting" and taxonomic "lumping".

The subdivision and splitting of Gnathodus species through small variations in appearance has been attempted by many workers, often based on isolated studies of just a few Pa elements (Matthews and Naylor 1973, Metcalfe 1981). This approach will only be validated if the increase in number of species and subspecies results in the emergence of an overall phylogenetic pattern; whereby subtly differentiated Gnathodus species produce a closely defined biostratigraphical scheme, which is widely applicable. In reality, as more studies are made, continued splitting seems only to make the situation increasingly complex and untidy. It appears likely that there is no finely differentiated temporal series of linear variation in Gnathodus, and that many of the so-called species and subspecies are just phenotypical variations of little worldwide biostratigraphical significance. Further, the elucidation of phylogenetic lineages is hindered by nomenclatural clutter.

Taxonomic "lumping" allows for the inclusion of a range of characteristics

within a single definition. This approach has been employed by Lane et al. (1980) who recognise four groups of Gnathodus on the basis of parapet length and degree of expansion of the posterior tip of the carina. Three of these four groups are used in an attempt to divide the Gnathodus stock into separate lineages. Although the inclusion of several similar "species" within a single redefined species plexus is extremely useful for taxonomic purposes, the application of the Lane et al. (1980) phylogenetic scheme to actual Gnathodus populations (including that of this study) often produces unsatisfactory results. Minor variations in ornament result in co- occurring specimens being placed in entirely separate lineages, (see section 1.4b,iv).

Development of the posterior tip does not appear to be a genetically significant character. In specimens of the present study increased lateral development is often associated with increased ontogenetic development, and in otherwise indistinguishable forms a continuous succession of development can be seen. The criteria used to rationalise Gnathodus phylogeny can not be as simple and as rigidly applied as those of the Lane et al. (1980) system. Future work should involve an overall balanced appraisal of each Gnathodus group, and endeavour to apply biological considerations to their speciation.

In light of the situation reviewed above, the recognition of Gnathodus species in this study is based on Pa elements, and their taxonomy is simplified by informally dividing the genus into two: "Gnathodus sensu stricto" and "the homopunctatus group". The rationale behind this procedure is discussed in the introduction to section 1.4f.

Gnathodus sensu stricto includes forms with an asymmetrical platform (in upper view), which often takes up less than half the length of the unit (in mature forms). The narrower inner platform meets the blade further anteriorly than the broader outer platform. A parapet is usually strongly developed on the inner platform with a smaller parapet, nodes or no ornamentation on the outer platform. There is a characteristic lateral profile to the free blade with two or three taller and broader denticles near the anterior end.

The homopunctatus group includes forms with a simple sub-symmetrical platform which is often approximately half the length of the unit. The platform may either be unornamented or bears nodes or small denticles which may form ridges parallel to the platform margin (in upper view). There is no differential development of the posterior tip and in lateral view little or no arching of the lower margin of the cup. The carina is always approximately twice the height of the platform, and the free blade has a characteristic rectangular or weakly arched lateral profile, in which denticle height often decreases toward the anterior.

The material recovered in this study is not sufficient to formally split the homopunctatus group from Gnathodus, although other authors have alluded to it being a possibility following further work (Rhodes and Austin 1971, Higgins

1975, Norby 1976).

The Gnathodus species designations which follow are given an expanded definition (where necessary); and each includes a plexus of broadly similar types, many of which may have been designated as separate species by previous authors. The use of more closely defined and exact species designations is precluded by: the limited nature of the material recovered in this study, the confusion presently existing in the literature, and the continuous nature of the variations in Gnathodus Pa element morphology. This approach is favoured because it is thought to reflect more closely the original biological situation, and to aid in future clarification of the present confusion. Use of this method of classification is not viewed as "an abdication of taxonomic responsibility" (Matthews 1973), but as a valuable adjunct to the use of open nomenclature (Richter 1948, Matthews 1973, Bengtson 1988).

Gnathodus sensu stricto

Gnathodus cuneiformis Mehl and Thomas 1947

Pa element

Plate: 2 figs 1-2.

Synonymy:

1947 Gnathodus cuneiformis n. sp. Mehl and Thomas Plate 1 fig 2, page 10.

non1969 Gnathodus cuneiformis Mehl and Thomas. Rhodes et al. Plate 8 figs 6a-c.

p1973 Gnathodus delicatus Branson and Mehl. Matthews and Naylor Plate 35 figs 17, 25-26 only.

p1973 Gnathodus delicatus Branson and Mehl. Butler Plate 56 figs 7-9.

1974 Gnathodus cuneiformis Branson and Mehl. Austin and Husri Plate 4 fig 3.

1980 Gnathodus cuneiformis Mehl and Thomas. Lane et al. Plate 4 figs 6-8 and Plate 10 fig 7, page 130 (this includes a full synonymy and a re-illustration of the holotype, see 1947).

.1981 Gnathodus antetexanus Rexroad and Scott. Metcalfe Plate 3 fig 1.

.1984 Gnathodus typicus Cooper. Austin and Davies Plate 2 fig 14.

p?1984 Gnathodus texanus pseudosemiglaber Thompson and Fellows. Austin and Davies Plate 2 figs 12-13.

1985 Gnathodus cuneiformis Mehl and Thomas. Belka Plate 3 figs 4-5 (Fig 4 is termed "juvenile specimen"and is very similar to those designated as juvenile in this study).

1985 Gnathodus cuneiformis Mehl and Thomas. Varker and Sevastopulo Plate 5.1 figs 21, 25, page 192.

1986 Gnathodus cuneiformis Mehl and Thomas. Belka and Groessens Plate 4 figs 13-16.

.1986 Gnathodus cuneiformis Mehl and Thomas -> Gnathodus

pseudosemiglaber Thompson and Fellows. Belka and Groessens Plate 5 figs 4-9.

.1987 Gnathodus typicus Cooper. Austin Plates 13.1, 13.2 and 13.3.

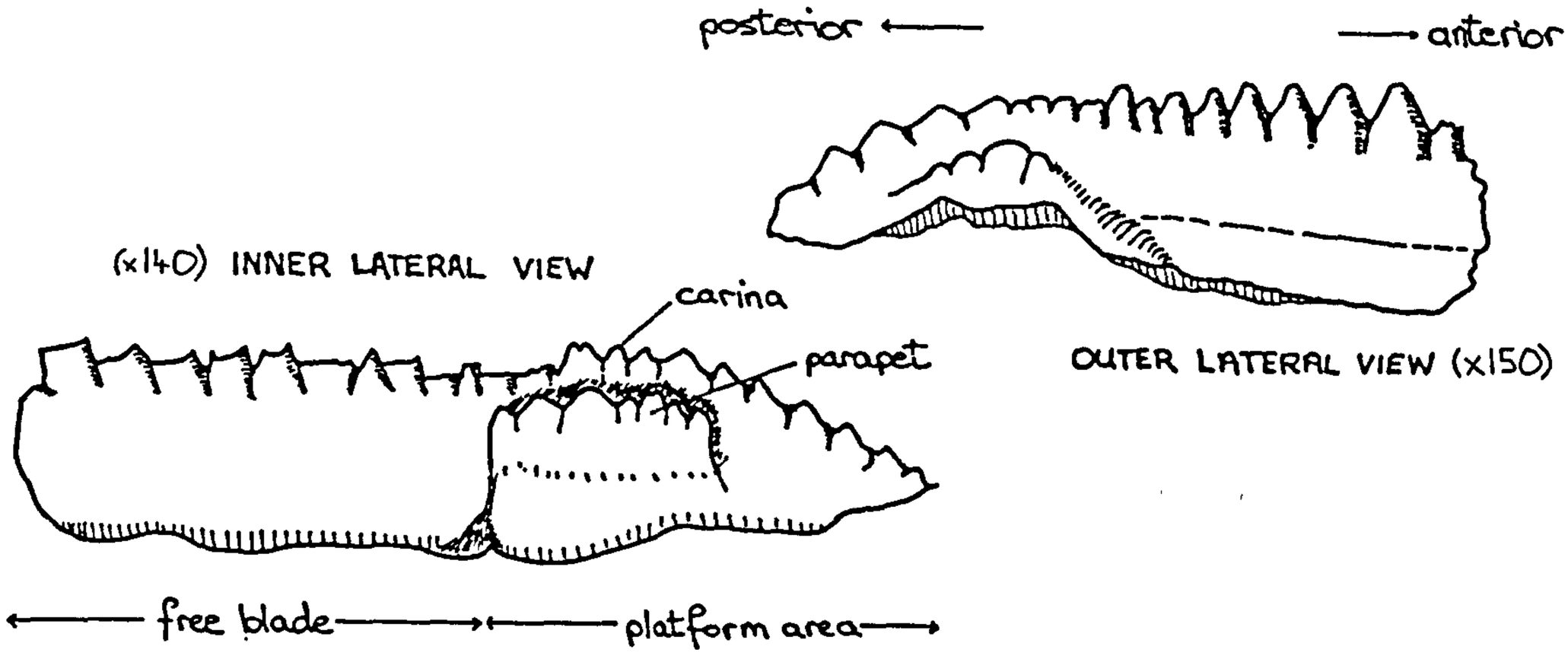
Description:

The mature specimens recovered in this study have an asymmetrical platform with a markedly flared outer side, and narrower inner side. The basal margin of both inner and outer platforms is marked by a lateral flaring to produce "basal skirts", these are best developed on the outer platform. The inner platform starts anterior to the outer platform, and the "skirts" on both sides extend to the posterior tip of the unit.

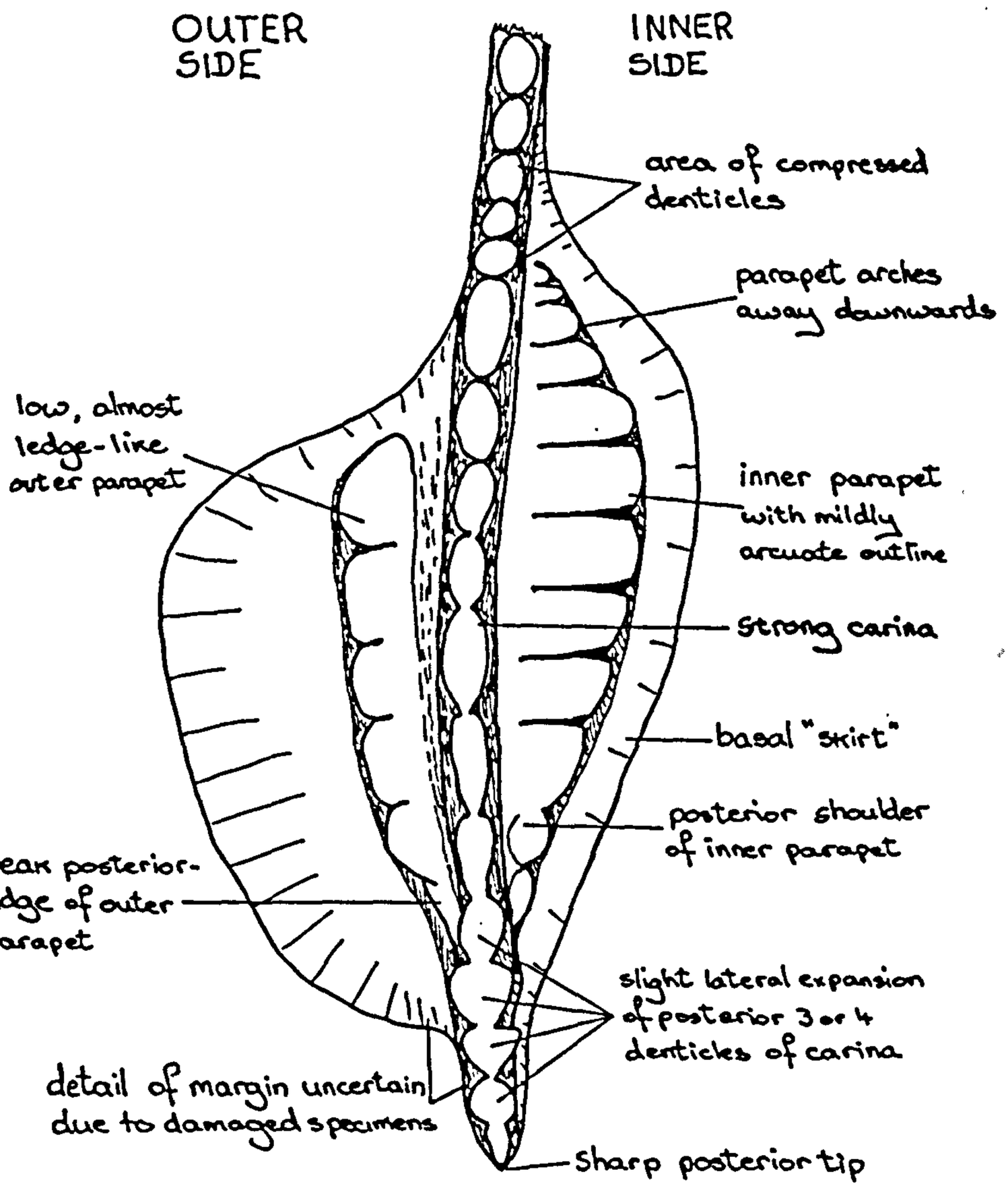
Parapets are developed on both sides of the platform. The inner parapet is strongly formed and consists of 6 to 9 fused denticles and a posterior shoulder (see interpretive sketch 2.2.5). The anterior denticles may be so developed as to form lateral ridges. The parapet drops vertically away to the side, and runs parallel to the carina decreasing in size uniformly toward the posterior, until it dies out just anterior of the posterior tip. In upper view the outer margin of the parapet is mildly arcuate. The inner parapet is almost as tall as the carina, from which it is separated by a well-formed adcarinal trough.

The outer parapet is lower and shorter, and consists of five-or-so fused nodes and a weak posterior ridge running subparallel to the carina. The outer parapet is angled-in toward the carina as it runs to the posterior, and eventually terminates as a weak ridge which runs into the carina approximately half way between its upper and lower margins. The carina is very slightly laterally expanded for the posterior 3 fused nodes, but the posterior tip itself reverts to being quite thin. In the anterior part of the carina, the denticles are rather crowded (see interpretive sketch 2.2.5), and may be fused to an extent where it is difficult to discern individual denticles. In mature specimens the free blade is at least 1.5 times the length of the platform, and in upper view is laterally compressed, and in lateral view appears comparatively tall.

Interpretive sketch 2.2.4 Gnathodus cuneiformis Pa element, lateral-views (samples CM B4 and CM 2).



Interpretive sketch 2.2.5 Gnathodus cuneiformis Pa element, upper view sample CM 2).



Discussion:

Specimens intermediate in size and development between the mature form illustrated in Plate 2 figure 1 and the juvenile form in Plate 2 figure 2 are found throughout the range of this species, and suggest a series of ontogenetic stages. The inner platform is first to develop with its relatively strong parapet (which often appears darker in immature specimens). Later the outer platform expands laterally and eventually the outer parapet develops. The carina gets taller and more defined, and in fully mature specimens the penultimate three denticles of the posterior tip begin to expand laterally. Throughout this development the unit increases in size, darkens and takes on a more robust and less rounded appearance.

Lane et al. (1980) expanded the definition of G. cuneiformis to include a series of three morphotypes, and the specimens of this study agree closely with their illustrations of morphotype 3 (the youngest of the three). The Lane et al. (1980) definition of G. cuneiformis includes a plexus of similar types, some specimens of which were previously assigned to G. typicus, G. antetexanus, G. delicatus and G. girtyi.

Sample range: CM B1 to CM 9, SQ 1, LS 2.
Distribution: outer ramp and distal mid-ramp.
Material: 37 specimens (7 mature, 30 immature).

Gnathodus aff. girtyi Hass 1953
Pa element

Plate: 2 figs 3-6.
Synonymy:

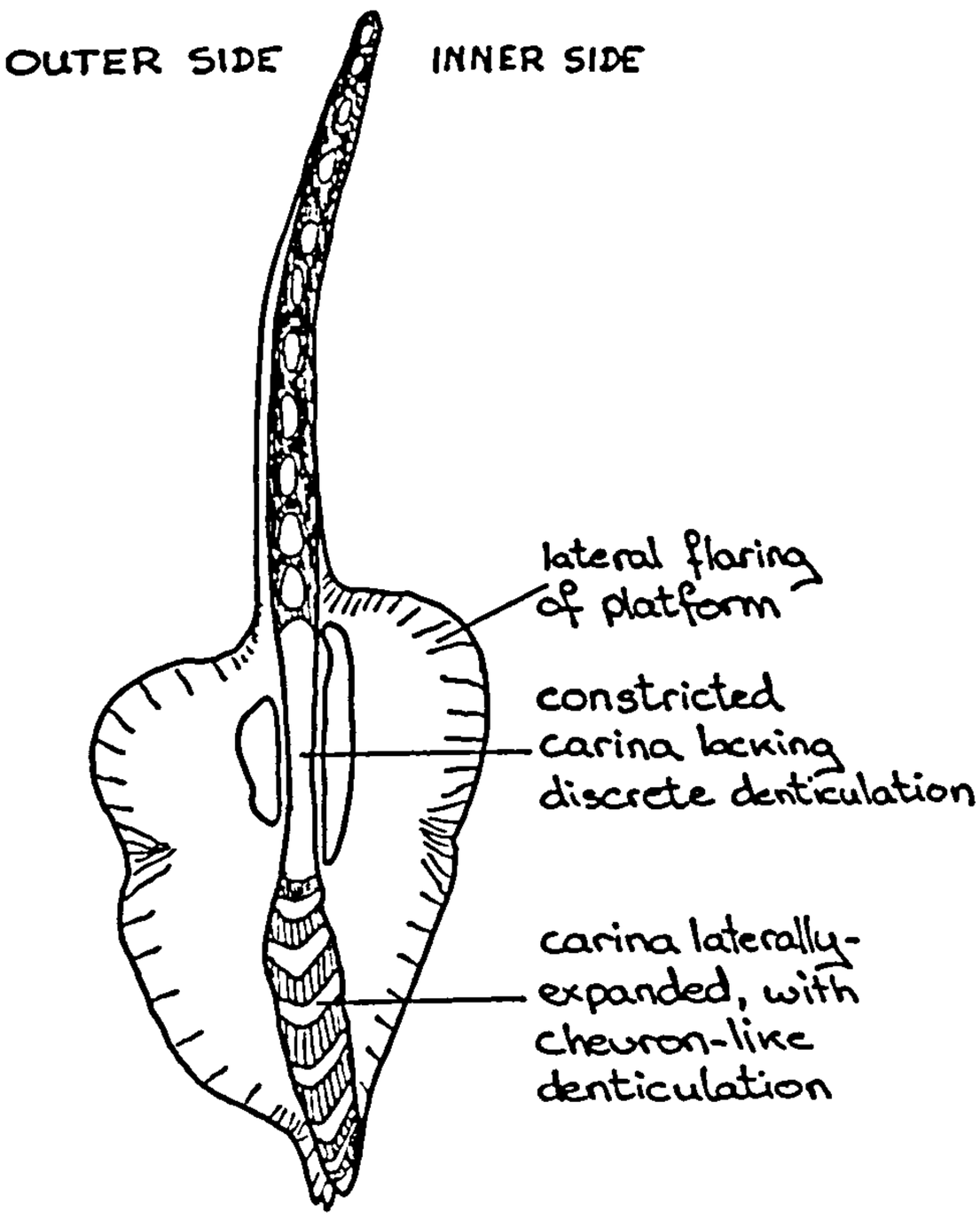
.?1969 Gnathodus cuneiformis Mehl and Thomas. Rhodes et al. Plate 8 figs 6a-c.

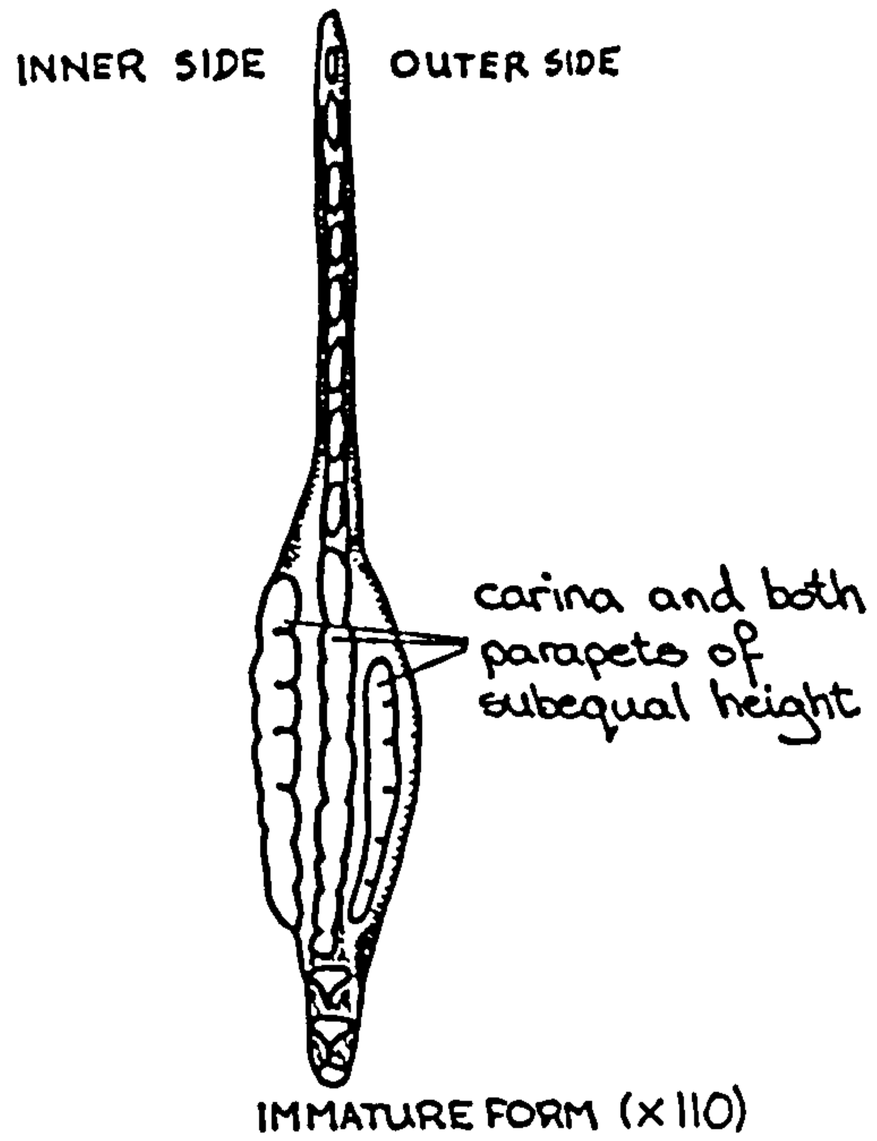
p?1981 Gnathodus girtyi Hass. Metcalfe Plate 4 figs 2-3.

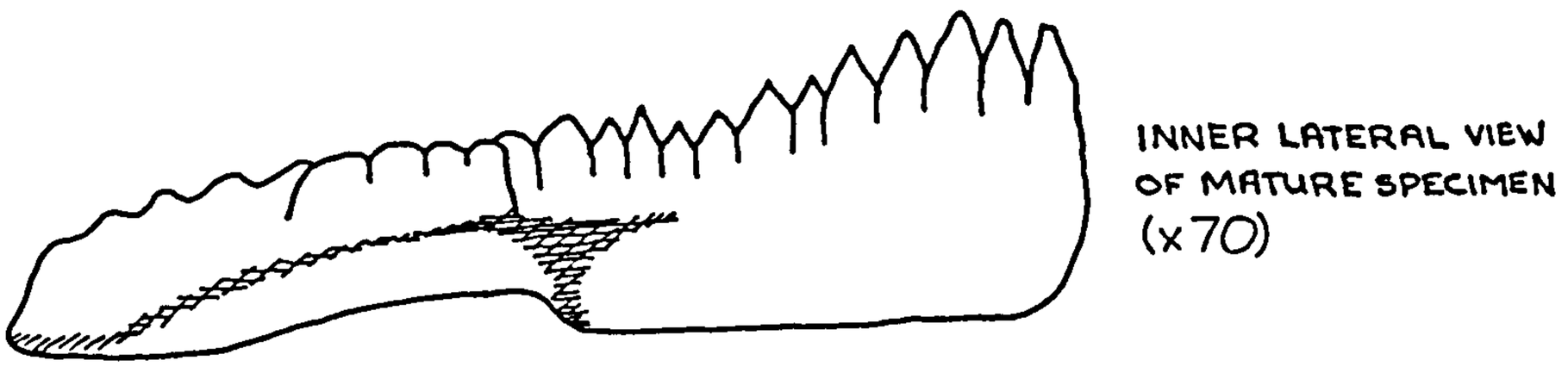
Description:

Mature specimens have a broad, steep sided, asymmetrical platform which flares laterally on both sides. The outer margins of the platform are typically lighter coloured and less robust than the central portion. The inner platform is slightly narrower, and starts and finishes anterior of the outer platform - which continues to or beyond the posterior tip of the carina. In upper view the parapet area is comparatively restricted. Both parapets and the carina are of similar height. The inner parapet is slightly longer than the outer parapet and starts further anteriorly. The parapets run subparallel to the carina, and either run back weakly into the carina or remain separated from it for their entire length by weakly formed adcarinal grooves.

Interpretive sketch 2.2.6 Gnathodus aff. girtyi Pa elements (sample CM 22).







The inner parapet may be slightly more strongly developed and taller than the outer (and the carina), and may have weakly developed lateral ridges at its anterior end. In general the parapets are rather smooth and undifferentiated (particularly in upper view), and extend for between one third and three quarters of the length of the platform. Between the parapets the carina is constricted and is often reduced to a weak ridge. Posterior to the termination of the parapets the carina is laterally expanded and may exhibit chevron-like denticulation.

Specimens intermediate in size and development between the mature and immature forms illustrated in interpretive sketch 2.2.6 and Plate 2 figs 3-5 are

found throughout the range of this species. Immature specimens are smaller and often have relatively long parapets (see interpretive sketch 2.2.6). In upper view the lateral flaring of the platform may be completely absent and there is only very minor lateral expansion of the posterior tip of the carina. Ontogenetic development involves lateral flaring of the platform (simultaneously on both sides), and relative lengthening and further lateral development of the posterior tip. The parapets become smoother and undergo very little further elongation.

Discussion:

Most of the specimens recovered, although distinctive, do not readily fit into any established Gnathodus species. However within the population there is a continual gradation to forms (particularly in the upper Arundian) which could be included within a broad definition of G. girtyi: these forms have long, low parapets of subequal height developed on both sides of the platform, extending back toward the posterior tip and fusing with the carina to produce marked lateral flaring (Rhodes et al. 1969 page 99). Although in most cases the parapets do not continue far enough posteriorly to fit the specific designation unequivocally, the nature of the expanded platform and relative development of parapets and carina coupled with lateral flaring of the posterior tip all suggest a girtyi affinity. This is an early occurrence for G. girtyi, which is documented by Varker and Sevastopulo (1985) as originating early in the Asbian Stage.

To account for the slight degree of ambiguity, the open nomenclatural symbol aff. is inserted before the species name as suggested by Bengtson (1988) to imply: the specimens are considered to be a new, previously undescribed species or subspecies, but the material is insufficient for the formal naming of a new taxon. The specimens can be most closely related to the species indicated. Gnathodus girtyi has been subspeciated by numerous authors (e.g. Dunn 1965, Globensky 1967, Rhodes et al. 1969, Higgins 1975), and is therefore already viewed as a plexus of similar types. Metcalfe (1981) noted that the range of the various girtyi subspecies appears to be anomalous from area to area, and that the species should not be classified at subspecific level before detailed biometrical work establishes satisfactory criteria for subdivision. These sentiments are echoed by Higgins (1985) who writes of a "Gnathodus girtyi complex", and implies a need for further detailed work prior to any alterations or additions to the group. Dean (1987) points out that because the different types of girtyi were not geographically isolated populations, the term "morphotype" should more correctly be used in place of "subspecies" to describe the variations within the group.

The distinctive features of the specimens recovered include a high, turret-like platform which is typical of many forms of G. girtyi, such as globenskyi and turritus. Also there are simple sub-equal parapets which are at least of equal height to, and more strongly developed than, the carina; and lateral expansion

of the posterior tip. All these characteristics are shared by some of the Namurian Idiognathidontidae (e.g. Declinognathodus and some species of Neognathodus). The similarity in the above characteristics between G. aff. girtyi of this study and D. noduliferous might imply a lineage from G. aff. girtyi in late Arundian times, through G. girtyi and D. noduliferous to Neognathodus in the early Chokierian (as suggested by Merrill 1972). More recently however, Grayson et al. (1988) have compared Pb elements of the various groups and place Neognathodus in a clade with G. girtyi, but remove Declinognathodus and Idiognathoides to a separate clade with G. bilineatus as an ancestor. In the future, clarification may be achieved through multielement studies of continuous lineages, and may result in the division of a G. girtyi lineage into separate Declinognathodus and Neognathodus stems.

Sample range: CM 22 - CM 43, SQ 3-4, LS 12, PE 1.
Distribution: Outer and distal mid-ramp.
Material: 91 specimens (38 mature, 43 immature)

Gnathodus texanus Roundy 1926

Pa element

Plate: 3 figs 1-5.
Synonymy:

1926 Gnathodus texanus Roundy. In: Roundy, Girty and Goldman Plate 2 figs 7-8, page 12.

1965 Gnathodus texanus Roundy. Rexroad and Collinson Plate 1 figs 33 to 38, pages 8-9.

.p1970 Gnathodus texanus pseudosemiglaber ssp. nov. Thompson and Fellows Plate 2 figs 6, 8-9, 11-13, page 88.

1980 Gnathodus texanus Roundy. Lane et al. Plate 6 figs 8-9, 11-12, 16, page 133, (with extended synonymy).

.1980 Gnathodus pseudosemiglaber Thompson and Fellows. Lane et al. Plate 4 figs 15-17, 19; Plate 5 figs 8-15; Plate 6 fig 14. (with extended synonymy).

.1981 Gnathodus texanus pseudosemiglaber Thompson and Fellows. Metcalfe Plate 6 figs 1-3.

1981 Gnathodus texanus texanus Roundy. Metcalfe Plate 6 figs 5-7.

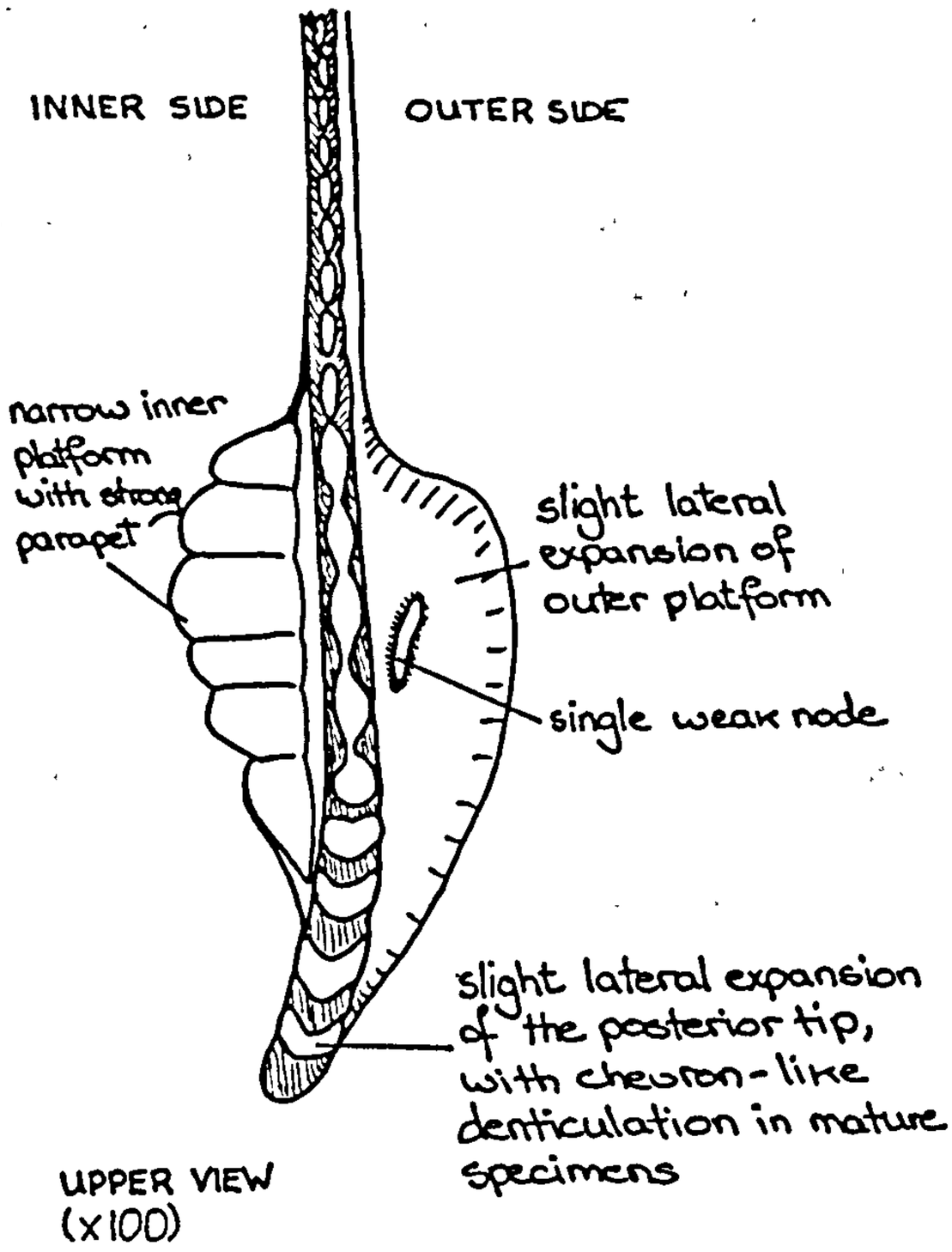
.p1984 Gnathodus texanus pseudosemiglaber Thompson and Fellows. Austin and Davies Plate 3 figs 15-16.

1984 Gnathodus texanus texanus Roundy. Austin and Davies Plate 3 fig 14.

.1985 Gnathodus austini n. sp. Belka Plate 4 figs 2-3, 7-8, 10-11, page 38.

.1985 Gnathodus pseudosemiglaber Thompson and Fellows. Varker and Sevastopulo Plate 5.3 figs 15, 18, page 196.

Interpretive sketch 2.2.7 Gnathodus texanus Pa element (sample CM 7).



Diagnosis:

Comparatively elongate and narrow, asymmetrical platform with strong, often buttress-like inner parapet which is higher than the carina; and a slightly expanded outer platform on which ornamentation is much-reduced or absent. There may be slight lateral expansion of the posterior tip.

Description:

The inner platform is extremely narrow and often consists only of a strong buttress-like parapet which may parallel the carina or may be slightly arcuate (concave inward), there may be a more weakly formed posterior "tail" to the parapet. The inner platform terminates before the posterior tip, and at its anterior end the inner parapet is higher than the carina. The outer platform is only slightly laterally expanded and bears: a short but strong pillar adjoined to the carina, a much reduced single elongate node, a weakly formed shoulder sub-parallel to the carina or no ornamentation. The outer platform may reach to

the posterior tip or terminate just anterior to it. The posterior tip of the carina usually exhibits some manifestation of lateral expansion, at the posterior termination of the inner parapet, but this is not usually particularly marked in the present specimens.

Discussion:

Specimens conforming to the above description have been assigned to at least three different species: G. texanus, G. pseudosemiglaber and G. austini (and all their transitional forms). On the evidence of the present study there is little justification for separation of the species and the specimens are grouped as part of a G. texanus plexus. This is because: a series of continuous variation exists between the three "marker" species named above, they share the same sample range and there is little agreement in the literature on how to distinguish these forms.

Thompson and Fellows (1970) defined G. texanus pseudosemiglaber as a subspecies of G. texanus, transitional between G. bulbosus and G. texanus texanus. They differentiated between the two by assigning to G. pseudosemiglaber forms with ornamentation on both platforms and a laterally expanded posterior tip which extends posteriorly beyond the end of the platform. Later, Thompson (1979) proposed separate phylogenies for the two forms and promoted them to full species status. Lane et al. (1980) placed these forms in a G. punctatus group, and redefined G. texanus to include forms with a single high node on the outer cup and a degree of lateral expansion of the posterior tip. They also altered the definition of G. pseudosemiglaber such that the posterior tip does not extend posteriorly beyond the platform. Lane et al. (1980) noted transitional forms between: G. semiglaber and G. pseudosemiglaber; G. texanus and G. pseudosemiglaber; and G. texanus and G. semiglaber.

Belka (1985) erected G. austini as a species transitional between G. texanus and G. girtyi, although he did not define his concepts of the latter two. Belka's G. austini is here considered as a morphotype of G. texanus and there is no ambiguity in distinguishing between G. texanus and G. aff. girtyi of this study. Forms with a markedly asymmetrical platform (in upper view) bearing a strong inner parapet separated from the carina by a distinct adcarinal groove, and a weakly developed outer parapet which is lower than the carina - are assigned to G. texanus. Forms with an expanded platform bearing sub-equal rounded parapets without strongly developed adcarinal grooves, are assigned to G. aff. girtyi.

It is evident that G. texanus is at the centre of a plexus of similar forms, and that there is lack of agreement amongst conodont workers on how to differentiate between elements of this group; some favour the original Thompson and Fellows (1970) concept, some follow Lane et al. (1980) and

others combine elements of both. Future clarification of the situation would benefit from a monographic multielement study, involving reassesment of many of the original types, and as many stratigraphically confined and correlated lineages as possible.

Sample range: CM 6 to CM 21, SQ 1 to SQ 2, LS 3.
Distribution: outer ramp and distal mid-ramp.
Material: 87 specimens

The homopunctatus group

Gnathodus homopunctatus Ziegler 1960

Pa element

Plate: 3 figs 6-9.

Synonymy:

1957 Gnathodus commutatus punctatus Bischoff Plate 4 figs 7-11, 14, page 24.

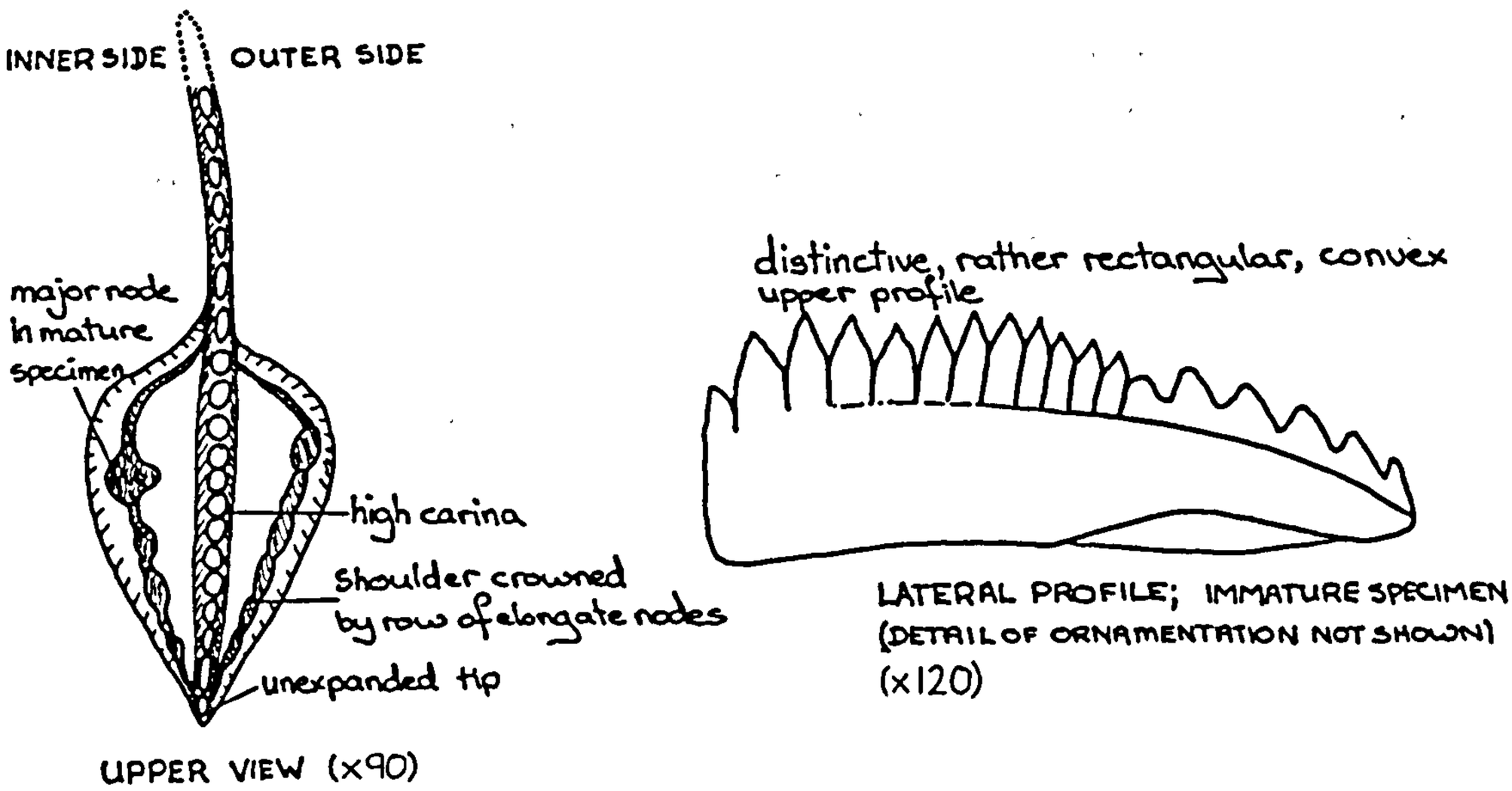
non1957 Gnathodus commutatus punctatus Bischoff. Ziegler In: Flügel and Ziegler Plate 3 figs 16-17, 24, page 40.

1959 Gnathodus commutatus homopunctatus [Ziegler]. Voges page 281.

1960 Gnathodus commutatus homopunctatus Ziegler Plate 4 fig 3, page 39 (nom. nov. for G. commutatus punctatus Bischoff 1957, non Cooper 1939).

1969 Gnathodus homopunctatus Ziegler. Rhodes et al. Plate 19 figs 5-8.

Interpretive sketch 2.2.8 Gnathodus homopunctatus Pa element (sample CM 2).



Description:

In upper view, mature specimens have a sub-symmetrical, lachrymiform platform with the sharp end to the posterior. The platform is always at least as long as it is wide. There is a high central carina, approximately twice the height of the platform, consisting of 10-12 denticles. The posterior tip of the carina is unexpanded. The upper surface of the platform dips gently away from the carina on both sides, and then drops away steeply to form shoulders approximately half way between the carina and the platform margin (in upper view). On both sides of the platform an irregular row of elongate nodes forms darker ridges which crown the shoulders of the platform and run subparallel to the platform margin. There is often a more strongly developed, major node toward the anterior of one of the rows of nodes.

Discussion:

Immature Pa elements of the homopunctatus group are very similar (see introduction to section 1.4f, and remarks at the beginning of this section), and the distinction between G. homopunctatus, G. mermaidus, and G. symmutatus can only be made in mature forms. However, in sample CM 2 a series of specimens which shows a progressive increase in size, robustness and development of ornamentation appears to illustrate an ontogenetic progression in G. homopunctatus (see Plate 3 figs 7-9). In immature specimens the platform is comparatively smooth and lanceolate in upper view. The major node develops first and is followed by part of the opposing ridge, slightly posterior of the major node. The early development shows up as darker, slightly elevated areas. Eventually ridges develop all the way around the platform, and the anterior margin of the platform becomes expanded such that the platform outline in upper view is more lachrymiform than lanceolate. The shoulders of the platform become more pronounced and the free blade elongates to be of equal length to the platform.

Although their stratigraphic ranges are similar, the results of this study suggest that G. homopunctatus may have lived in a deeper water or more offshore environment than G. symmutatus. Metcalfe (1981) does not discriminate between G. homopunctatus, G. symmutatus, G. mermaidus and G. lineatus Austin and Husri 1974; and classifies them all under G. homopunctatus, as he believes these to be variations within a single species. While it appears reasonable to synonymise G. lineatus with G. homopunctatus, further work is required before this proposal can be fully substantiated or refuted.

Sample range: CM 2 to CM 43.
Distribution: outer ramp.
Material: 31 specimens

Gnathodus mermaidus Austin and Husri 1974

Pa element

Plate: 4 figs 1-2.

Synonymy:

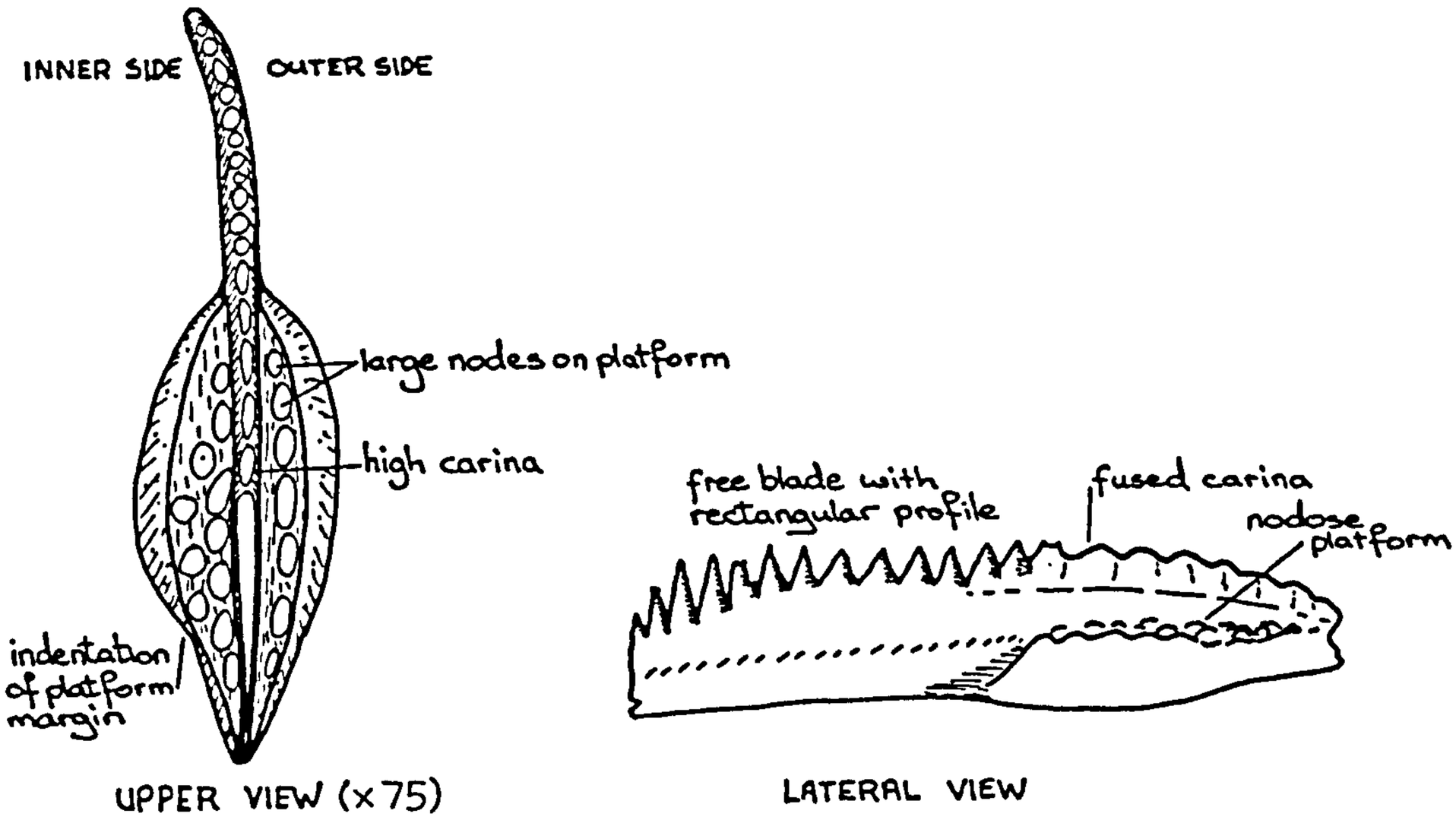
1974 Gnathodus symmutatus mermaidus Austin and Husri Plate 3 fig 11 (N.B. due to a printing error, Plate 3 is actually the second Plate of this paper), page 54.

1985 Gnathodus mermaidus Austin and Husri. Belka Plate 7 fig 9.

Description:

In upper view mature specimens have an elongate oval platform in which both sides start and terminate opposite each other. There is commonly a slight indentation in the platform margin toward the posterior on one side (see interpretive sketch 2.2.9). The platform cross-section is similar to that of G. homopunctatus, although the gently-dipping upper platform area is narrower. The upper platform is covered in strongly formed nodes, some of which may exhibit a crude alignment parallel with the carina. The carina is approximately twice as high as the platform. There is a characteristic homopunctatus-group lateral profile to the specimens (see interpretive sketch 2.2.9) and the free blade is roughly of equal length to the platform.

Interpretive sketch 2.2.9 Gnathodus mermaidus Pa element (sample CM 42)



Discussion:

Although the platform cross-section is similar to that of G. homopunctatus, the platform outline in upper view is more similar to that of G. symmutatus, and G. mermaidus appears to represent a morphological half-way stage between the two.

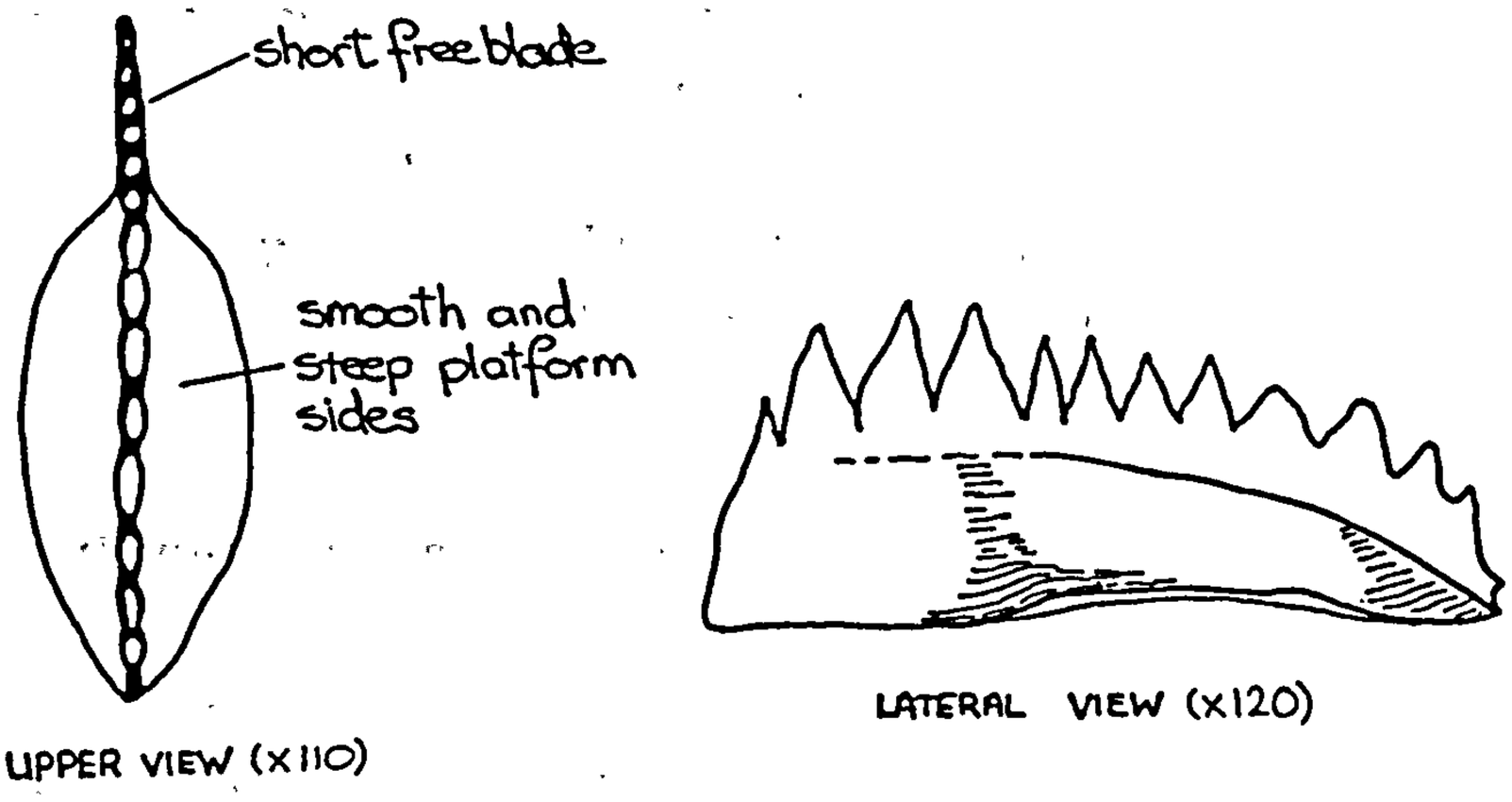
Sample range: CM 24 to CM 43,
Distribution: outer ramp.
Material: 15 specimens

Gnathodus symmutatus Rhodes Austin and Druce 1969
Pa element

Plate: 4 figs 3-5.
Synonymy:

1969 Gnathodus symmutatus Rhodes et al. Plate 19 figs 1a-4c, page 108.
1974 Gnathodus symmutatus symmutatus Rhodes et al. Austin and Husri Plate 3 fig 10 Plate 4 figs 6-7.
1975 Gnathodus symmutatus Rhodes et al. Higgins Plate 10 figs 8-9, page 34.
p1987 Gnathodus symmutatus Rhodes et al. Austin Plate 13.2 figs 1, 16-17 only, Plate 13.3 fig 17.

Interpretive sketch 2.2.10 Gnathodus symmutatus Pa element (sample CM 2).

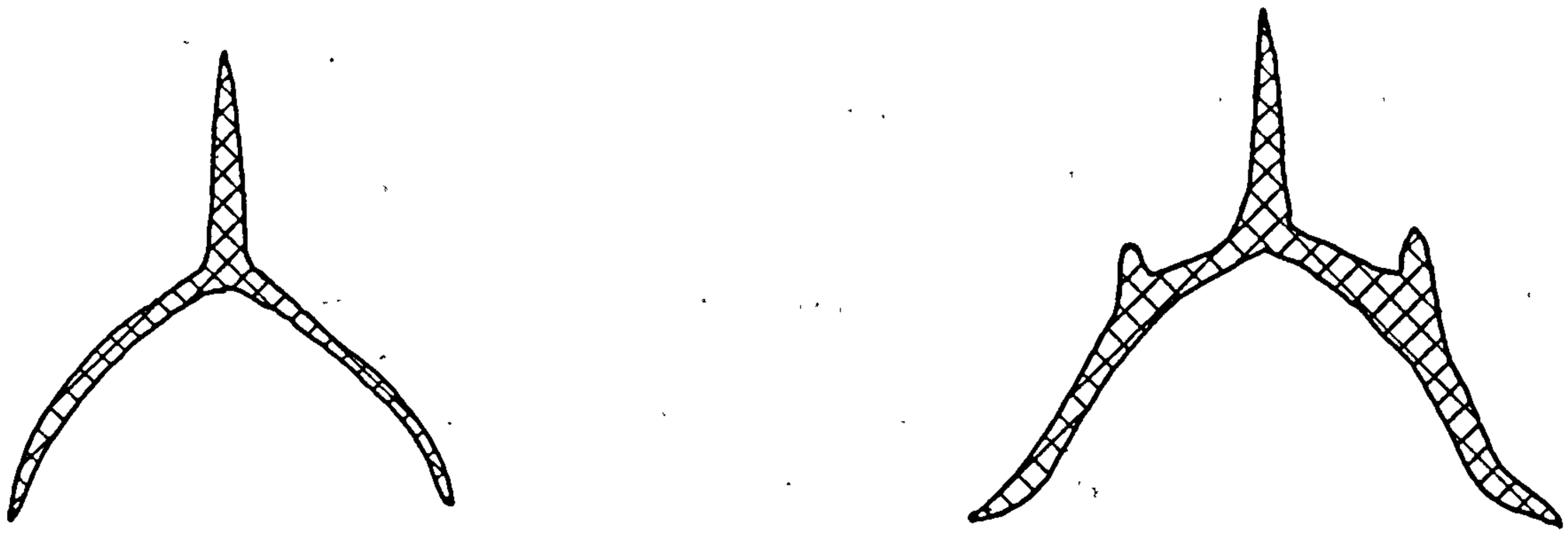


Description:

Mature forms have a sub-symmetrical, lanceolate to oval, elongate platform which is unornamented, biconvex in cross-section and often steep sided. There is a short free blade, shorter than or of equal length to the platform. In upper view the free blade and carina are not laterally expanded. The lateral profile is typical of the homopunctatus group. It is common for the

G. symmutatus elements in this study to be of a delicate and thin appearance, and they are often recovered in a flattened and mis-shapen state.

Mature Pa elements of G. symmutatus and G. homopunctatus have distinctively different cross-sections (see diagram below):



G. symmutatus

G. homopunctatus

Discussion:

Austin (1987) worked on the Chadian/Arundian boundary of the Castle Martin succession, and suggested that the first occurrence of G. symmutatus may be used to indicate Arundian strata. Further studies will show whether this is a universally applicable indicator. Some of the specimens referred to G. symmutatus by Austin (1987) may be immature examples of G. homopunctatus, as no allowance is made for ontogeny (e.g. Austin 1987, Plate 13.2 figs 18-19).

Sample range: CM 2 to CM 34, LS 7, GL 14, T 5.
Distribution: outer ramp to proximal mid-ramp.
Material: 34 specimens

Gnathodus Non-platform elements:

Remarks:

As explained above the non-platform elements for Gnathodus are discussed collectively, based on the findings of Norby (1976), who studied bedding-plane apparatus assemblages of G. bilineatus. It should however be borne in mind that future multielement studies may result in differences being established between the non-platform elements of Gnathodus sensu stricto and the homopunctatus group (of this study), or even between different species of Gnathodus sensu stricto. Gnathodus non-platform elements are illustrated in Plate 4 figs 6-12.

Pb element

Synonymy:

1926 Ctenognathus sp. B Roundy Plate 2 figs 4-5, page 16.

1941 Ozarkodina delicatula (Stauffer and Plummer). Ellison Plate 20 figs 40-42, 47, page 120.

?1952 Scottella typica Rhodes Ozarkodina component; Rhodes Plate 126 figs 2-3, 8-11, page 892.

1953 Subryantodus roundyi Hass Plate 14 figs 3-6, page 40.

1957 Ozarkodina roundyi (Hass). Rexroad Plate 2 fig 7, page 37.

1961 Ozarkodina delicatula Ellison (sic). Higgins Plate 12 fig 13, page 220.

1961 Ozarkodina delicatula (Stauffer and Plummer). Rexroad and Burton Plate 141 fig 12, page 1156.

1965 Ozarkodina roundyi (Hass). Dunn Plate 140 figs 19-20, page 1149.

1967 Ozarkodina delicatula (Stauffer and Plummer). Globensky Plate 56 fig 19, page 446.

1969 Ozarkodina delicatula (Stauffer and Plummer). Rhodes et al. Plate 27 figs 15, 19, page 170.

1969 Ozarkodina cf. delicatula (Stauffer and Plummer). Rhodes et al. Plate 27 fig 14, page 177.

1974 Ozarkodina delicatula (Stauffer and Plummer). Austin and Husri Plate 12 fig 5.

1975 Ozarkodina delicatula (Stauffer and Plummer). Higgins Plate 5 figs 9, 11, 16, Plate 6 figs 15-16 (specimen fused with Pa element of Idiognathoides sulcatus parvus), page 69.

1975 Ozarkodina cf. delicatula (Stauffer and Plummer). Higgins Plate 5 fig 2, page 69.

vic1976 Gnathodus bilineatus (Roundy) O element; Norby Plate 6 figs 6a-8c, page 110.

1981 Ozarkodina delicatula (Stauffer and Plummer). Metcalfe Plate 19 figs 3-4.

1984 Ozarkodina delicatula (Stauffer and Plummer). Austin and Davies Plate 3 fig 24.

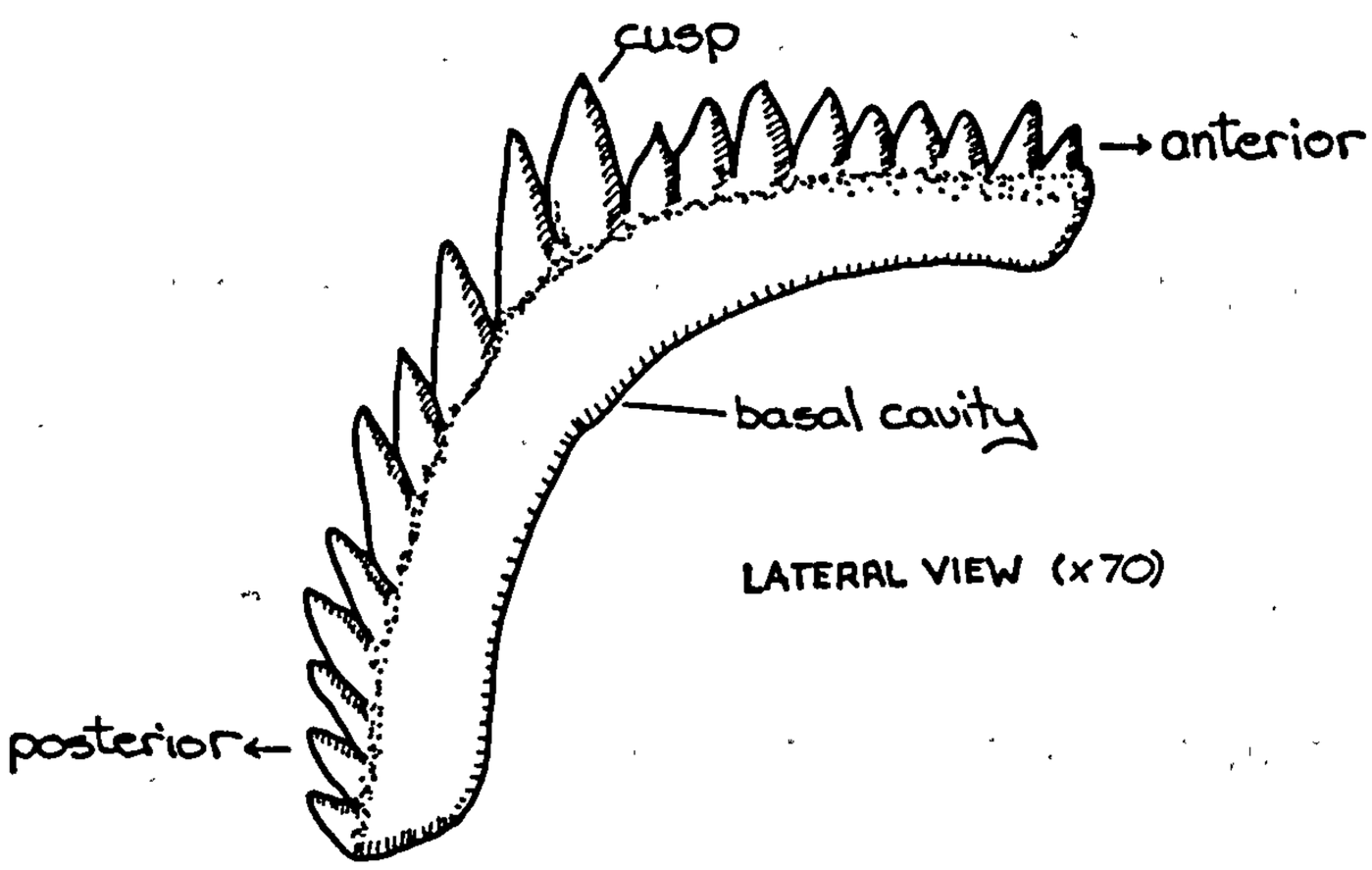
1987 Ozarkodina sp. cf. O. delicatula (Stauffer and Plummer). Austin Plate 13.4 fig 20.

Description:

Elongate, angulate blade-like element with little or no lateral flexure. The anterior and posterior denticulate bars meet to form an arch. The posterior bar is one and a half to two times longer than the anterior bar (cf. description of Subryantodus roundyi by Hass 1953). There is a degree of variation in the curvature of the posterior bar, particularly towards its distal end, which in some

specimens is slightly flexed inwards. The anterior bar is uniformly straight in upper view. The cusp lies above the small, elongate basal cavity, where the two bars meet. The cusp is slightly longer than the bar denticles and may be twice as wide. The anterior bar bears nine to twelve denticles of subequal size, which are fused for about two thirds of their length. These denticles are normal to the bar and in alignment with the cusp in lateral view. The denticles of the posterior bar are of the same general form but may be slightly larger, and subtend an angle of approximately 60° to 70° with the bar such that these denticles are also aligned with the cusp in lateral view.

Interpretive sketch 2.2.11 Gnathodus Pb element (sample CM 2).



Discussion:

Comparatively few complete specimens have been recovered as the element seems to snap in half quite easily. The broken bars are difficult to identify to species level and may even be mistaken for other types of element. Dean (1987) notes that there is a greater degree of variation within the Gnathodus Pb element than with the other non-platform elements, and this is borne-out by the findings of the present study. Norby (1976) lists several characteristics which may be used to discern the Gnathodus Pb element, among which are: a distinct apical denticle, elongate bar denticles, a distinct oval-shaped basal cavity with distinct lips and the relatively equal length of the anterior and posterior bars.

Sample range: CM 2 to CM 35, SQ 1 to SQ 4.
Distribution: outer ramp.
Material: 22 specimens.

M element

Synonymy:

1933 Synprioniodina sp. Gunnell Plate 31 fig 6, page 269.

1941 Synprioniodina microdenta Ellison Plate 20 figs 43-46, page 119.

?1952 Scottella typica Rhodes Synprioniodina component; Rhodes Plate 126 figs 4, 8-11, page 892.

1961 Synprioniodina forsenta Stauffer. Higgins Plate xii fig 8.

1968 Synprioniodina microdenta Ellison. Higgins and Bouckaert Plate 1 fig 6, page 47.

1969 Euprioniodina caverna Collinson and Druce (nom. nud.). Rhodes et al. Plate 22 figs 11a-b, page 90.

1969 Euprioniodina microdenta Ellison. Rhodes et al. Plate 22 figs 16a-b, page 91.

1969 Euprioniodina sp. Rhodes et al. Plate 22 figs 15a-b, page 92.

vic1972 Streptognathodus and Idiognathodus Ne element; von Bitter Plate 9 figs 2a-b, page 60.

vic1973 Idiognathodus delicatus Gunnell N element; Baesemann Plate 1 fig 14, page 701.

?1974 Euprioniodina caverna (Collinson and Druce) sic. Austin and Husri Plate 12 figs 20, 23.

1974 Euprioniodina microdentata (Ellison). Austin and Husri Plate 13, figs 19-20.

1975 Synprioniodina microdenta Ellison. Higgins Plate 3 figs 10, 15-16, page 75.

vic1976 Gnathodus bilineatus (Roundy) N element; Norby Plate 6 figs 1- 5, page 112.

1981 Synprioniodina microdenta Ellison. Metcalfe Plate 19 figs 8-9.

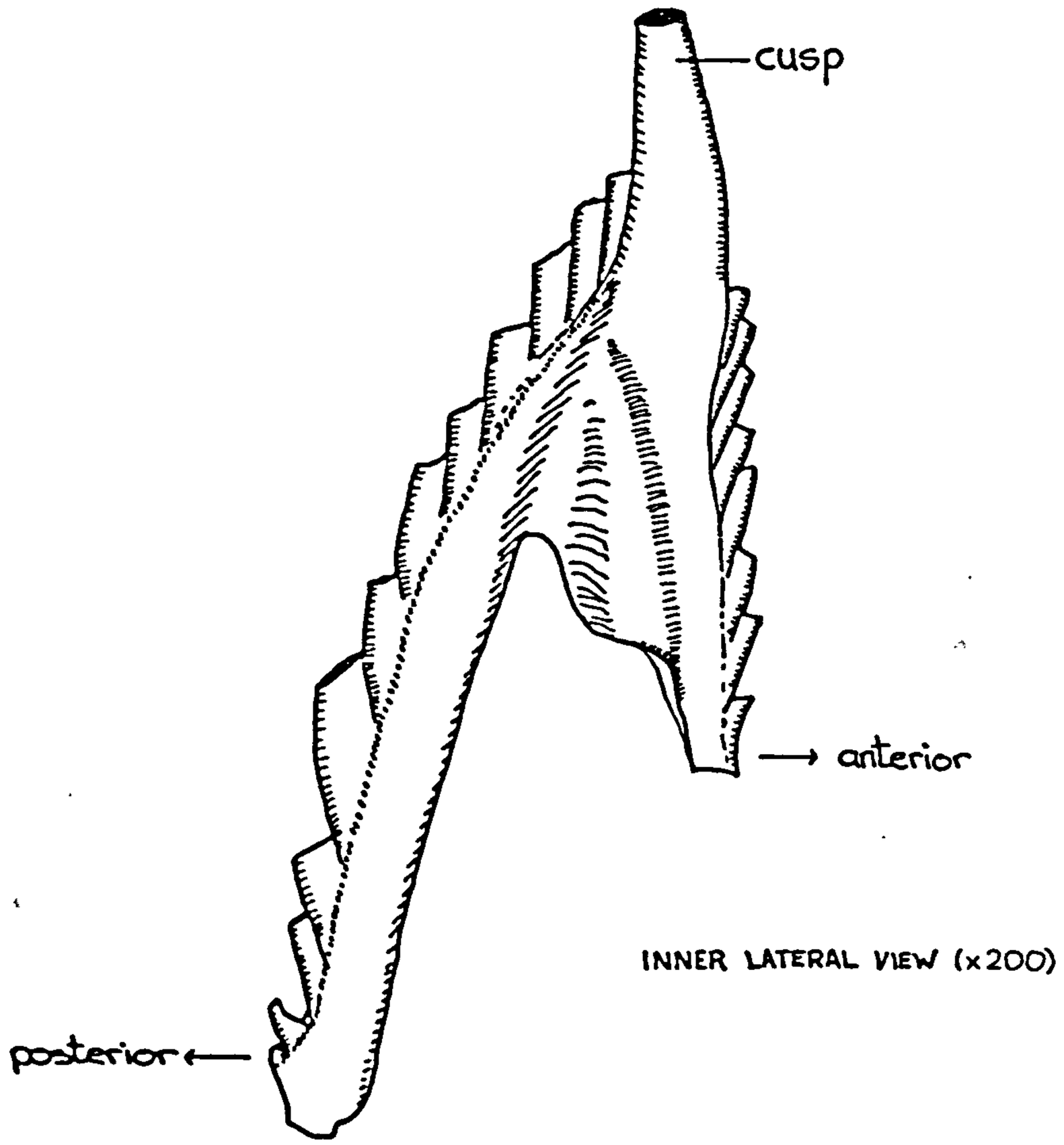
Description:

Dolabrate element with a long, downward-pointing posterior process and a distinctive denticulate anticusp which forms a shorter anterior process. The cusp is two to three times longer and wider than any of the bar denticles, and is laterally compressed and bowed inwards. Beneath the cusp, the moderately deep and conical basal cavity has a distinctively flared asymmetrical lip on the inner side (see interpretive sketch 2.2.12) and a less flared lip on the outer side.

The two processes subtend an angle of between 30° and 60°. The posterior process bears up to at least twelve subequal, laterally flattened denticles. The distal two or three denticles may be somewhat smaller than the others. The denticles are fused for approximately two thirds of their length, and grow at an angle to the bar so as to point upwards, subparallel to the cusp. The denticles of the anterior process are generally similar to, but smaller than, those of the posterior process. The only element with a complete anterior process recovered

in this study has thirteen denticles thereon.

Interpretive sketch 2.2.12 Gnathodus M element (sample CM 2).



Discussion:

Although not readily apparent from the often fragmentary specimens recovered in this study, the dentition of the posterior bar may occur as regularly or irregularly alternating sets of larger and smaller denticles (Norby 1976). Higgins (1975) highlights the variable nature of this element, and records up to thirty large denticles on the posterior bar of a single specimen. In some cases there may be parts of the bar with only minor denticles. The number of denticles on the anterior process is seen to vary from one to twenty. Variation is also noted in the shape of the anterior bar, bar thickness and denticle shape.

Sample range: CM 2 to CM 29, GL 15.
Distribution: outer ramp and distal mid-ramp.
Material: 10 specimens.

Sa element

Synonymy:

?1941 Hindeodella pulchra Ellison Plate 20 fig 20, page 117.

1961 Hibbardella fragilis Higgins Plate 12 fig 4, text-fig 2, page 213.

1965 Hibbardella acuta Murray and Chronic Plate 73 figs 3-5, page 598.

1969 Hibbardella (Hibbardella) acuta Murray and Chronic. Rhodes et al. Plate 25 figs 19-20, page 112.

vic1972 Streptognathodus and Idiognathodus Tr element; von Bitter Plate 16 figs 4a-d, page 61.

vic1973 Idiognathodus delicatus Gunnell A_3 element; Baesemann Plate 1 fig 20, page 702.

1974 Hibbardella (Hibbardella) acuta Murray and Chronic. Austin and Husri Plate 13 figs 10, 12.

1975 Hibbardella acuta Murray and Chronic. Higgins Plate 1 figs 7, 9, Plate 6 fig 13 (pars), text-fig 7g, page 34.

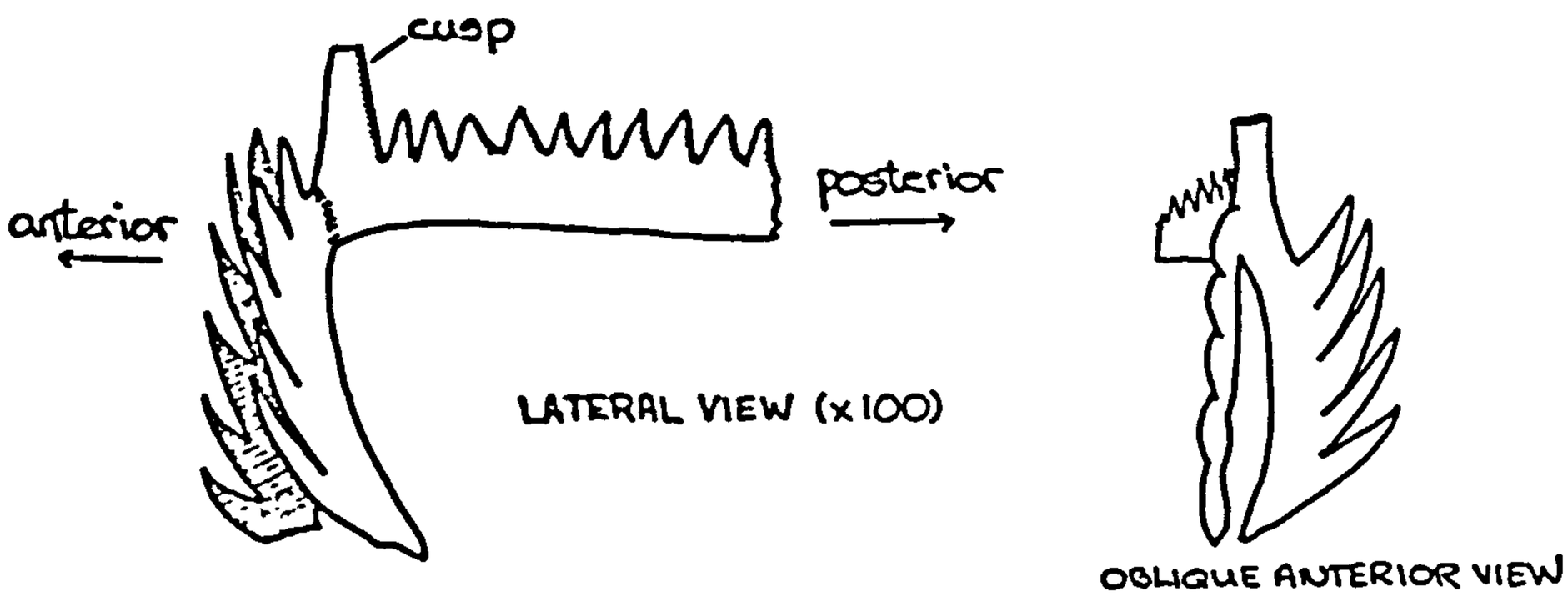
vic1976 Gnathodus bilineatus (Roundy) A_3 element; Norby Plate 7 figs 12-13, page 122.

1981 Hibbardella acuta Murray and Chronic. Metcalfe Plate 14 fig 6.

1984 Hibbardella acuta Murray and Chronic. Austin and Davies Plate 3 fig 21.

.1987 Hibbardella sp. Austin Plate 13.4 fig 13.

Interpretive sketch 2.2.13 Gnathodus Sa element (sample CM 20).



Description:

Alate element with distinctively elongate and downward-pointing lateral processes which subtend an acute angle of approximately 30°. The lateral processes bear at least seven or eight elongate, discrete upward pointing

denticles, and the bars themselves are slightly twisted and curved backwards so that their planar surfaces are not in the same plane.

The cusp is at least twice as large as any of the bar denticles, and is angled posteriorly. The posterior process, which curves slightly downwards, is of approximately the same length as the lateral processes and bears a series of alternating large and small denticles.

Discussion:

The delicate nature of this unit reduces its preservation potential, and only one complete specimen was recovered in this study. Higgins (1975) discusses variations in the denticulation and relative lengths of the processes.

Sample range: CM 2 to CM 20.
Distribution: outer ramp.
Material: 4 specimens.

Sb element

Synonymy:

1943 Hindeodella ampla Cooper and Sloss Plate 28 fig 30, page 173.
?1957 Angulodus walrathi (Hibbard). Bischoff Plate 5 figs 44-45, page 17.
1961 Angulodus walrathi (Hibbard). Higgins Plate 10 fig 16.
1964 Hindeodella paradelicatula Igo and Koike Plate 27 figs 3-4, page 183.
1968 Angulodus simplex Higgins and Bouckaert Plate 1 fig 7, page 28.
1969 Hindeodella hibbardi Collinson and Druce (nom. nud.). Rhodes et al. Plate 28 figs 18-20, page 122.
vic1973 Idiognathodus delicatus Gunnell A_2 element; Baesemann Plate 1 fig 12, page 702.
1974 Hindeodella hibbardi Collinson and Druce (sic). Austin and Husri Plate 15 figs 9-10.
1975 Hindeodella simplex (Higgins and Bouckaert). Higgins Plate 5 figs 10, 12-13, page 42.
vic1976 Gnathodus bilineatus (Roundy) A_2 element; Norby Pate 7 figs 1, 7, page 120.
1981 Hindeodella simplex (Higgins and Bouckaert). Metcalfe Plate 15, figs 1 and at least the lowest specimen of the cluster in fig 7.
.?1987 Hindeodella sp. A Austin Plate 13.4 fig 28.

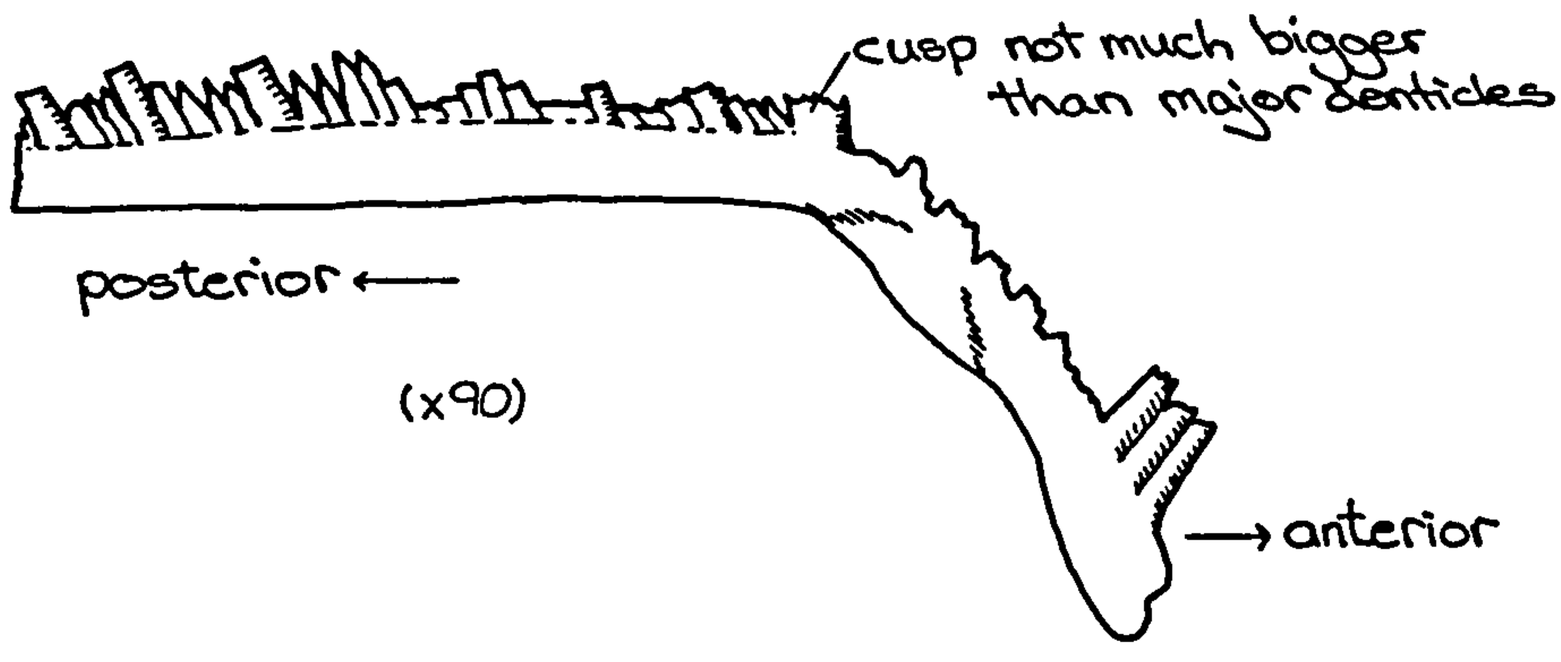
Description:

Elongate and delicate, bipennate, hindeodellan element. The anterior process is relatively long (approximately one third the length of the posterior process, although no complete specimens were recovered). The anterior process is deflected down from the posterior process such that the angle between them is approximately 125°. Immediately anterior to the cusp, the lower

margin of the anterior process flares outwards (particularly on the inner side), and at the point where it constricts again, the process is flexed inwards. At its distal end the anterior process is bluntly spatulate or paddle-shaped and slightly deflected downwards. The distal three denticles are larger and more robust than the other bar denticles.

The cusp is not much larger than the other bar denticles, but points up more vertically. The denticles of the posterior process alternate in size in typical hindeodellan fashion and are angled posteriorly at approximately 55°. There is a conspicuous groove along the under-side of both processes and an elongate pit beneath, and anterior to, the cusp.

Interpretive sketch 2.2.14 Gnathodus Sb element (sample CM 15).



Discussion:

Rhodes et al. (1969) give a full description of this element which agrees very closely with the above. From their study of complete specimens they report that the anterior process typically bears about ten denticles and that the posterior third of the posterior process is deflected downwards and slightly twisted laterally. The denticles of the anterior process are discrete and tend to increase in size anteriorly, while those of the posterior process alternate in size (in typical hindeodellan fashion) and are deflected inwards.

The delicate nature of such elements means that, although numerous hindeodellan bar fragments are recovered, detailed identification is rarely possible.

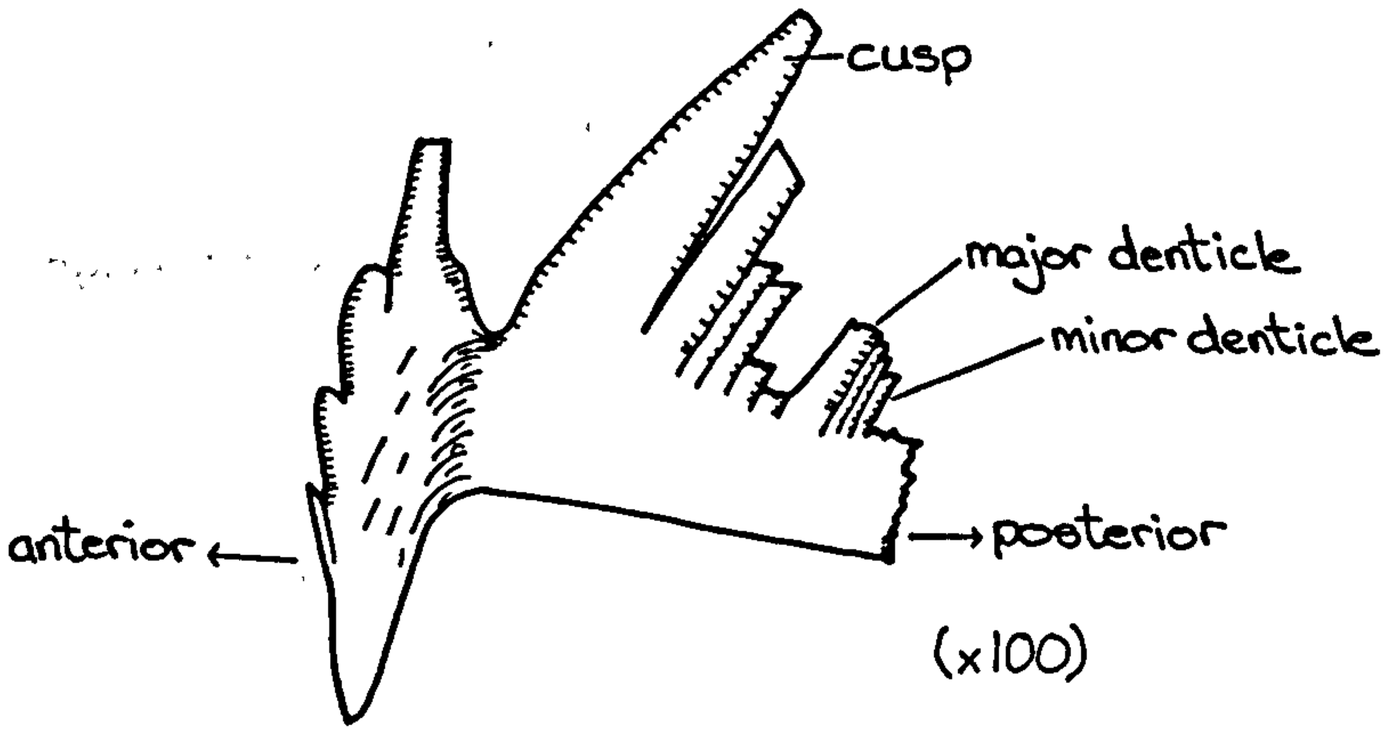
Sample range: CM 15 to CM 23.
Distribution: outer ramp.
Material: 3 specimens (but see final paragraph of discussion above).

Sc_1 element

Synonymy:

p1957 Hindeodella ibergensis Bischoff Plate 6 fig 33, page 28.
p1964 Hindeodella asiatica Igo and Koike Plate 27 fig 7, page 183.
p1968 Hindeodella ibergensis Bischoff. Higgins and Bouckaert Plate 1 fig 2, page 37.
1969 Hindeodella cooperi (Elias). Rhodes et al. Plate 31 figs 18-19 page 120.
vic1973 Idiognathodus delicatus Gunnell A_{1a} element; Baesemann Plate 1 fig 13, page 702.
p1974 Hindeodella ibergensis Bischoff. Austin and Husri Plate 15, fig 18.
p1975 Hindeodella ibergensis Bischoff. Higgins Plate 4 figs 10-11, 14, (The specimen illustrated on Plate 6 fig 13 is partially obscured and identification is equivocal), text-fig 8a-d and f, page 38.
vic1976 Gnathodus bilineatus (Roundy) A_{1a} element; Norby Plate 7 figs 2, 4-5, page 115.
1981 Hindeodella ibergensis Bischoff. Metcalfe Plate 15 figs 5-6.
.1987 Hindeodella sp. Austin Plate 13.4 figs 26-27.

Interpretive sketch 2.2.15 Gnathodus Sc_1 element (sample CM 4).



Description:

Bipennate hindeodellan element with short, flexed, spatulate, hook-like anterior process (see interpretive sketch 2.2.15). The anterior process bears three or four stocky, upward pointing denticles, and is curved round to subtend a 90° angle with the long posterior process. The distal portion of the anterior process is adenticulate (cf. the Sc_2 element below).

In lateral view there is a distinct gap in the denticulation immediately anterior of the cusp. The cusp is two or three times wider than any of the bar

denticles and usually somewhat taller. The cusp and denticles of the posterior process are angled posteriorly at an angle of approximately 50°. The posterior process bears a series of alternating larger and (three or four) smaller denticles.

Discussion:

(See discussion under Sc_2 element below).

Sample range: CM4 to CM 21.
Distribution: outer ramp.
Material: 4 specimens.

Sc_2 element

Synonymy:

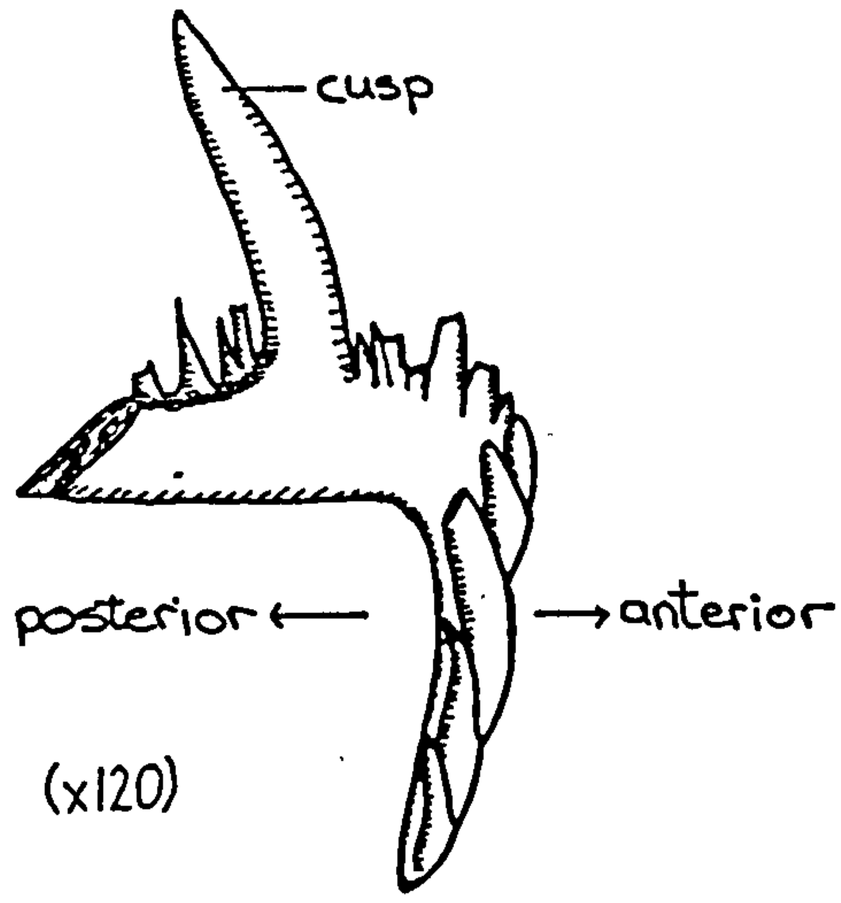
p1941 Indeterminate hindeodellids Ellison Plate 20 fig 18, page 118.
p1941 Hindeodella sp. Ellison and Graves Plate 1 fig 6, page 2.
p1957 Hindeodella ibergensis Bischoff Plate 6 figs 37, 39, page 28.
1957 Hindeodella germana Holmes. Ziegler In: Flügel and Ziegler Plate 5 fig 16, page 41.
1958 Hindeodella redunca Stanley Plate 63 figs 1-4, page 466.
1967 Hindeodella asiatica Igo and Koike. Koike Plate 4 figs 1-2, page 303.
p1968 Hindeodella ibergensis Bischoff. Higgins and Bouckaert Plate figs 1, 3, page 37.
1969 Hindeodella ibergensis Bischoff. Rhodes et al. Plate 28 figs 22-24, 30-31, page 123.
?vic1972 Streptognathodus and Idiognathodus Hi element; von Bitter Plate 10 figs 4a-d, Plate 11 figs 3a-d, page 60.
vic1973 Idiognathodus delicatus Gunnell A_{1b} element; Baesemann Plate 1 fig 15, page 702.
p1974 Hindeodella ibergensis Bischoff. Austin and Husri Plate 12 fig 26.
p1975 Hindeodella ibergensis Bischoff. Higgins Plate 4 fig 15 (NB, angle of photograph makes this identification equivocal), text-fig 8e, page 38.
vic1976 Gnathodus bilineatus (Roundy) A_{1b} element; Norby Plate 7 figs 10a-b, 14-15, page 115.

Description:

Bipennate hindeodellan element with stoutly-denticulate, hook-like anterior process. The anterior process is slightly flexed inwards and bent downwards at 90° to the posterior process. Denticulation continues to the distal tip of the anterior process, and the denticles are large, discrete, upward-pointing and slightly posteriorly-curved. The anterior bar denticles increase in size

toward the distal tip of the process, except for the last two, smaller denticles.

Interpretive sketch 2.2.16 Gnathodus Sc_2 element (sample CM 4).



The cusp is notably larger than any of the bar denticles and curves back posteriorly. Immediately anterior of the cusp several small, congruent bar denticles occur, before the flexure of the anterior process begins. The posterior process is relatively long and delicate, and probably bears standard hindeodellan alternating larger and smaller denticles (no elements were recovered with a posterior process).

Discussion:

The Sc_2 element differs from the Sc_1 element in having a more elongate anterior process with a denticulate distal tip and larger, more discrete denticles. Also there is continuous denticulation anterior of the cusp, between the anterior flexure and the cusp itself.

Several of the early workers included the Sc_1 and Sc_2 elements under the same designation, but noted a substantial degree of variation within the form (e.g. Higgins and Bouckaert 1968, von Bitter 1972). In his reconstruction of Idiognathodus delicatus, Baesemann (1973) recognised two distinct forms. Norby (1976) concluded from bedding-plane apparatus studies that two distinct forms did exist in any one animal, but that throughout an entire population there was a considerable degree of intergradation.

As with all the elongate, delicate bipennate units, these elements tend to break easily and very few pristine specimens are recovered. Because of the essential similarity of the hindeodellan forms, relatively few are sufficiently well-preserved to be identified.

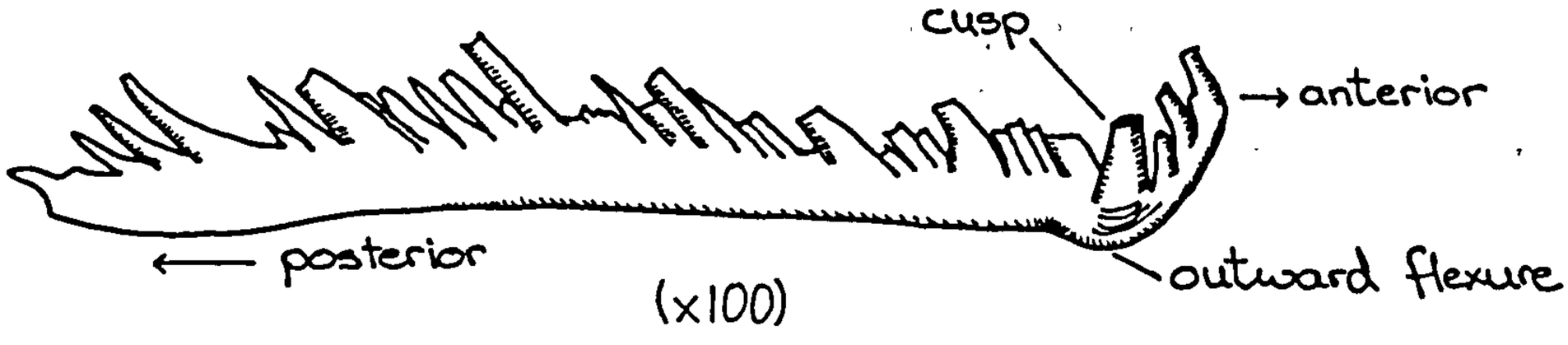
Sample range: CM 17 to CM 21.
Distribution: outer ramp.
Material: 2 specimens.

Sd element

Synonymy:

1941 Hindeodella parva Ellison Plate 20 fig 29, page 117.
1952 Hindeodella component Rhodes Plate 126 fig 10(h), page 891.
1965 Hindeodella pulchra Ellison. Murray and Chronic Plate 72 fig 28, page 559.
?1968 Hindeodella uncata (Hass). Higgins and Bouckaert Plate 1 fig 5 page 37.
?1969 Hindeodella croka Collinson and Druce (nom. nud.). Rhodes et al. Plate 28 figs 15-17, page 121.
1972 Hindeodella parva Ellison. von Bitter Plate 11 figs 4a-d, page 76.
1973 A_1 element (Hindeodella parva); Baesemann Plate 1 fig 8, page 708.
1974 Hindeodella uncata (Hass). Austin and Husri Plate 15 fig 13.
1975 Hindeodella uncata (Hass). Higgins Plate 4 figs 1-3, page 44.
vic1976 Gnathodus bilineatus (Roundy) A_{1c} element; Norby Plate 7 figs 6, 8-9, 11, page 117.
1981 Hindeodella uncata (Hass). Metcalfe Plate 15 fig 2.

Interpretive sketch 2.2.17 Gnathodus Sd element (sample CM 23).



Description:

Bipennate hindeodellan element with denticulate anterior process at 90° to the posterior process; both being in the same horizontal plane. In upper view there is a distinctive outward flexure of the proximal posterior and anterior processes, around the cusp area (see interpretive sketch 2.2.17). The anterior process is relatively straight and bears several large, discrete denticles; and there is a distinctive downward hook at the distal tip (cf. Lochriea Sc_2 element).

The cusp is of a similar size to the larger bar denticles, but lies in a different orientation and is slightly angled outwards from the geniculation. The posterior bar is typically hindeodellan, and the bar denticles are posteriorly inclined.

Discussion:

This element is particularly delicate and is rarely recovered in recognisable form (Norby 1976).

Sample range: CM 23 to CM 43.
Distribution: outer ramp.
Material: 2 specimens.

2.2e Genus: Hindeodus Rexroad and Furnish 1964

Type species: Trichonodella imperfecta Rexroad 1957, by designation of Rexroad and Furnish 1964; junior synonym for Hindeodus cristulus (Youngquist and Miller 1949), see remarks below.

Synonymy: 1970 Anchignathodus Sweet.
1976 Ozarkodina Branson and Mehl. Norby.
1977 Hindeodus Rexroad and Furnish. Sweet In: Ziegler.

Remarks:

Sweet (In: Ziegler 1977) proposes that Trichonodella imperfecta s.f. Rexroad 1957 is the Sa element of an apparatus in which the Pa element was Spathognathodus cristulus s.f. Youngquist and Miller 1949. As the oldest established form-species of the apparatus, cristulus has priority and the type species of multielement Hindeodus should be Hindeodus cristulus.

Hindeodus cristulus (Youngquist and Miller 1949)

Plate 5 figs 1-4.

Pa element

Synonymy:

?p1900 Polygnathus scitulus Hinde Plate 9 fig 10, page 343.

?1941 Spathognathodus minutus (Ellison). Ellison and Graves Plate 2 figs 1, 3, 5, page 3.

1949 Spathognathodus cristula Youngquist and Miller Plate 101 figs 1-3, page 621.

1957 Spathognathodus cristula Youngquist and Miller. Rexroad Plate 3 figs 16-17, page 38.

1960 Spathognathodus minutus? (Ellison). Clarke Plate 3 figs 9, 12, 14, page 20.

1964 Spathognathodus cristula Youngquist and Miller. Rexroad and Furnish Plate 111 fig 15.

1967 Spathognathodus cristulus Youngquist and Miller. Globensky Plate 57 figs 15-16, page 447.

1969 Spathognathodus cristulus Youngquist and Miller. Rhodes et al. Plate 8 figs 14-18, page 227.

1969 Spathognathodus cf. cristulus Youngquist and Miller. Rhodes et al. Plate 8 figs 7-8, 12-13, page 233.

1974 Spathognathodus cristulus Youngquist and Miller. Austin and Husri Plate 8 fig 1.

1974 Spathognathodus cf. cristulus Youngquist and Miller. Austin and Husri Plate 8 fig 2.

1976 Ozarkodina cristula (Youngquist and Miller) P element; Norby Plate 15 figs 9-12, page 160.

1977 Hindeodus cristulus (Youngquist and Miller) Pa element; Sweet In: Ziegler Plate 1 (of Hindeodus) fig 1, page 209.

p1981 Hindeodus cristula (Youngquist and Miller). Rexroad Plate 2 fig 1 (fig 2 is indistinct but looks more akin to Synprioniodina? spicula Pa).

1981 Hindeodus cristulus (Youngquist and Miller) Pa element; Sweet and Clark In: Clark et al. Fig 114 (1f), page 167.

1981 Spathognathodus cristulus Youngquist and Miller. Metcalfe Plate 8, fig 6.

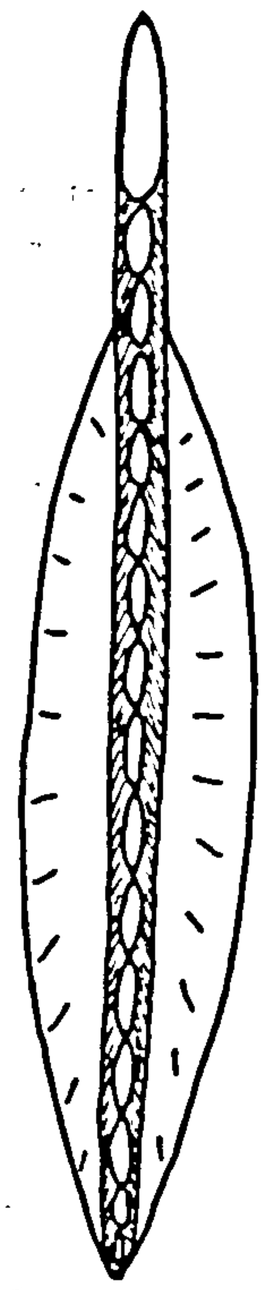
1984 Hindeodus cristulus (Youngquist and Miller) Sp element; Austin and Davies Plate 1 fig 14, Plate 3 fig 11.

1985 Hindeodus? cf. cristulus (Youngquist and Miller). Varker and Sevastopulo Plate 5.2 fig 20.

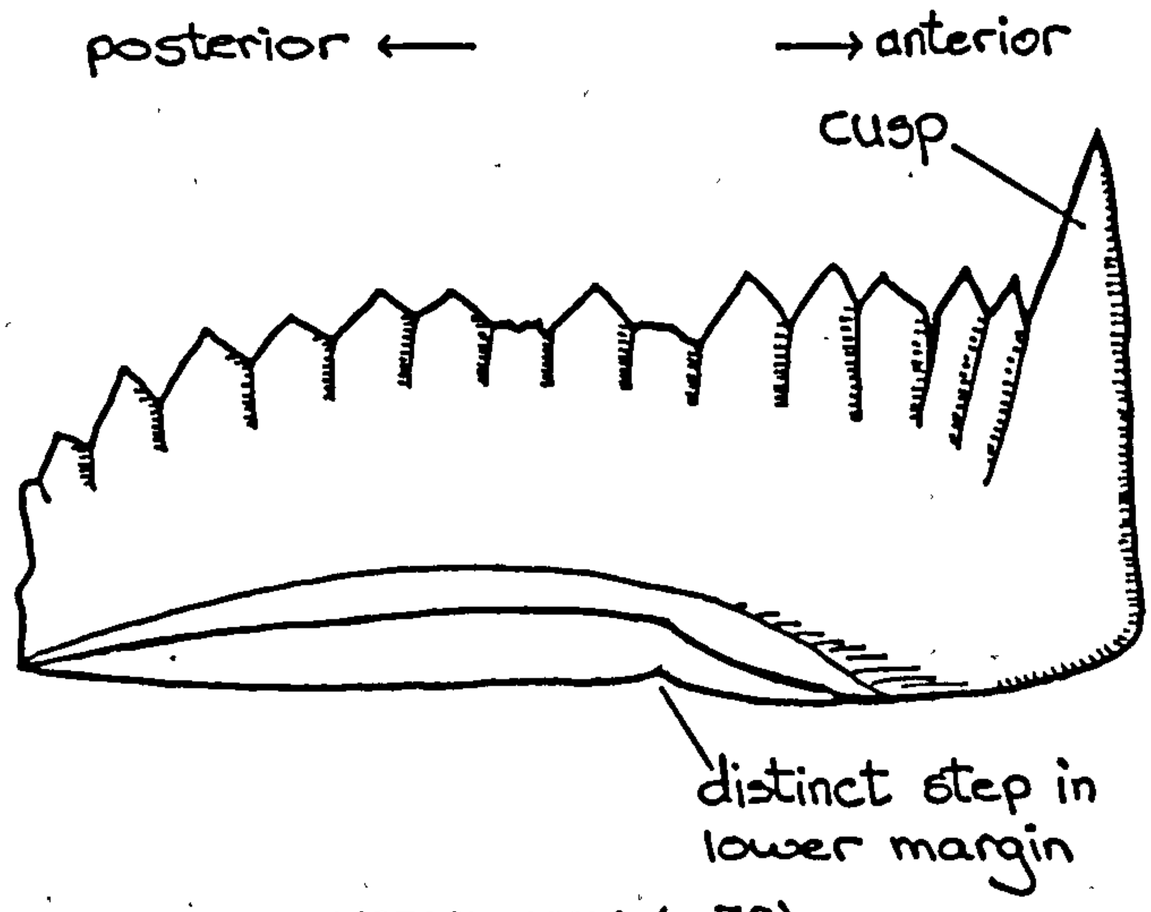
p1987 Spathognathodus cristulus Youngquist and Miller. Austin Plate 13.4 fig 4 (fig 5 looks more akin to a ?Hindeodus scitulus Pa element).

1988 Hindeodus cristulus (Youngquist and Miller) Pa element; Sweet text-fig 5.54, page 116.

Interpretive sketch 2.2.18 Hindeodus cristulus Pa element (sample CM 4)



UPPER VIEW



LATERAL VIEW (x70)

Description:

Blade-like spathognathodontan platform element. In lateral view, the massive, triangular cusp is anterior-most. It is substantially taller and at least three times wider than the other denticles. The anterior margin of the cusp is angled posteriorly from its base, and the anterobasal corner is bluntly rounded. The nine to fifteen (or-so) blade-denticles are stout and fused to their tips, which are chevron shaped. The two denticles immediately posterior of the cusp may be slightly thinner, sharper and angled more anteriorly than the other blade denticles. Most of the blade denticles reach approximately the same height, with a slight decrease toward the posterior, until the posterior-most two or three denticles - which decrease in height markedly. The posterior blade denticles tend to be more fused and less discrete than those at the anterior.

The elongate, flared basal cavity is distinctive (cf. ?Hindeodus scitulus Pa element). It extends for approximately three quarters of the length of the unit, starting just posterior to the base of the main cusp and extends to the posterior tip of the unit. In lateral view there is a distinctive upward kink in the anterior part of the lower margin of the basal cavity. Toward the posterior, the lower

margin gives a generally flat profile. In upper view the basal cavity is subsymmetrical and lanceolate.

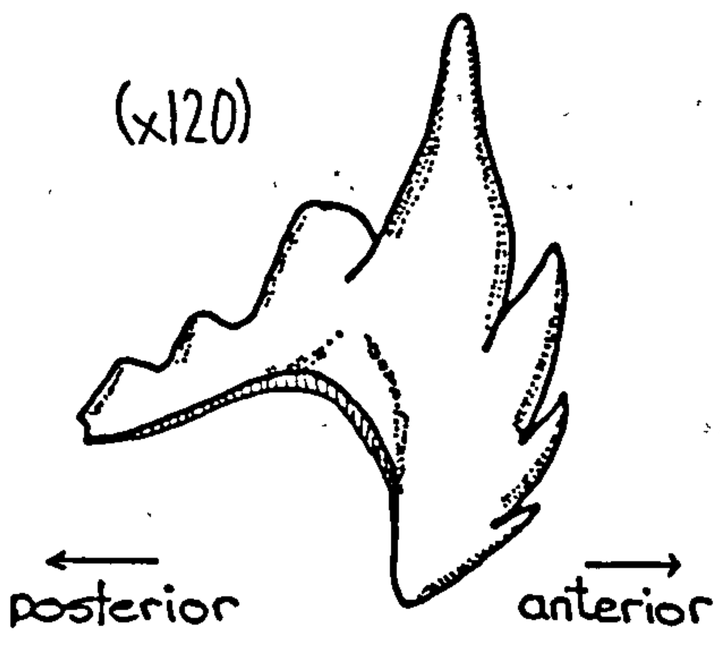
Sample range: CM B4 to CM 33, GL 16, (?)T 5.
Distribution: outer ramp to distal mid-ramp.
Material: 9 specimens.

Pb element

Synonymy:

1958 Ozarkodina curvata Rexroad Plate 4 figs 1-3, page 24.
1965 Ozarkodina curvata Rexroad. Rexroad and Nicoll Plate 2 figs 1-2, page 25.
1969 Ozarkodina curvata Rexroad. Rhodes et al. Plate 27 fig 6, page 168.
1976 Ozarkodina cristula (Youngquist and Miller) O element; Norby Plate 15 figs 1-4, page 162.
1977 Hindeodus cristulus (Youngquist and Miller) Pb element; Sweet In: Ziegler Plate 1 (of Hindeodus) fig 4, page 209.
1981 Hindeodus cristulus (Youngquist and Miller) Pb element; Sweet and Clark In: Clark et al. Fig 114 (1e), page 167.
1988 Hindeodus cristulus (Youngquist and Miller) Pb element; Sweet text-fig 5.54, page 116.

Interpretive sketch 2.2.19 Hindeodus cristulus Pb element (sample CM 29).



Description:

Comparatively short, strongly arched and flexured angulate ozarkodinan element. In inner lateral view the anterior bar is short and strongly down-curved, it is relatively deep and straight and bears three strong denticles which are congruent with the cusp and get progressively smaller toward the distal tip of the process.

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The apical dentical is approximately twice the height of the largest bar-denticle and two to three times wider. It is recurved posteriorly but has a relatively straight anterior edge. The asymmetrical basal cavity is marked by a slight flaring of the lower margin beneath the cusp. A pronounced slit continues from the basal cavity along the underside of both processes.

The two processes subtend an angle of approximately 90°. The posterior process is longer and less deep than the anterior process, and bears three more-upright but less discrete denticles. The process is curved inwardly.

Discussion:

Although the above is consistent with previous descriptions of Ozarkodina curvata s.f. (e.g. Rhodes et al. 1969), comparison suggests the single element recovered in this study to be a juvenile specimen. During ontogeny the posterior bar could be expected to elongate and the bar denticles to become more discrete. Dean (1987) observed a wide degree of morphological variation in Hindeodus cristula Pb elements from upper Dinantian/lower Namurian rocks of the Midland Valley of Scotland, and tentatively synonymised Hindeodus sp. s.f. Rhodes Austin and Druce 1969. This latter form is similar to the above but has longer and more robust processes. The material recovered in this study is not sufficient to allow for any comment on this, but the variation does seem within that which might be expected during ontogeny.

Sample range: CM 29.
Distribution: outer ramp.
Material: 1 specimen.

M element

(Not recovered in this study, presumably due to the general paucity of Hindeodus elements).

Synonymy:

1957 Neoprioniodus camurus Rexroad Plate 2 figs 18-20, page 33.
1961 Neoprioniodus camurus Rexroad. Rexroad and Burton Plate 140 fig 11, page 1155.
1962 Synprioniodina denticamura Rexroad and Liebe text-fig 2, page 513.
1965 Synprioniodina denticamura Rexroad and Liebe. Rexroad and Nicoll Plate 2 figs 16-17, page 27.
1965 Neoprioniodus camurus Rexroad. Rexroad and Nicoll Plate 2 figs 19-20, page 23.
1969 Neoprioniodus cf. N. camurus Rexroad. Rhodes et al. Plate 22 figs 1-4, page 167.
1974 Neoprioniodus camurus Rexroad. Austin and Husri Plate 15 fig 15.
1976 Ozarkodina cristula (Youngquist and Miller) N element; Norby Plate

16 figs 1-2, 6, 9, page 163

1977 Hindeodus cristulus (Youngquist and Miller) M element; Sweet In: Ziegler Plate 1 (of Hindeodus) fig 3, page 209.

1981 Hindeodus cristulus (Youngquist and Miller) M element; Sweet and Clark In: Clark et al. Fig 114 (1d), page 167.

1988 Hindeodus cristulus (Youngquist and Miller) M element; Sweet text-fig 5.54, page 116.

Discussion:

Norby (1976) notes that the Hindeodus M element is similar to those of Vogelgnathus and Cavusgnathus, but can be distinguished by the relatively small degree of basal flaring, which forms the lateral margin of the basal cavity.

Sa element

Synonymy:

1957 Trichonodella imperfecta Rexroad Plate 4 figs 4-5, page 41.

1961 Elsonella? imperfecta (Rexroad). Rexroad and Burton Plate 141 fig 1, page 1152.

1964 Hindeodus imperfectus (Rexroad). Rexroad and Furnish Plate 111 figs 13-14, page 672.

?1969 Hindeodus imperfectus (Rexroad). Rhodes et al. Plate 31 fig 8 page 129.

1976 Ozarkodina cristula (Youngquist and Miller) A_3 element; Norby Plate 16 figs 4-5, page 167.

1977 Hindeodus cristulus (Youngquist and Miller) Sa element; Sweet In: Ziegler Plate 1 (of Hindeodus) fig 6, page 209.

1981 Hindeodus cristulus (Youngquist and Miller) Sa element; Sweet and Clark In: Clark et al. Fig 114 (1a), page 167.

1988 Hindeodus cristulus (Youngquist and Miller) Sa element; Sweet text-fig 5.54, page 116.

Description:

Alate element lacking a posterior process. The two lateral processes are in the same horizontal plane and subtend an angle of approximately 90°; where they meet there is a very slight flaring to form a restricted basal pit.

The cusp is approximately three times wider than any of the bar denticles, but is broken in the one recovered specimen. The bar denticles tend to increase in size away from the cusp. The processes are laterally compressed but comparatively deep, and give a blade-like appearance. The two processes are not quite symmetrical.

Discussion:

Norby (1976) states that perfectly symmetrical Hindeodus Sa elements are uncommon; and there appears to be a series of transitions between Sa and Sb elements. Dean (1987) corroborates Norby's findings and describes a range of variations in inter-bar angle, bar length and depth and denticulation.

Sample range: PE 1
Distribution: mid-ramp
Material: 1 specimen

Sb element

(Not recovered in this study, presumably due to the general paucity of all Hindeodus cristulus elements).

Synonymy:

1961 Falcodus? alatoides Rexroad and Burton Plate 140 fig 8, page 1152.

1964 Hindeodus alatoides (Rexroad and Burton). Rexroad and Furnish Plate 111 figs 18-19, page 672.

1967 Hindeodus alatoides (Rexroad and Burton). Globensky Plate 55 fig 8, page 442.

1976 Ozarkodina cristula (Youngquist and Miller) A_2 element; Norby Plate 16 fig 3, page 167.

1977 Hindeodus cristulus (Youngquist and Miller) Sb element; Sweet In: Ziegler Plate 1 (of Hindeodus) fig 2, page 209.

1981 Hindeodus cristulus (Youngquist and Miller) Sb element; Sweet and Clark In: Clark et al. fig 114 (1b), page 167.

1988 Hindeodus cristulus (Youngquist and Miller) Sb element; Sweet text-fig 5.54, page 116.

Discussion:

The Sb element is transitional between the Sa and Sc elements and there is a wide range of variation in its morphology; it is rarely recovered complete (Norby 1976).

Sc element

(Not recovered in this study, presumably due to the general paucity of all Hindeodus cristulus elements).

Synonymy:

p1957 Hindeodella spp. Rexroad Plate 3 fig 2 (only), page 32.

p1964 Hindeodella spp. Rexroad and Furnish Plate 111 fig 12 (only), page 671.

?1969 Hindeodus alatoides (Rexroad and Burton). Rhodes et al. Plate 31 figs 7, 10, page 129.

1976 Ozarkodina cristula (Youngquist and Miller) A_1 element; Norby Plate 16 figs 7-8, page 165.
1977 Hindeodus cristulus (Youngquist and Miller) Sc element; Sweet In: Ziegler Plate 1 (of Hindeodus) fig 5, page 209.
1981 Hindeodus cristulus (Youngquist and Miller) Sc element; Sweet and Clark In: Clark et al. Fig 114 (1c), page 167.
1988 Hindeodus cristulus (Youngquist and Miller) Sc element; Sweet text-fig 5.54, page 116.

Discussion:

The Sc element is seen as an end member of the Hindeodus cristula S element transition series, and is transitional with the Sb element. It is characterised by a spatulate anterior process which curves uniformly inwards and downwards to approximately 90°, and bears six or more subequal, laterally compressed denticles. The cusp is elongate and erect or only slightly angled posteriorly (Norby 1976).

?Hindeodus scitulus Hinde 1900

Plate 5 figs 5-8.

Remarks:

The nature of the apparatus in which Spathognathodus scitulus s.f. occupied the Pa position has been discussed by several authors (see section 1.4i and Higgins and Varker 1982 page 165). Austin and Rhodes (1969) reported a fused cluster from Asbian (equivalent) rocks of the Avon Gorge, comprising S. scitulus s.f. and four elements (three species?) of 'Apatognathus' s.f.; which they believed to represent a natural association. Rexroad and Thompson (1979) noted that the association between S. scitulus s.f. and species of Apatognathus s.f. is consistently documented in the literature (e.g. Rexroad and Collinson 1963), and this grouping was given further credence by the findings of Nicoll (1980) who concluded from a study of Viséan rocks in the Carnarvon Basin of Australia that there is an association between the form species S. scitulus, 'A.' porcata, 'A.' geminus and Ozarkodina laevipostica.

Druce et al. (1972) indicated a statistical association between the form species 'A.' varians Branson and Mehl (? see Nicoll 1980 page 137), Hibbardella separata Branson and Mehl and Lonchodina sp. A Rhodes et al. The possibility of this association providing the missing elements of the apparatus represented by the fused cluster mentioned above was suggested by Rexroad and Thompson (1979), but they thought it most likely that 'A.' varians s.f. was in a different apparatus from S. scitulus s.f.

It is reasonable to assume that the association outlined by Nicoll (1980) which includes S. scitulus s.f. represents at least part of a multielement

apparatus. The most suitable systematic terminology for this apparatus is uncertain. The choice of species name is between scitulus and porcatus, both of Hinde 1900; and Rexroad and Thompson (1979) recommend scitulus on the grounds that it is greatly preferable for the Pa element to be the name bearer where there is a choice. Deciding on the most suitable generic name is more controversial. The nature of this apparatus is markedly different from that of the multielement genus Ozarkodina, and therefore neither Ozarkodina nor its junior synonym Spathognathodus are available. Rexroad and Thompson (1979) noted that there was a stratigraphical gap between the disappearance of the originally described Upper Devonian species of Apatognathus and the Middle Mississippian forms found in association with S. scitulus s.f.; however they concluded that until new information dictates otherwise, the generic name Apatognathus should be adopted. Nicoll (1980) did not include the Carboniferous apatognathan forms in his Apatognathus multielement concept, but suggested no alternative generic designation.

Sweet (1988) expands the criteria for designating species to the family Anchignathodontidae Clark 1972, and includes apparatuses with a spathognathodontan Pa element, an angulate Pb element with a relatively large cusp and short processes and an alate Sa element lacking a posterior process. Apart from the one species of Aethotaxis, all other species within this group are included in the genus Hindeodus. Sweet implies that this genus is probably too broadly interpreted, but pending further studies refers the present apparatus loosely to Hindeodus. This procedure is adopted here, with the proviso of a question mark inserted before the generic name.

Rexroad and Collinson (1963), Austin and Rhodes (1969), Rexroad and Thompson (1979) and Nicoll (1980) all cite at least two types of apatognathan unit in association with S. scitulus s.f. It can be inferred that in each of these reports one element is of a type which has a large inclined cusp, strong and regular denticulation on both bars and a swivelling of the posterior process resulting in a flattened bar. The other element is more asymmetrical and has relatively small bar-denticles interspersed with single large denticles. The first type has been termed 'A.' porcata s.f. (Rexroad and Collinson 1963, Rexroad and Thompson 1979, Nicoll 1980) and 'A.' cuspidatus s.f. (Austin and Rhodes 1969). The second type has been termed 'A.' gemina s.f. (Rexroad and Collinson 1963, Nicoll 1980), 'A.' chaulodius s.f. (Austin and Rhodes 1969) and 'A.' scalenus s.f. (Rexroad and Thompson 1979).

Much of the confusion over the terminology appears to have arisen because of the rather incomplete original descriptions of 'A.' porcata s.f. and 'A.' gemina s.f. by Hinde (1900). The interpretation of the present study is based on the apatognathan elements illustrated by Rexroad and Collinson (1963), and the diagnoses and descriptions of Varker (1967). From reviewing the literature it is assumed that 'A.' gemina s.f. and 'A.' scalena s.f. as described by Varker (1967)

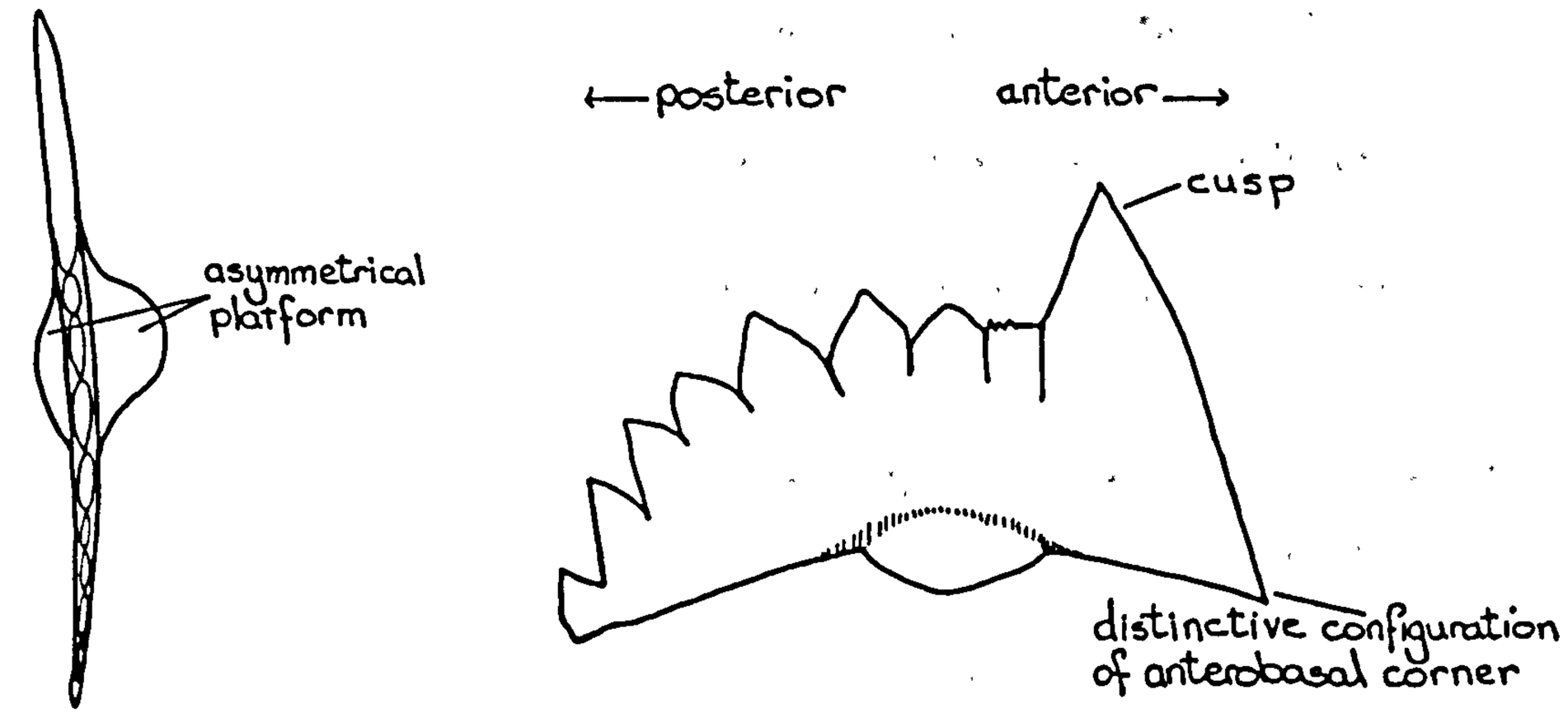
are the most appropriate form names for the apatognathan units of this association. It is possible that 'A.' chaulodius s.f. Varker 1967 is also included, as suggested by Austin and Rhodes (1969), although it has not been recovered in the present study.

Pa element

Synonymy:

p1900 Polygnathus scitulus Hinde Plate 9 figs 9, 11, page 343.
p1928 Panderodella scitula (Hinde). Holmes Plate 6 figs 26, 28, page 16.
1960 Spathognathodus scitulus (Hinde). Clarke Plate 3 figs 12-13, page 21.
1963 Spathognathodus scitulus (Hinde). Rexroad and Collinson Plate2 figs 14, 19, 21-31, page 20.
1969 Spathognathodus scitulus (Hinde). Austin and Rhodes (not discernable in illustrations).
1969 Spathognathodus scitulus (Hinde). Rhodes et al. Plate 8 figs 9-11, page 232.
1974 Spathognathodus scitulus (Hinde). Austin and Husri Plate 7 fig 10, Plate 8 fig 6.
1975 Spathognathodus scitulus (Hinde). Austin and Mitchell Plate 2 fig 26.
1981 Spathognathodus scitulus (Hinde). Metcalfe Plate 8 fig 4.
1982 Spathognathodus scitulus (Hinde). Higgins and Varker Plate 19 fig 14, page 164.
1984 Spathognathodus scitulus (Hinde). Austin and Davies Plate 1 fig 15, Plate 3 fig 18.
?1987 Spathognathodus scitulus (Hinde). Austin Plate 13.4 figs 2-3.
.p?1987 Spathognathodus cristulus Youngquist and Miller. Austin Plate 13.4 fig 5 (only).
1988 Hindeodus scitulus (Hinde) Pa element; Sweet text-fig 5.54, page 115.

Interpretive sketch 2.2.20 ?Hindeodus scitulus Pa element (sample CM 14).



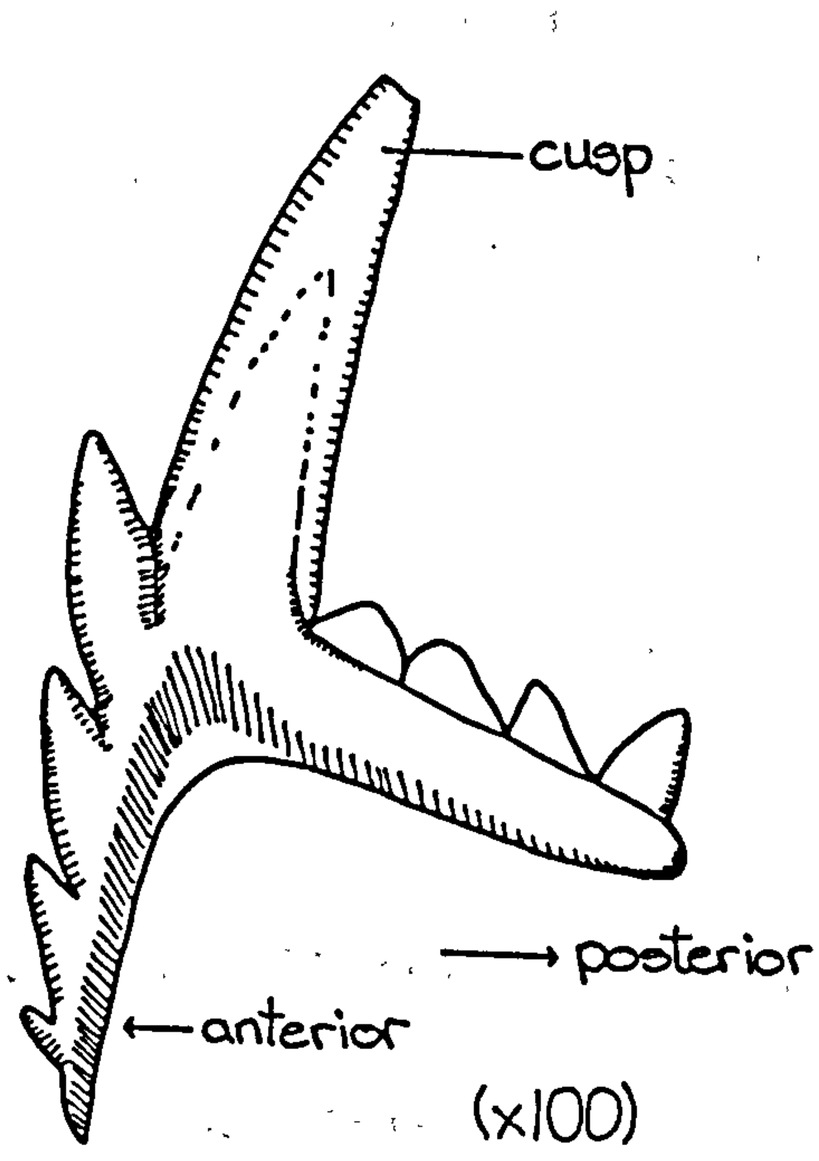
flexured inwards.

The anterior process is directed downwards and may appear as an over-developed anticusp. It bears three or four bulbous, discrete denticles which are angled upwards at about 45° to the cusp, and which get progressively smaller toward the sharply pointed, adenticulate distal tip. The posterior (or lower) edge of the anterior process is flattened and angled-in steeply to form a sharp edge.

The posterior process is approximately at 90° to the cusp, and is straight and subcylindrical with a bluntly rounded distal tip. It bears four (or less) laterally flattened, plate-like denticles.

The basal cavity is asymmetrical and slightly flared on the outer side. It continues as a slit along the underside of the posterior process.

Interpretive sketch 2.2.21 ?Hindeodus scitulus Pb element (sample SQ 1)



Discussion:

Dean (1987) notes variation in denticulation, bar length and size of basal cavity in this unit. In the original description by Rexroad and Collinson (1963) the posterior limb was said to typically have just one or two denticles or be adenticulate, but Rhodes et al. (1969) report up to five closely set denticles.

Sample range: CM 18, SQ 1, GL 13, LL 3.
Distribution: across the entire shelf.
Material: 5 specimens.

apatognathan elements

Remarks:

Because of the idiosyncratic morphology of apatognathan elements, application of the notational scheme of Sweet (In: Clark et al. 1981) is not straightforward. Austin et al. (In: Clark et al. 1981) were first to use this notation (although there was a delay in publication), and designated all species of Apatognathus s.f. as Sa elements. Nicoll (1980) reconstructed a Devonian apparatus containing three types of apatognathan element and designated them as M, Sa and Sc elements. Sweet (1988 text-fig 5.54) illustrates a reconstruction of the apparatus of Hindeodus scitulus (without referencing his sources), and includes apatognathan elements in the Sa, Sb, Sc and M positions. This is taken as a basis for the designations used in this section, although it is recognised that further work is necessary for confirmation.

M element

Synonymy:

?1900 Prioniodus geminus Hinde Plate 10 fig 25, page 344.
?1900 Prioniodus porcata Hinde Plate 10 fig 26, page 344.
1928 Prioniodina? gemina (Hinde). Holmes Plate 5 fig 10, page 19.
1960 Apatognathus geminus (Hinde). Clarke Plate 1 figs 1-2, page 4.
p1963 Apatognathus? porcata (Hinde). Rexroad and Collinson Plate 1 figs 7-9 (figs 10-11 look transitional with 'A.' cuspidata s.f.), page 8.
1967 Apatognathus? gemina (Hinde). Varker Plate 17 figs 9, 12-13, page 133.
?1969 Apatognathus geminus (Hinde). Rhodes et al. Plate 20 figs 3-4, 6-7, page 71.
?1969 Apatognathus porcatus (Hinde). Rhodes et al. Plate 31 fig 27, page 73.
?1974 Apatognathus geminus (Hinde). Austin and Husri Plate 10 fig 10 (fig 17 = 'A.' cuspidata s.f.?).
?1974 Apatognathus varians Branson and Mehl. Austin and Husri Plate 10 fig 11.
?1974 Apatognathus sp. Matthews and Thomas Plate 50 figs 1-2.
p?1981 Apatognathus cuspidatus Varker. Metcalfe Plate 13 fig 9 (only).
1981 Apatognathus petilus Varker. Austin and Davies Plate 3 fig 20.
1988 Hindeodus scitulus (Hinde) M element; Sweet text-fig 5.54, page 116.

Description:

An elongate apatognathan unit with a thickened (or "tumescent") posterior process (orientation of element sensu Varker 1967) and a more bar-like anterior process of approximately the same length (although no complete specimens have been recovered in the present study). The cusp is two or three times larger than the bar denticles neighbouring it, is relatively straight and in mature specimens is almost lozenge shaped.

The two processes may be slightly twisted relative to one another, such that they are not in the same horizontal plane, and the posterior process is flexed inwards. In mature specimens each process may bear up to 16-or-so denticles. The denticles are angled toward the apex and are of subequal size, although the more distal denticles are commonly slightly smaller.

The angle subtended by the processes varies from approximately 35° to 45°, and where the two processes meet a thin flange may be developed which extends along the "aboral" margin of the posterior process for a short distance.

Discussion:

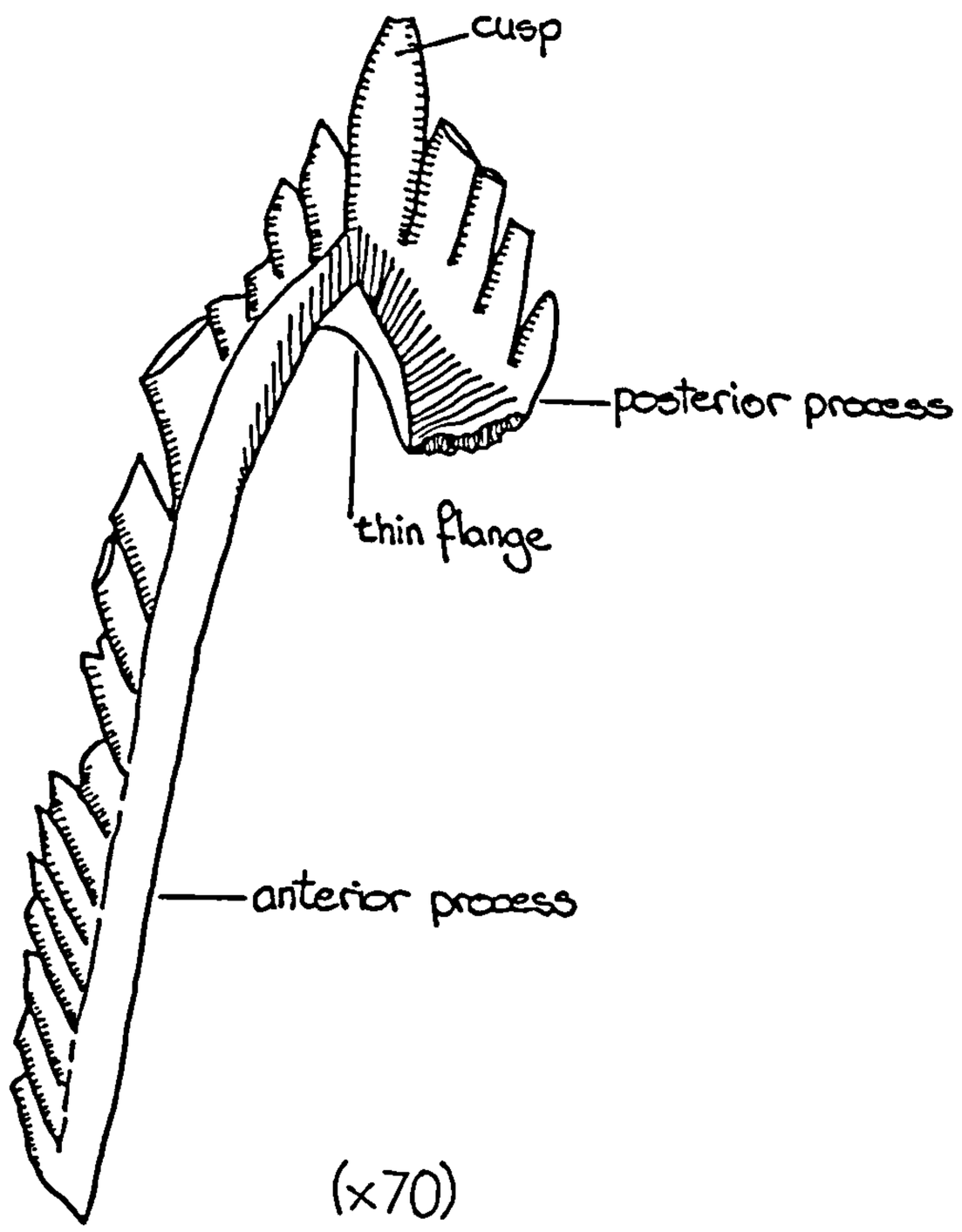
The specimen figured below (interpretive sketch 2.2.22) agrees very closely with the specimen illustrated as 'A.' porcata by Rexroad and Collinson (1963 Plate 1 fig 7) from the Upper St. Louis Formation of the Illinois Basin (= Holkerian/Asbian).

As with all apatognathan elements there is a range of variation within the forms included in this designation; and there is a gradation between the above and forms described by Varker (1967) as 'A.' cuspidata s.f. and 'A.' petila s.f. Future work may show these forms to all have been associated as part of a transition series (see discussion under ?H. scitulus Sc element).

In the present study units designated as 'A.' cuspidatus s.f. have virtually no thickening of the posterior process, and a larger more elongate cusp than the above, in which the cusp appears to be a continuation of the processes (see interpretive sketch 2.2.43). Elements assigned to 'A.' petilus s.f. are less elongate, have a marked thickening of the posterior process, and a cusp of subequal size to its surrounding denticles (see interpretive sketch 2.2.44).

In the present study apatognathan elements are most frequently recovered broken, with only the base of the cusp and fragments of the proximal parts of the processes. Thus it is often difficult to identify apatognathan elements definitively beyond the generic level (s.f.).

Interpretive sketch 2.2.22 ?Hindeodus scitulus M element (sample CM 43)



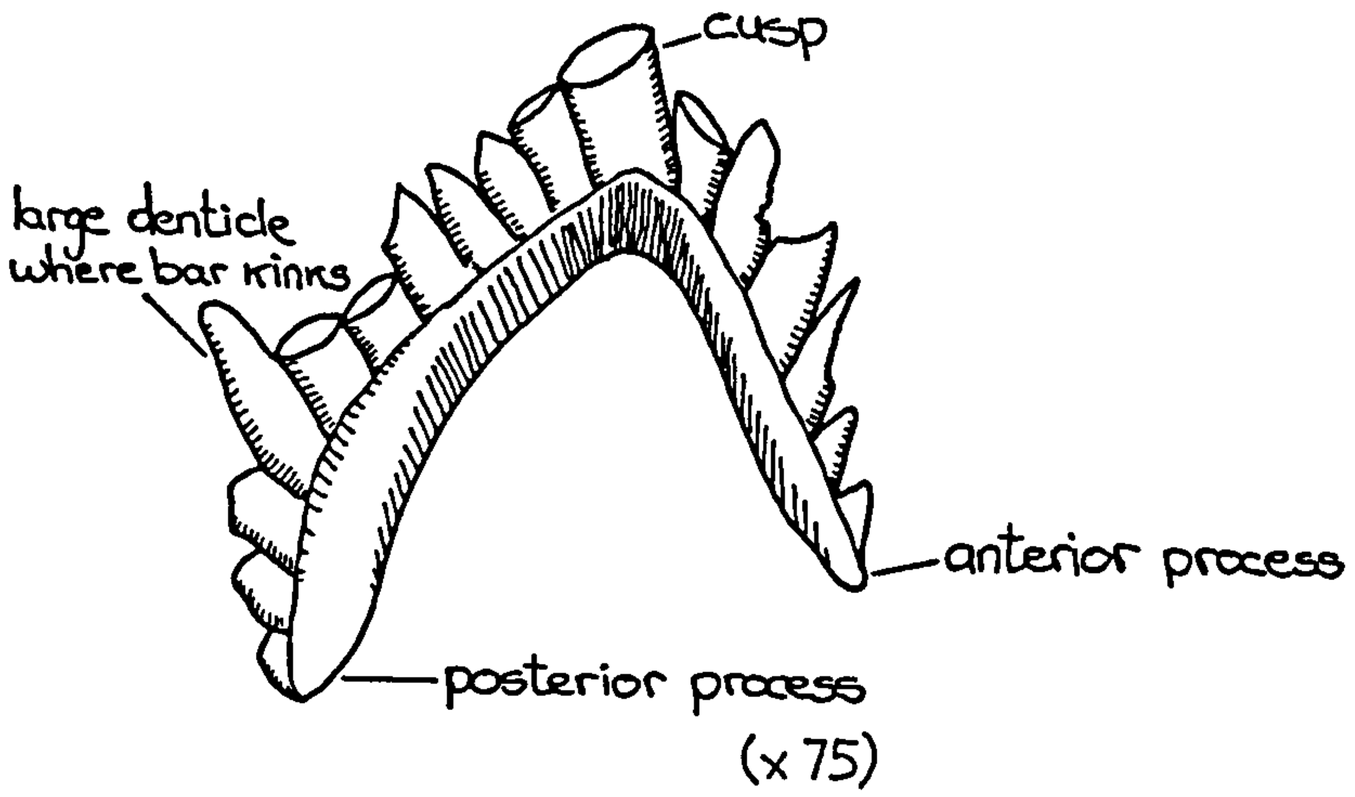
Sample range: CM 15 to CM 43, GL 15, T 5.
Distribution: outer to proximal inner ramp.
Material: 12 specimens.

Sc element

Synonomy:

1963 Apatognathus? gemina (Hinde). Rexroad and Collinson Plate 1 figs 12-17, page 7.
1967 Apatognathus? scalena Varker Plate 18 figs 1-2, 4-5. page 136.
1969 Apatognathus scalena Varker. Rhodes et al. Plate 20 figs 9-11.
1974 Apatognathus scalenus Varker. Austin and Husri Plate 10 fig 12.
1981 Apatognathus scalenus Varker. Metcalfe Plate 13 fig 3.
1988 Hindeodus scitulus (Hinde) Sc element; Sweet text-fig 5.54.

Interpretive sketch 2.2.23 ?Hindeodus scitulus Sc element (sample CM 43).



Description:

A markedly asymmetrical apatognathan unit with a kinked posterior process which bears a bar denticle of subequal size to the cusp.

The anterior process is unthickened and bears between six and sixteen discrete, stout, subequal denticles (except for the distal one or two which may be smaller). The posterior process is one third longer than the anterior, and bears approximately ten stout denticles. Approximately two thirds along its length the bar kinks, and at this point there is an unusually large bar-denticle (see interpretive sketch 2.2.23). The posterior bar is thickened and twisted over its distal portion.

The angle which the two processes subtend is highly variable and may be between 80° and 20°.

Discussion:

Forms intermediate between the ?H. scitulus M and Sc elements have been recovered in this study; and it seems likely that as with H. cristulus the non-platform elements intergrade with one another (Norby 1976). Consequently it may be difficult to designate them in terms of Sweet's notation (In: Clark et al. 1981) when they are studied in isolation.

Sample range: CM 29 to CM 43, LS 6.
Distribution: outer and distal mid-ramp.
Material: 3 specimens.

2.2f Genus: Idioprioniodus Gunnell 1933

Type species: Idioprioniodus typus Gunnell 1933

Synonymy: 1952 Duboisella Rhodes.

1972 Neoprioniodus Rhodes and Müller. von Bitter.

1973 Idioprioniodus Gunnell. Baesemann.

Remarks:

The use of cf. below in describing the single species recognised in this study, reflects a degree of ambiguity regarding the nature of the M elements recovered (see comments under M element below).

Idioprioniodus cf. healdi (Roundy 1926)

Plate 6 figs 1-5.

Pb element

Synonymy:

p1900 Polygnathus (Centrodus) convexus Pander. Hinde Plate 9 fig 8 (only), page 342.

1931 Prioniodus bidentatus Gunnell Plate 29 fig 6, page 247.

1941 Metalonchodina bidentata (Gunnell). Branson and Mehl Plate 19 fig 34, page 106.

1941 Metalonchognathus bidentata (Gunnell). Ellison Plate 20 figs 35-36, page 116.

1952 Duboisella typica Rhodes Metalonchodina component (of text-fig 3) Plate 128 (m), page 897.

1953 Metalonchodina sp. A Hass Plate 16 figs 17-18, page 85.

1956 Lonchodina regularis Elias Plate 5 figs 19-21, page 122.

1960 Metalonchodina conflecta Clarke Plate 2 fig 14, page 17.

1965 Metalonchodina bidentata (Gunnell). Murray and Chronic Plate 73 fig 4, page 604.

1965 Metalonchodina fragilis Murray and Chronic Plate 73 figs 19-20, page 605.

1969 Metalonchodina bidentata (Gunnell). Rhodes et al. Plate 24 figs 8-11, page 154.

1974 Metalonchodina bidentata (Gunnell). Austin and Husri Plate 11 figs 1, 6-7, 11-13.

1975 Metalonchodina bidentata (Gunnell). Higgins Plate 1 fig 13, page 63.

1975 Metalonchodina multidentata Higgins Plate 1 figs 14-16, page 63.

1975 Idioprioniodus paraclaviger (Rexroad) aff. bidentata element; Nicoll and Rexroad Plate 3 figs 12-14, page 25.

1976 Idioprioniodus healdi (Roundy) N_2 element; Norby Plate 9 figs 6, 13, page 130.

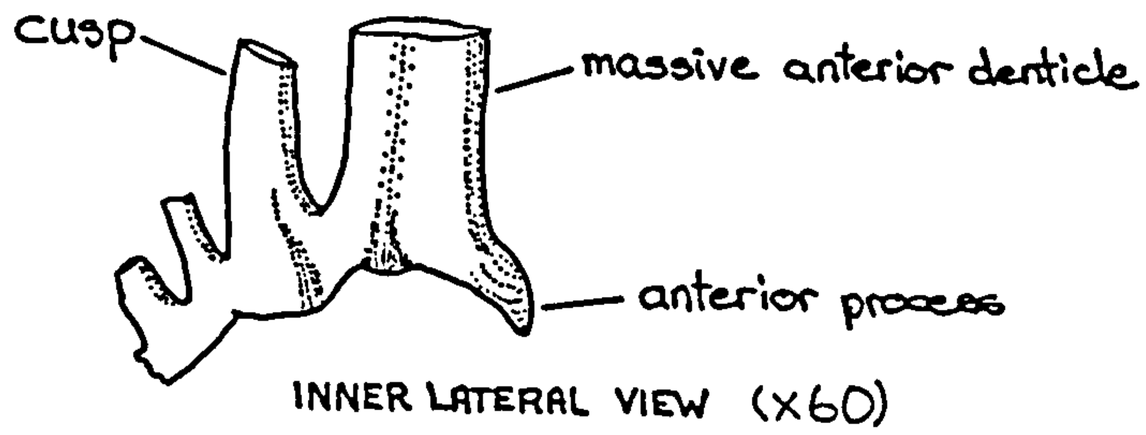
1981 Metalonchodina bidentata (Gunnell). Metcalfe Plate 17 fig 1.

1981 Idioprioniodus typus Gunnell Pb element; Clark et al. Fig 98 (2a), page 149.

p1983 Idioprioniodus? conleyharpi Sb_2 element; Chauff Plate 3 fig 23.

1988 Idioprioniodus Pa element. Sweet text-fig 5.31, page 83.

Interpretive sketch 2.2.24 Idioprioniodus cf. healdi Pb element (sample CM 14).



Description:

Unusual digyrate/bipennate element with a massive anterior denticle which is two to three times wider than the cusp. The anterior process is short and consists only of the anterior denticle and its anterobasal corner which is extended to form a slight projection. The anterior process is twisted to subtend an angle of approximately 100° with the posterior process.

The cusp lies immediately behind the anterior denticle, and exhibits marked lateral flaring of its base; particularly on the inner side. The cusp is curved anteriorly.

The posterior process of the only identifiable specimen recovered is broken, but bears at least two discrete denticles with a rounded cross-section. The bar is deflected downwards at an angle of approximately 45° from the base of the cusp.

Discussion:

Rhodes et al. (1969) give a full description of this element as Metalonchodina bidentata, and note that the posterior bar may bear two or three denticles, inclined toward the anterior; and that considerable variation is seen in this unit and in some cases one or two smaller denticles may be developed in font of the massive anterior denticle.

Sample range: CM 14.
Distribution: outer ramp.
Material: 1 specimen

M element

No unequivocally idioprioniodontan M elements were recovered in this study, but see comments below for discussion and tentative explanation.

Synonymy:

1931 Prioniodus conjunctus Gunnell Plate 29 fig 7, page 247.

?p1952 Duboisella typica Rhodes Prioniodus component; Plate 128 (b),page 897.

1962 Neoprioniodus conjunctus (Gunnell). Higgins Plate 1 fig 2, page 10.

1969 Euprioniodina sp. nov. A Rhodes et al. Plate 22 fig 13, page 91.

1969 Neoprioniodus conjunctus (Gunnell). Rhodes et al. Plate 21 figs 16-17, 20, page 159.

1972 Neoprioniodus conjunctus (Gunnell) Ne element; von Bitter Plate 9 fig 6, page 69.

1973 Idioprioniodus lexingtonensis (Gunnell) N element; Baesemann Plate 3 fig 7, page 703.

1975 Neoprioniodus conjunctus (Gunnell). Higgins Plate 3 fig 7, page 66.

1975 Idioprioniodus paraclaviger (Rexroad) conjunctus element; Nicoll and Rexroad Plate 3 figs 1-3, page 24.

1976 Idioprioniodus healdi (Roundy) N_1 element; Norby Plate 9 figs 4, 7, 9, 12, 15, page 129.

1981 Neoprioniodus conjunctus (Gunnell). Metcalfe Plate 18, figs 7, 9.

p?1983 Idioprioniodus? conleyharpi M element; Chauff Plate 3 fig 27.

1988 Idioprioniodus M element. Sweet text-fig 5.31, page 83.

Comments:

The Idioprioniodus M element which is cited above and in the apparatus reconstructions of Rhodes (1952), von Bitter (1972), Baesemann (1973), and Merrill and Merrill (1974) has not been recovered in this study. This is surprising given: the general robustness of M elements, the relatively high number of other Idioprioniodus elements recorded and the high number of neoprioniodan M elements recovered in this study.

The workers referenced above studied Upper Pennsylvanian faunas. Nicoll and Rexroad (1975) and Norby (1976) have reported multielement Idioprioniodus from rocks as old as the Chesterian Stage (equivalent to upper Viséan/lower Namurian), but they also cite the same M element as the above workers. Sweet (1988) suggests it is likely that a variety of species of Prioniodinidae (his term for the superfamilies Hibbardellacea and Gondolellacea of Clark et al. 1981) is represented in Pre-Chesterian rocks; probably including early representatives of Idioprioniodus.

One explanation for the lack of Idioprioniodus M elements in this study is that, although originally present, they were subsequently lost during taphonomy or processing. Alternatively it is possible that Idioprioniodus in Arundian times

may have had slightly different M elements from later forms. Unfortunately the present fauna is too limited to allow for further elucidation through statistical analyses.

Circumstantial evidence supports the linking of the plexus of forms described under "Kladognathus M element" with Idioprioniodus as well as Kladognathus. In initial studies of the present fauna, and without knowledge of the multielement nature of Idioprioniodus, such M elements were linked empirically with other elements of the Idioprioniodus apparatus. Further, this type of M element was the only one recovered from sample CM 14, from which the single recorded Idioprioniodus Pb element was recovered; and it was of the same general size and appearance as the Pb element. This association may prove to be ecological rather than physiological, however more detailed bulk-sampling would be needed to fully investigate the situation.

In the present fauna there is a plexus of neoprioniodontan M elements showing a range of continuous variation through several form species previously referred to the genus Neoprioniodus s.f. (peracutus/scitulus/barbatus). Without further studies it is impossible to consistently separate these forms in the recovered fauna (although Horowitz and Rexroad 1982 state peracutus and scitulus to be distinct). Norby (1976) and Dean (1987) both synonymised peracutus and scitulus, and Norby also included Neoprioniodus cassilaris s.f. Branson and Mehl 1940 within a general plexus of such neoprioniodontan forms.

The generalised M element description given under Kladognathus may eventually be found to also refer to Idioprioniodus, and further detailed studies may result in the splitting of the plexus into separate Idioprioniodus and Kladognathus elements.

Sa element

(Not recovered in this study)

Synonymy:

1931 Prioniodus subacodus Gunnell Plate 29 fig 5, page 246.

1931 Prioniodus missouriensis Gunnell Plate 29 fig 9, page 247.

1941 Hibbardella subacoda (Gunnell). Ellison Plate 20 figs 22, 26, page 118.

1952 Duboisella typica Rhodes Hibbardella component; Plate 128 (c), page 897.

1953 Roundya barnettana Hass Plate 16 figs 8-9, page 89.

1969 Hibbardella (Roundya) barnettana Hass. Rhodes et al. Plate 25 figs 2-5, page 116.

1969 Hibbardella (Roundya) sp. Rhodes et al. Plate 25 fig 1, page 116.

1972 Neoprioniodus conjunctus (Gunnell) Tr element; von Bitter Plate 16 fig 2, page 70.

1973 Idioprioniodus lexingtonensis (Gunnell) B_{3a} element; Baesemann Plate 3 fig 9, page 704.
1974 Hibbardella (Roundya) barnettana Hass. Austin and Husri Plate 13 figs 17-18.
1975 Roundya barnettana Hass. Higgins Plate 1 figs 1-3, 12, page 72.
1975 Idioprioniodus paraclaviger (Rexroad) aff. subacoda element. Nicoll and Rexroad Plate 3 fig 15, page 23.
1976 Idioprioniodus healdi (Roundy) B_3 element; Norby Plate 9 figs 16-17, page 138.
1981 Roundya barnettana Hass. Metcalfe Plate 16 fig 4.
1981 Idioprioniodus typus Gunnell Sa element; Clark et al. Fig 98 (2b), page 149.
1983 Idioprioniodus? conleyharpi Sa element; Chauff plate 3 fig 29.
1984 Roundya barnettana Hass. Austin and Davies Plate 3 fig 5.

Comments:

The lack of any Idioprioniodus Sa elements in this study may be the result of: loss through taphonomy or processing, misidentification, or the species represented in the Arundian Stage may have had different Sa elements from I. healdi sensu stricto (see comments under M element above).

Sb element

Synonymy:

1926 Prioniodus healdi Roundy Plate 4 fig 5, page 10.
1931 Prioniodus lexingtonensis Gunnell Plate 29 fig 4, page 246.
1931 Prioniodus tridentatus Gunnell Plate 29 fig 3, page 246.
1941 Ligonodina lexingtonensis (Gunnell). Ellison Plate 20 figs 13-15, page 115.
p?1953 Geniculatus claviger Hass Plate 15 fig 17 (only).
1958 Lonchodina furnishi Rexroad Plate 4 figs 11-13, page 22.
1968 Lonchodina clarki (Gunnell). Higgins and Bouckaert Plate 2 fig 1, page 43.
p1969 Lonchodina furnishi Rexroad. Rhodes et al. Plate 24 figs 20-22 (only), page 141.
1972 Ligonodina lexingtonensis (Gunnell). von Bitter Plate 12 fig 2, page 76.
1973 Idioprioniodus lexingtonensis (Gunnell) B_2 element; Baesemann Plate 3 figs 3, 8, page 704.
1973 Lonchodina furnishi Rexroad. Austin and Aldridge Plate 1 fig 9.
1974 Lonchodina furnishi Rexroad. Austin and Husri Plate 11 figs 2, 16, 18.
1976 Idioprioniodus healdi (Roundy) B_{2a} element; Norby Plate 9 figs 2, 5,

The anterior process is thicker and more robust than the posterior process, and in mature specimens becomes rather square in cross-section, such that the bar denticles sit on a flattened platform. The denticles are larger and more conical than those of the posterior process, and number between five and eight; they are slightly recurved posteriorly, and often appear confluent with the cusp. The two processes subtend an angle of approximately 100°.

Discussion:

This unit exhibits a range of variation in regard to relative lengths of processes, robustness and number of bar denticles. It is probable that many of these variations occur through ontogeny. The single most important diagnostic feature is the symmetry of the basal cavity (Rhodes et al. 1969).

Sample range: CM B1 to CM 22A, SQ 1 to SQ 2, GL 10, T5.
Distribution: outer and mid-ramp.
Material: 10 specimens.

Sc_1 element

Synonymy:

1931 Prioniodus clarki Gunnell Plate 29 fig 8, page 247.
1941 Lonchodina clarki (Gunnell). Ellison Plate 20 figs 21, 27, 30, 31, page 116.
1952 Duboisella typica Rhodes Lonchodina component; Plate 128 (l), page 896.
1953 Lonchodina paraclarki Hass Plate 16 figs 15-16, page 83.
1957 Lonchodina c.f. projecta Ulrich and bassler. Bischoff Plate 1 fig 20, page 34.
1968 Lonchodina bischoffi Higgins and Bouckaert page 43.
1969 Lonchodina bolbosa Collinson and Druce. Rhodes et al. Plate 24 figs 12-14, page 140.
?1969 Lonchodina paraclarki Hass. Rhodes et al. Plate 24 fig 16, page 143.
?1969 Lonchodina transitans Collinson and Druce (nom. nud.). Rhodes et al. Plate 31 fig 14, page 144.
1972 Neoprioniodus conjunctus (Gunnell) Pl element; von Bitter Plate 12 fig 4, page 69.
1973 Idioprioniodus lexingtonensis (Gunnell) B_{1b} element; Baesemann Plate 3 fig 2, page 704.
1974 Lonchodina transitans Collinson and Druce (nom. nud.). Austin and Husri Plate 11 fig 3, Plate 14 fig 6.
?1974 Lonchodina paraclarki Hass. Austin and Husri Plate 11 fig 17.
1975 Idioprioniodus paraclaviger (Rexroad) clarki element; Nicoll and Rexroad Plate 3 figs 8-11, page 23.

Rexroad Plate 3 figs 8-11, page 23.

1976 Idioprioniodus healdi (Roundy) B_{2b} element; Norby Plate 9 figs 2, 5, 10, page 134.

1981 Lonchodina bischoffi Higgins and Bouckaert. Metcalfe Plate 16 fig 2.

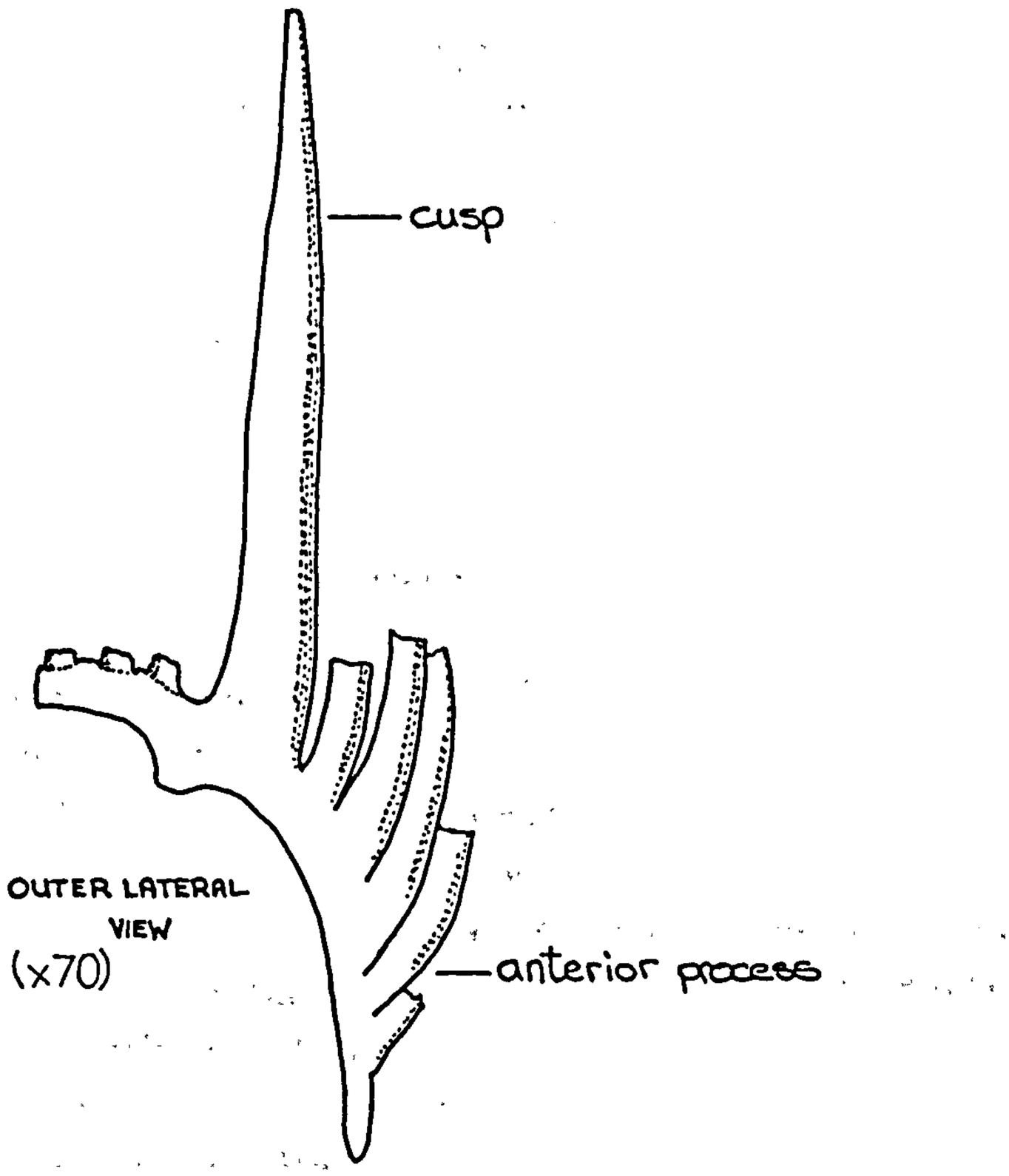
1981 Lonchodina transitans Rhodes et al. (sic). Metcalfe Plate 16 fig 3, page 31.

1981 Idioprioniodus typus Gunnell Sc element; Clark et al. Fig 98 (2c), page 149.

.p1987 Lonchodina sp. Austin Plate 13.4 fig 16 (and possibly fig 15).

1988 Idioprioniodus Pb element. Sweet text-fig 5.31, page 83.

Interpretive sketch 2.2.26 Idioprioniodus cf. healdi Sc_1 element (sample CM 24).



Description:

Digyrate lonchodinan element with relatively short anterior and posterior processes, and a very elongate and pointed cusp.

The anterior process (sensu Hass 1953) arches downwards in its proximal part and is straight in its distal part, where it tapers to a rounded point. It bears

curve around parallel to the cusp.

The cusp is massive, relatively straight and longer than either of the processes. On the outer side of the unit there is marked basal flaring of the cusp which continues posteriorly to form an asymmetrical basal cavity.

The posterior process is slightly shorter and shallower than the anterior process, and bears three relatively small and separate denticles which, although normal to the bar, curve toward the outer side. The angle subtended by the two processes varies, but is usually more than 90°.

Discussion:

Application of the apparatus notation of Sweet (In: Clark et al. 1981) is not fully established for Type 3 apparatuses such as that of Idioprioniodus. The above element (here designated Sc_1), is simply termed Sc by Klapper and Bergström (In: Clark et al. 1981), although the full apparatus is not illustrated. Morphologically this element appears to intergrade between the Pb and Sc_2 elements of this study. Sweet (1988) designates this element as the Pb, and comparisons are made with the "Pb" of Ellisonia and its successors; such that Idioprioniodus is cited as a possible ancestor for Ellisonia and Xaniognathus - central stocks for the Ellisoniidae and Gondolellidae respectively.

Sample range: CM 2 to CM 24.
Distribution: outer ramp.
Material: 9 elements.

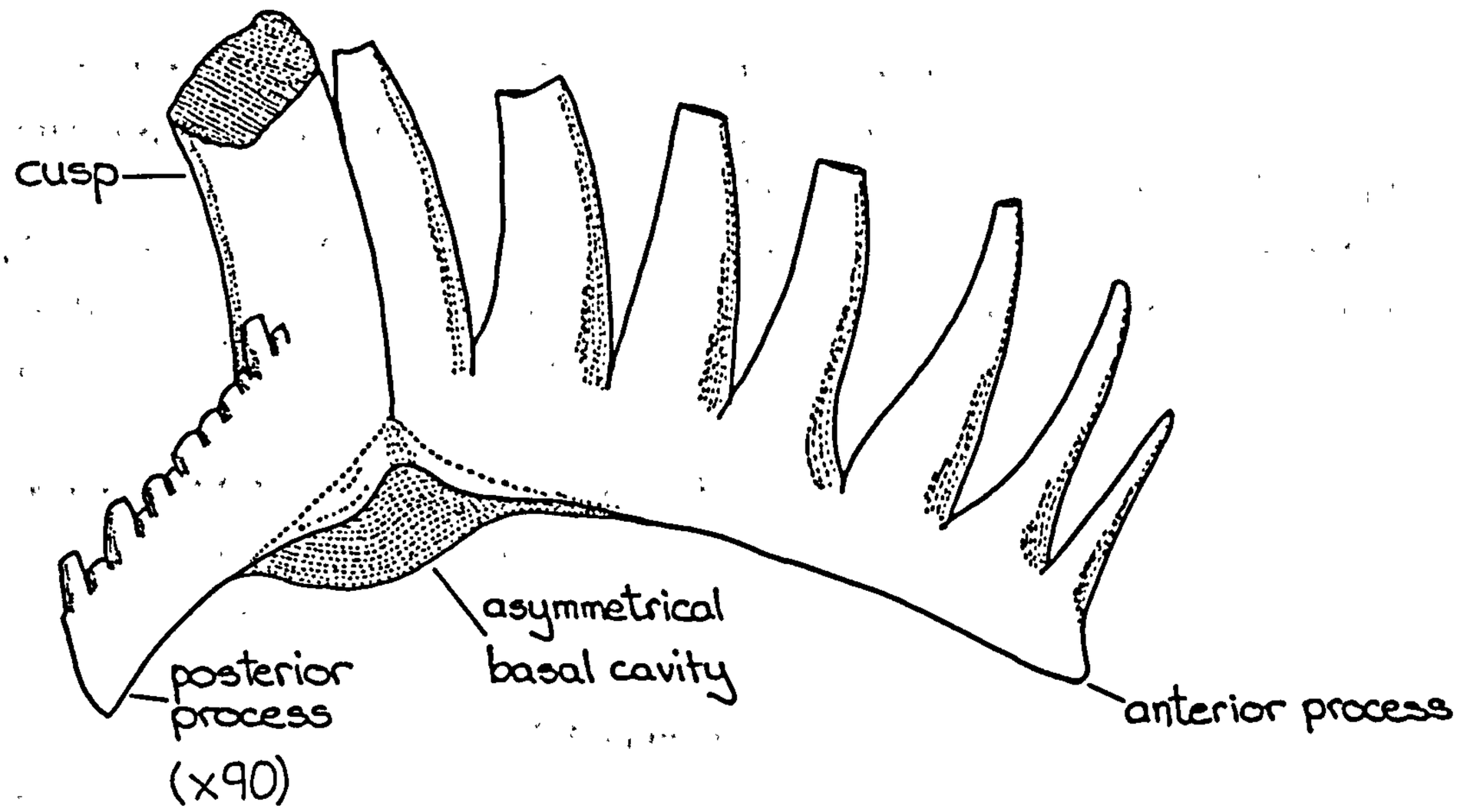
Sc_2 element

Synonymy:

p1926 Prioniodus sp. D Roundy Plate 4 fig 13 (only), page 11.
?1926 Polygnathus claviger Roundy Plate 4 figs 1-2, page 14.
?1941 Lonchodina? ponderosa Ellison Plate 20 figs 37-39, page 116.
p?1953 Geniculatus claviger Hass Plate 15 figs 13-14, page 77, (fig 1 represents a bar fragment which may be derived from a different element and fig 17 appears to be an Idioprioniodus Sb element).
1958 Lonchodina paraclaviger Rexroad Plate 4 figs 7-10, page 22.
1968 Lonchodina? sp. Higgins and Bouckaert Plate 1 fig 13, page 44.
1969 Lonchodina paraclaviger Rexroad . Rhodes et al. Plate 24 figs 15, 18, page 143.
p1969 Lonchodina furnishi Rexroad. Rhodes et al. Plate 24 fig 23 (only).
1972 Lonchodina? ponderosa Ellison. von Bitter Plate 12 fig 5, page 79.
1973 Idioprioniodus lexingtonensis (Gunnell) B_{3b} element; Baesemann Plate 3 figs 4-5, page 704.
1974 Lonchodina paraclaviger Rexroad. Austin and Husri Plate 11 figs 10-15.
1975 Lonchodina paraclaviger Rexroad. Higgins Plate 2 fig 9, page 60.

1975 Lonchodina paraclaviger Rexroad. Higgins Plate 2 fig 9, page 60.
1975 Idioprioniodus paraclaviger (Rexroad) paraclaviger element; Nicoll and Rexroad Plate 3 figs 16-17, page 25.
1976 Idioprioniodus healdi (Roundy) B_{2c} element; Norby Plate 9 figs 3, 8, page 137.
p1983 Idioprioniodus? conleyharpi Pb element; Chauff plate 3 figs 30, 33.
p1981 Geniculatus claviger (Roundy). Metcalfe Plate 12 fig 3 (only).

Interpretive sketch 2.2.27 Idioprioniodus cf. healdi Sc_2 element (sample SQ 1).



Description:

Stocky digyrate lonchodinan element with laterally thickened bars, a prominent conical cusp and an asymmetrical basal cavity.

The anterior process (sensu Rexroad 1958) is comparatively long and thickened, and more or less straight. It bears six to eight large, discrete, laterally compressed denticles (although in mature specimens there is some fusing toward the base). The denticles may be curved slightly inwards and posteriorly.

The cusp is usually slightly larger than the bar denticles, and often curves outwards and posteriorly (although in some specimens it may be relatively straight). There is an extension of the basal margin on the outer side, beneath the cusp, and a slight lateral flaring - to produce an asymmetrical and curved basal cavity. The general lack of flaring is useful in distinguishing this from the Sb and Sc elements.

the posterior process is one-third to half the length of the anterior process, and typically bears four or more small, laterally compressed, discrete denticles. It is often less thickened than the anterior process, and the two subtend an angle of between 90° and 120° in the horizontal plane and approximately 150o in the vertical.

Discussion:

A series of ontogenetic stages can be seen in the present material. As elements mature the basal cavity becomes less elongate, the processes (particularly the anterior) become stouter and more square in cross-section and overhanging shoulders may develop to produce a wide flattened platform, which over-grows the cup. Also, the anterior bar denticles become fused for their lower third.

The material recovered in the present study suggests there to be a continuous gradation of forms between mature Idioprioniodus Sc_2 elements and many of those previously assigned to Geniculatus claviger s.f. On the basis of the original diagnosis of Hass (1953) G. claviger s.f. is distinguished here by the excessive thickening of the anterior bar, its continually tapering outline in upper view, and the weak node-like denticles.

Sample range: CM 2 to CM 29, SQ 1, T5, CB 2.
Distribution: outer and mid-ramp.
Material: 21 specimens.

Sd element

Synonymy:

1926 Prioniodus sp. A Roundy Plate 4 fig 9, page 11.
1926 Prioniodus sp. C Roundy Plate 4 fig 11, page 11.
1933 Idioprioniodus typus Gunnell Plate 31 fig 47, page 265.
1933 Prioniodus? galesburgensis Gunnell Plate 31 fig 12, page 267.
1941 Ligonodina typa (Gunnell). Ellison Plate 20 figs 8-11, page 114.
1952 Duboisella typica Rhodes Ligonodina component; Plate 128 (a), page 896.
1953 Ligonodina roundyi Hass Plate 15 figs 5-9, page 82.
1958 Ligonodina roundyi Hass. Rexroad Plate 3 figs 1-4, page 21.
1968 Ligonodina typa (Gunnell). Higgins and Bouckaert Plate 2 fig 11, page 42.
1969 Ligonodina roundyi Hass. Rhodes et al. Plate 26 figs 13-14, 16, page 137.
1972 Neoprioniodus conjunctus (Gunnell) Hi element; von Bitter Plate 12 fig 3, page 69.
1973 Idioprioniodus lexingtonensis (Gunnell) B_{1a} element; Baesemann Plate

3 fig 1, page 703.

1974 Ligonodina typa (Gunnell). Varker and Austin Plate 6 fig 13.

1974 Ligonodina roundyi Hass. Austin and Husri Plate 14 figs 5, 8, 11.

1975 Ligonodina roundyi Hass. Higgins Plate 3 fig 14, page 58.

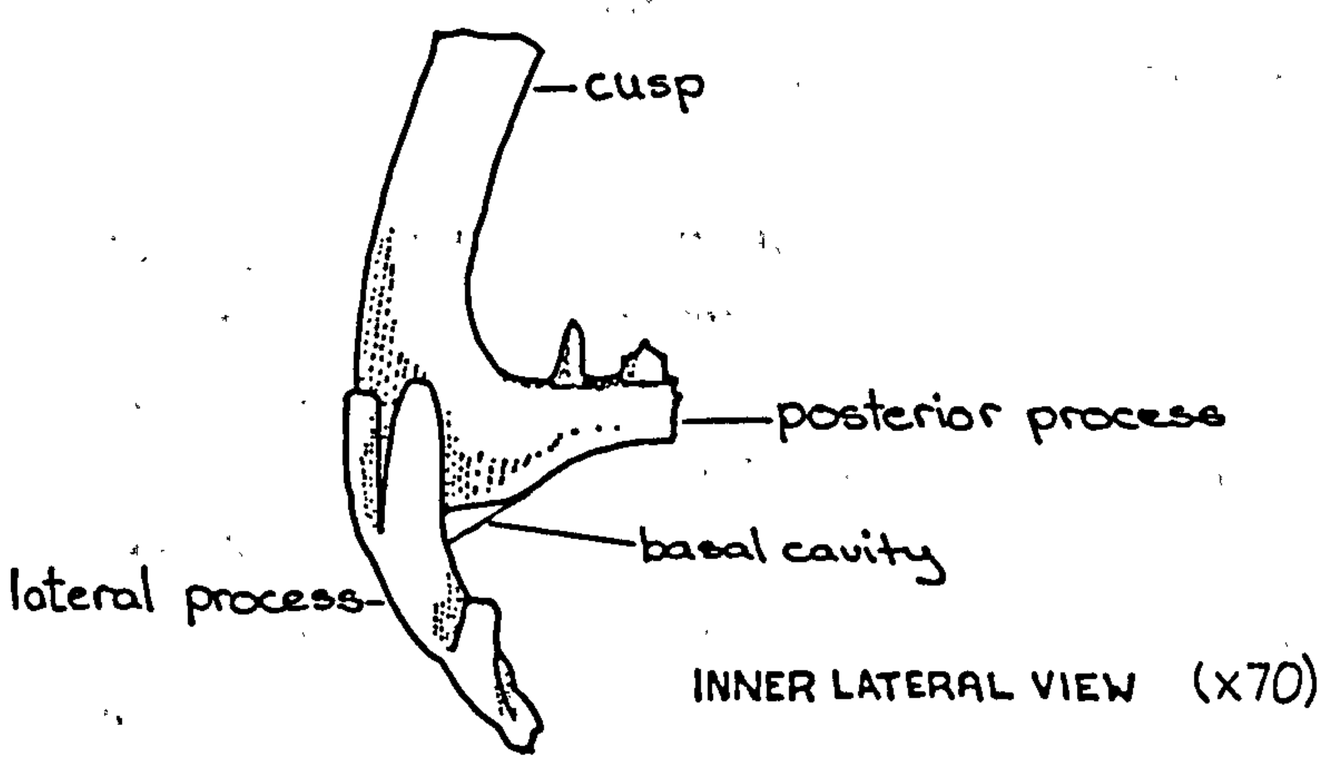
1975 Idioprioniodus paraclaviger (Rexroad) typus element. Nicoll and Rexroad Plate 3 figs 4-7, page 23.

1976 Idioprioniodus healdi (Roundy) B_1 element; Norby Plate 9 figs 1, 14, page 132.

non1981 Ligonodina roundyi Hass. Metcalfe Plate 15 figs 11-12, (probably Sd elements of Kladognathus tenuis).

p?1981 Idioprioniodus sp. aff. I. healdi (Roundy). Rexroad Plate 2 fig 7, page 11.

Interpretive sketch 2.2.28 Idioprioniodus cf. healdi Sd element (sample CM 37).



Description:

Ligonodinan element with a massive cusp, a strong downwardly directed lateral process and a relatively weak posterior process. The cusp is large and curved posteriorly, it is increasingly more rounded (in section) toward the distal tip and towards the base there is a groove on the posterior edge. The basal cavity is situated directly beneath the cusp and has slightly flared margins, particularly on the outer side. A groove extends from the basal cavity along the underside of both processes.

The posterior process is markedly thinner than the cusp in lateral view and bears two or three very feeble, discrete denticles. The lateral process continues down from the cusp in the form of an anticusp with little or no break in lateral profile. It is recurved posteriorly and bears between three and five large discrete denticles which point upwards. In anterior view the angle at which the lateral process diverges from the cusp varies between 30° and 40°.

Discussion:

Pristine specimens of ligonodinan elements are rare and there is a larger than usual degree of interpretation in the species designations. It is hoped that future studies, involving bulk resampling, will help to clarify the situation.

Sample range: CM 17 to CM 42 (only indeterminate ligonodinan fragments were recovered from any of the other sections).
Distribution: outer ramp, (but see above).
Material: 7 specimens

2.2g Genus: Kladognathus Rexroad 1958
Type species: Cladognathus prima Rexroad 1957
Synonymy: 1957 Cladognathus Rexroad.
1958 Kladognathus Rexroad.
1961 Cladognathodus Rexroad and Collinson.
1963 Magnilaterella Rexroad and Collinson.

Remarks:

The name Cladognathus Rexroad was found to be preoccupied by Cladognathus Burmeister 1847, a genus of the Coleoptera (an insect order which includes beetles). Therefore, Rexroad (1958) proposed the new name Kladognathus. However Ziegler (In: Rexroad and Collinson 1958) suggested that changing the initial C to a K was invalid under the rules of the International Code of Zoological Nomenclature. Accordingly, Rexroad and Collinson (1961) proposed Cladognathodus to replace the earlier terms. Article 56A of the I.C.Z.N. states that the changing of a single letter of a generic name does represent a valid distinction between two genera, hence Kladognathus Rexroad 1958 is now taken as the senior synonym.

Horowitz and Rexroad (1982) included the M, Sa and Sd elements discussed below in their tentatively proposed species K. levis. The form species Magnilaterella robusta s.f. Rexroad and Collinson 1963 was cited as the probable Sb element (being vicariously shared with all the described species of Kladognathus). However the magnilaterellan element recovered in this study is closer to Magnilaterella clarkei s.f. Rhodes Austin and Druce 1969. This explains the insertion of aff. in the binomen below (following the precepts of Bengtson 1988).

Kladognathus aff. levis (Branson and Mehl 1941)

Plate 6 figs 6-11.

M element

Synonymy: (see comments under Idioprioniodus M element).

p1900 Prioniodus peracutus Hinde Plate 10 fig 22 (only), page 343.

.1934 Prioniodus barbatus Branson and Mehl Plate 23 figs 19-20, page 288.

1934 Prioniodus corniger E.R. Branson Plate 28 fig 2, page 329.

1941 Prioniodus scitulus Branson and Mehl Plate 5 figs 5-6, page 173.

1949 Prioniodus spp. Youngquist and Miller Plate 101 figs 9-10, 14, page 62.

.1956 Prioniodina barbata (Branson and Mehl). Bischoff and Ziegler Plate 13 figs 19-20, page 160.

1957 Prioniodus cassilaris (Branson and Mehl). Bischoff Plate 5 figs 27-31, page 46.

1957 Neoprioniodus erectus Rexroad Plate 2 figs 23, 25, page 34.

1957 Neoprioniodus scitulus (Branson and Mehl). Rexroad Plate 2 figs 22, 26, page 35.

1957 Neoprioniodus striatus Rexroad Plate 2 figs 11-12, page 35.

1957 Neoprioniodus sp. B. Rexroad Plate 2 fig 24, page 36.

.1969 Neoprioniodus barbatus (Branson and Mehl). Rhodes et al. Plate 21 figs 4-7, page 158.

1969 Neoprioniodus peracutus (Hinde). Rhodes et al. Plate 21 figs 12-15, page 161.

1969 Neoprioniodus scitulus (Branson and Mehl). Rhodes et al. Plate 22 figs 9-10, 12, page 162.

1973 Neoprioniodus scitulus (Branson and Mehl). Austin and Aldridge Plate 2 fig 3.

.1974 Neoprioniodus barbatus (Branson and Mehl). Austin and Husri Plate 15 fig 1.

1974 Neoprioniodus scitulus (Branson and Mehl). Austin and Husri Plate 12 figs 12-13, 17.

1975 Neoprioniodus peracutus (Hinde). Higgins Plate 3 figs 1-4, 6, page 67.

1976 Neoprioniodus peracutus (Hinde) s.f. Norby Plate 20 figs3-5, 10-13, page 193.

.1981 Neoprioniodus barbatus (Branson and Mehl). Metcalfe Plate 18 fig 11.

1981 Neoprioniodus peracutus (Hinde). Metcalfe Plate 18 fig 10.

1981 Neoprioniodus scitulus (Branson and Mehl). Metcalfe Plate 18 fig 4.

vic1981 Kladognathus spp. M element; Rexroad Plate 2 figs 30-32, page 11.

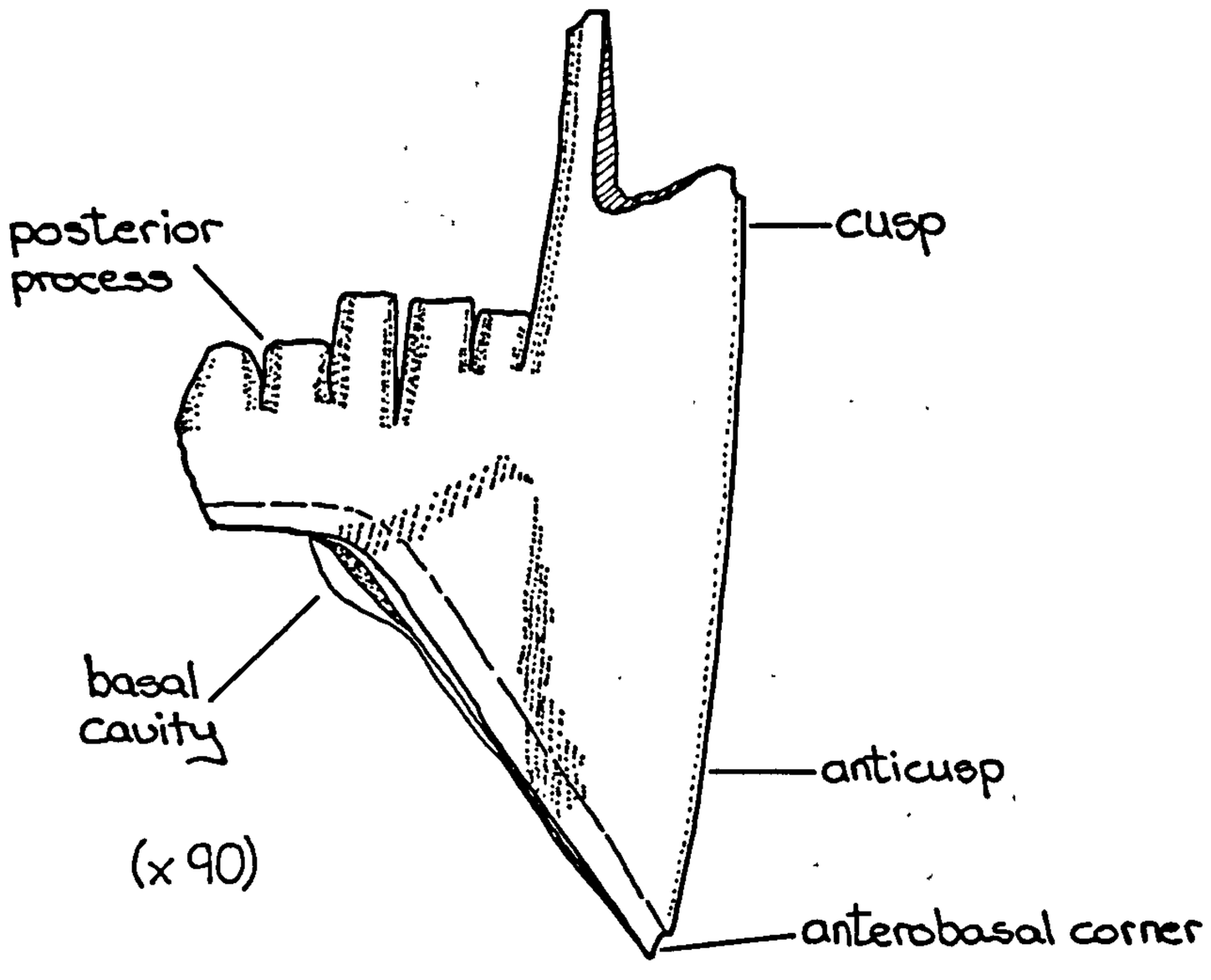
.1984 Neoprioniodus barbatus (Branson and Mehl). Austin and Davies Plate 3 fig 1.

vic1985 Kladognathus spp. M element; Rexroad and Merrill Plate 1 fig 21.

.1987 Neoprioniodus sp. cf. barbatus (Branson and Mehl). Austin Plate 13.4 figs 22-23.

1988 Kladognathus M element; Sweet text-fig 5.31.

Interpretive sketch 2.2.29 Kladognathus aff. levis M element (sample SQ 3).



Description:

Robust neoprioniodontan dolabrate element with a large, erect and laterally flattened cusp. There is a strong, triangular anticusp, and a more or less straight, blade-like denticulate posterior process.

In side view the anterior margin of the cusp is straight or marginally convex; it is rarely recovered complete, but tapers to a fine, increasingly flattened point in pristine specimens. The anterior margin of the cusp extends downwards to form a distinctive, plough-like anticusp (see interpretive sketch 2.2.29). The lateral profile of the anterobasal corner is variable and may be sharply pointed (as above), or slightly bulbous, and there is a range of variation between these two end members.

The lower margin of the anticusp extends towards the posterior at approximately 45° to the horizontal, and may be straight in profile or slightly convex. One side of the cusp is more flattened than the other; and on the flattened side there is a degree of flaring (which encloses the basal cavity) on the lateral face of the anticusp.

The posterior process is relatively straight and blade-like, and bears between five and ten discrete (or closely packed) denticles. The basal cavity continues as an excavated groove along the underside of the posterior process and the anticusp.

Discussion (see comments under Idioprioniodus M element):

Rexroad (1958) described this as a somewhat variable element, and noted differences in length of anticusp, outline of lower margin of the anticusp and the height and thickness of the posterior bar. Younger specimens were seen to have more flared lateral margins to the anticusp, and a more excavated underside than mature specimens. There is also ontogenetic variation in the shape and length of the anticusp.

Sample range: CM 14 to CM 31, SQ 3, GL 2, T 5, PE 1.
Distribution: outer to proximal mid-ramp.
Material: 14 specimens.

Sa element

Synonymy:

1957 Hibbardella n.sp. Rexroad Plate 1 fig 19, page 31.
?1957 Trichonodella fragilis Rexroad Plate 4 figs 6-7, page 40.
1958 Hibbardella milleri Rexroad Plate 2 figs 13-16, page 6.
1969 Hibbardella (Hibbardella) milleri Rexroad. Rhodes et al. Plate 25 figs 23-25, page 113.
1969 Hibbardella fragilis Rexroad. Thompson and Goebel Plate 2 figs 22-23, page 25.
1974 Hibbardella (Hibbardella) milleri Rexroad. Austin and Husri Plate 13 fig 16.
1976 Hibbardella milleri Rexroad. Norby Plate 20 figs 16-20, page 184.
?1981 Hibbardella milleri Rexroad. Metcalfe Plate 14 fig 2.
vic1981 Kladognathus spp. Sa element; Rexroad Plate 2 figs 22-23.
vic1985 Kladognathus spp. Sa element; Rexroad and Merrill Plate 1 fig 30.
1988 Kladognathus Sa element; Sweet text-fig 5.31.

Description:

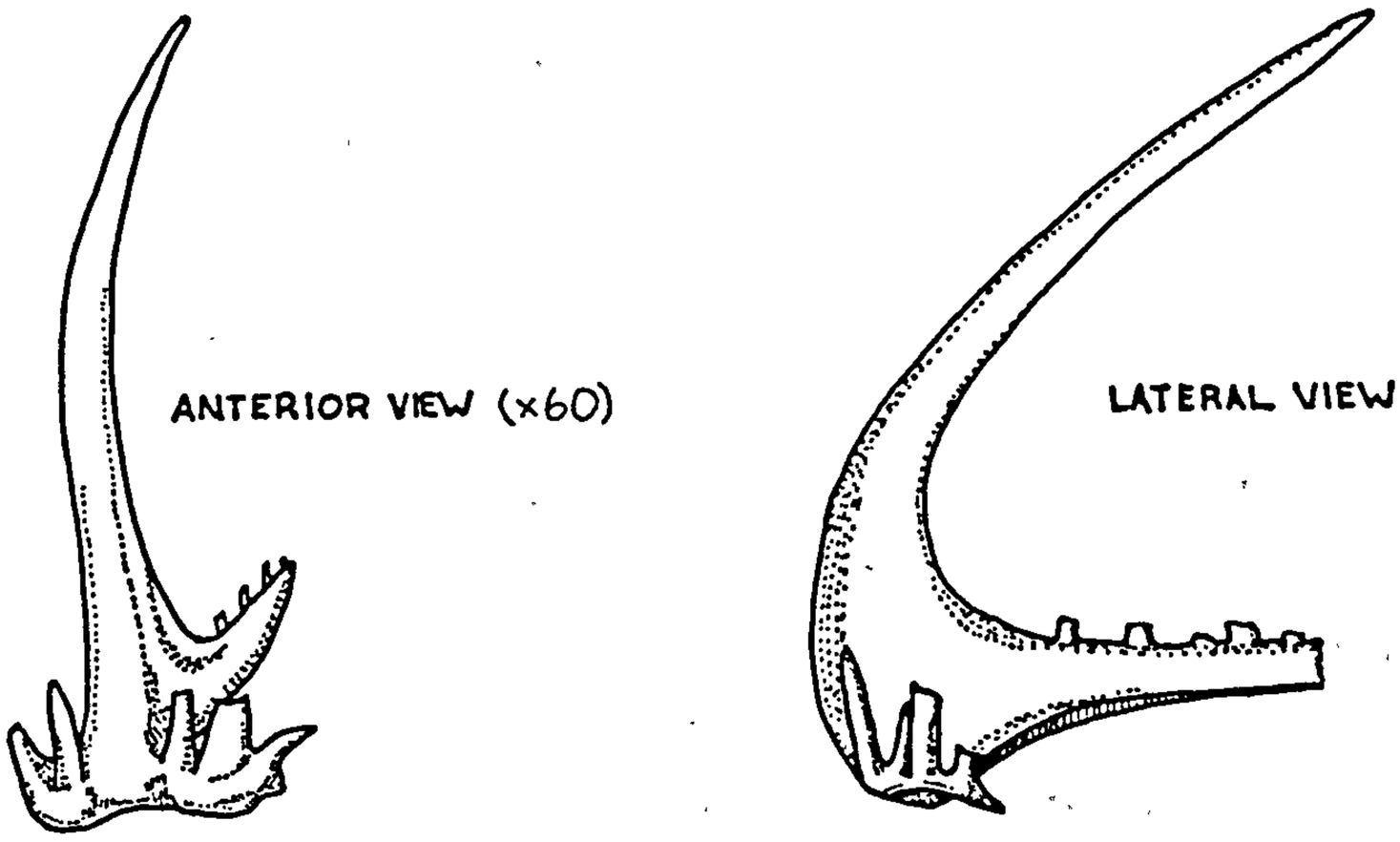
Hibbardellan alate element with an elegant elongate cusp and relatively short, subhorizontal lateral processes.

The cusp is curved posteriorly, with the maximum curvature toward the base. In mature specimens a slight groove may be developed on the posterior side of the cusp, near its base. The upper margin of the posterior process is straight in side view and bears five-or-so feeble, isolated denticles. The lower margin curves downwards anteriorly to form a blunt anterobasal corner with the

anterior margin of the cusp.

The nature of the lateral processes is the most distinctive feature of the unit. These are short, bear three or four erect and discrete denticles and may have spatulate or sharply pointed tips. The processes curve posteriorly to form an angle of between 85° to 70° with the posterior process. In anterior view the arch formed by the two lateral processes is extremely shallow and rounded.

Interpretive sketch 2.2.30 Kladognathus aff. levis Sa element (sample CM 23).



Discussion:

Rexroad (1958) notes that some specimens may have a denticle developed anterior to the cusp, and records a slightly more accentuated anterior arch than is seen in the present study.

Sample range: CM 23 to CM 40, GL 14, T 5.
Distribution: outer and mid-ramp.
Material: 5 specimens.

Sb element

Synonymy:

p1900 Polygnathus convexus Hinde Plate 9 fig 7, page 342.
p1928 Lonchodus convexus (Hinde). Holmes Plate 6 fig 14, page 14.
1960 "Gen. et sp. nov?" Clarke Plate 2 figs 10, 12-13, page 16.
1969 Magnilaterella clarkei Rhodes Austin and Druce Plate 23 figs 11-13, page 146.
1981 Magnilaterella clarkei Rhodes et al. Metcalfe Plate 16 figs 5-6. >pa

Description:

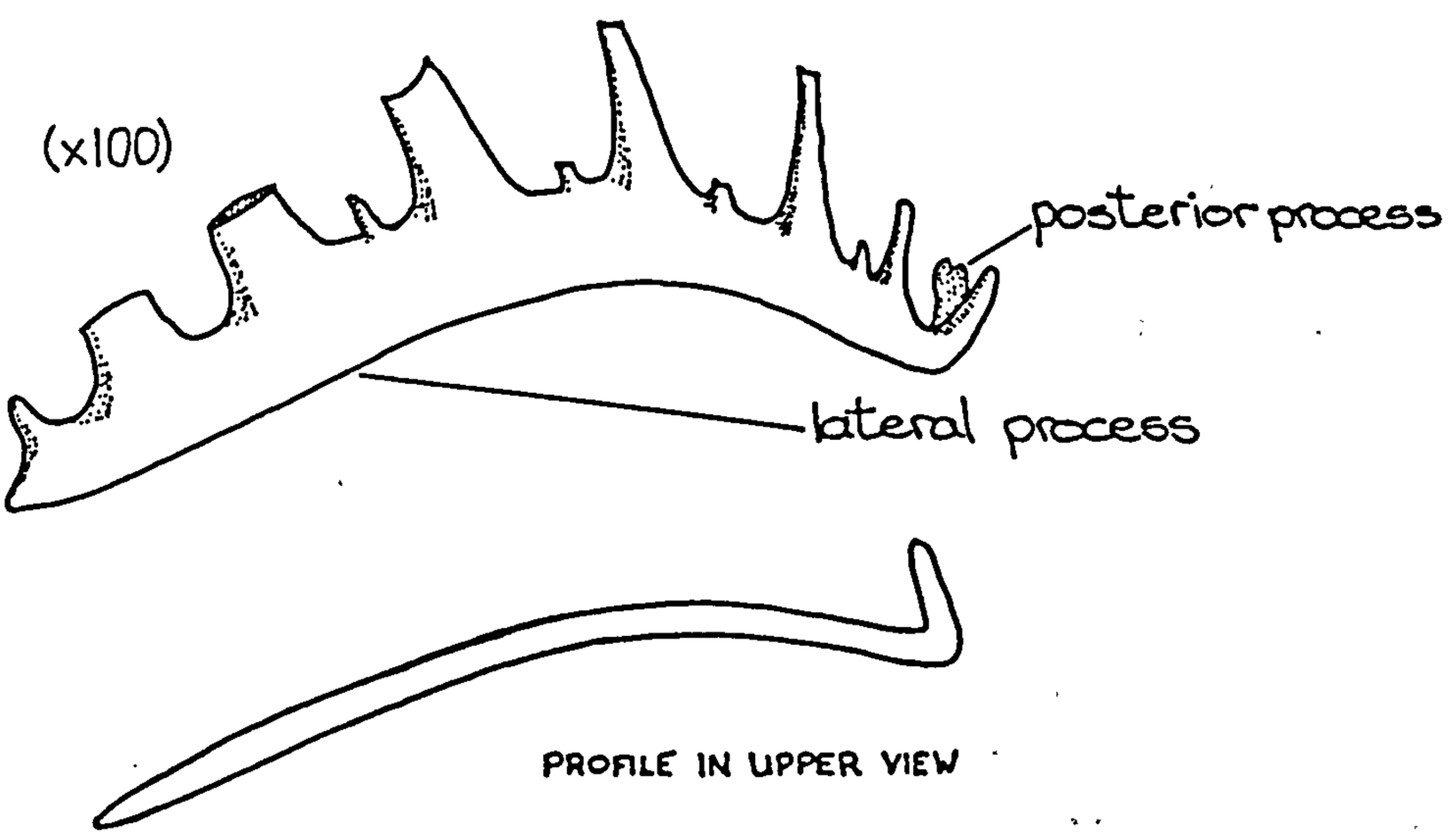
Bipennate magnilaterellan element with a relatively long lateral process (sensu Rexroad and Collinson 1963), which subtends an acute angle of approximately 30° with the short, spatulate posterior process.

The elongate lateral process is arched in side view and also slightly flexured in upper view. In side view the lower blade-like part of the process is deepest in its mid-third, where the denticles also tend to be largest. The process bears four to seven large, discrete denticles which may be angled toward the distal end of the bar. Over the proximal two thirds of the process, minor denticles alternate with the large denticles already described. These are six to seven times smaller than the large denticles. There is a weakly developed triangular denticle above the bluntly-triangular distal tip of the process. At the proximal end of the process, at the junction with the posterior process, a conical denticle is developed which is approximately half the size of the largest bar denticle.

The posterior process is short (approximately six times shorter than the lateral process), and bears three-or-so small denticles. The process is strongly flexured toward the lateral process and may also be twisted in side view. The distal end of the posterior process is spatulate.

In some specimens there is a conspicuous zone of recessive margin on the underside, particularly toward the inner-side. A slit extends along the underside of the lateral process, and continues along the posterior process although reduced in width.

Interpretive sketch 2.2.31 Kladognathus aff. levis Sb element (sample CM 7).



Discussion:

Supportive evidence for including the above in the Kladognathus apparatus comes from the fact that specimens were only recovered from samples in which the Kladognathus Sd element also occurred (see below). Rhodes et al. (1969) note that the depth of the lateral bar and the development of recessive margin are variable features in this form. The diagnosis and type description of Magnilaterella clarkei s.f. is somewhat ambiguous due to a series of misprints in which the lateral bar (sensu Rexroad and Collinson 1963) is termed the posterior bar.

Sweet (1988) suggests that magnilaterellan elements are more likely to have occupied P positions in the apparatus, rather than the Sb position suggested by Rexroad (1981); in which case the Sb position would be filled by species of Lambdagnathus s.f. or Kladognathus s.f. However, in the present study no elements assignable to either of these form genera have been recovered, and the elongate magnilaterellan component looks more like an Sb element than a P element. Hence the designation of Rexroad (1981) is retained.

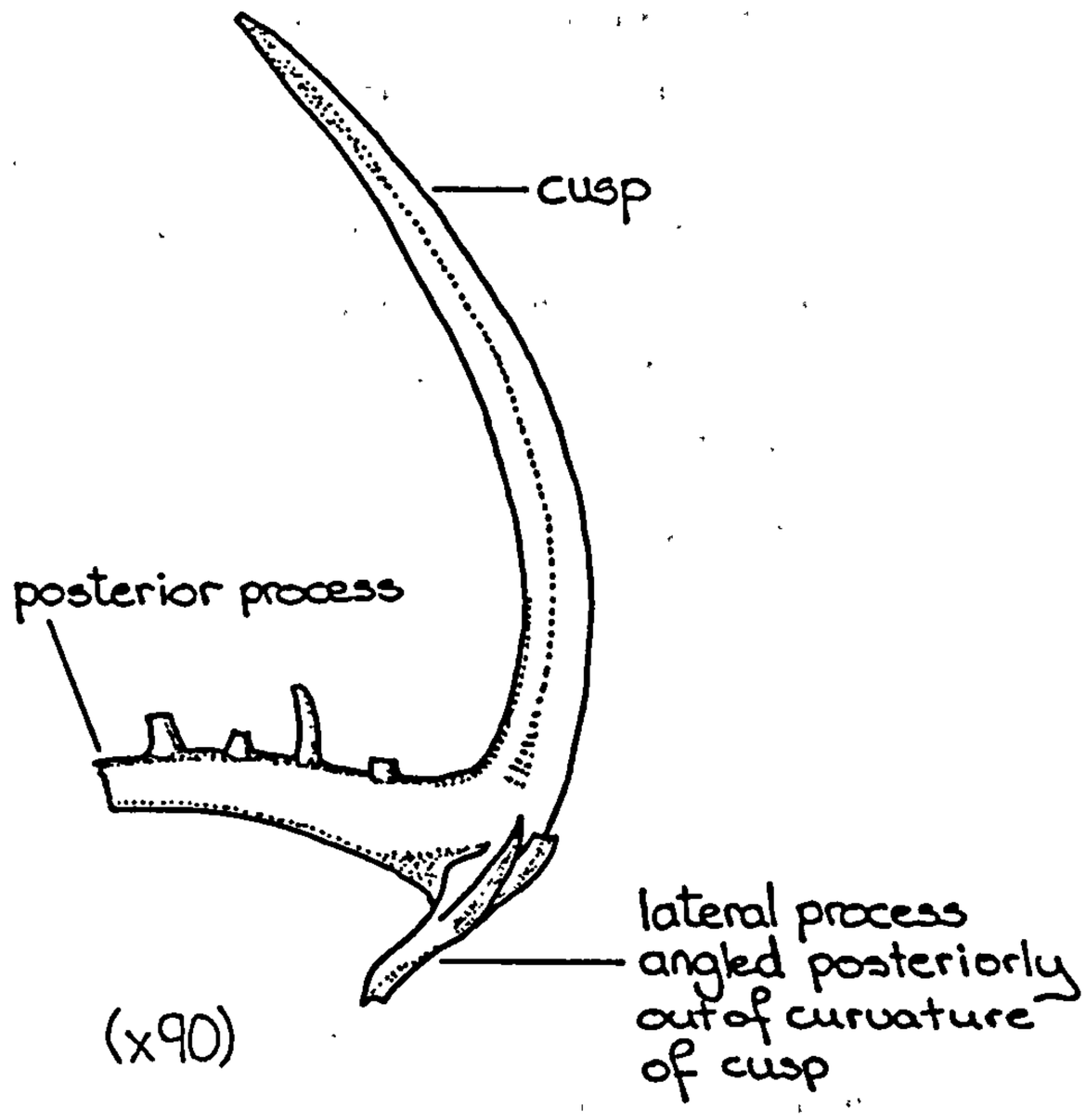
Sample range: CM 2 to CM 39.
Distribution: outer ramp.
Material: 6 specimens.

Sd element

Synonymy:

1941 Ligonodina levis Branson and Mehl Plate 6 fig 10, page 185.
1957 Ligonodina obunca Rexroad Plate 1 figs 22-23, page 32.
1958 Ligonodina obunca Rexroad. Rexroad Plate 3 figs 7-8, page 21.
1961 Ligonodina levis Branson and Mehl. Rexroad and Burton Plate 141 figs 7-8, page 1154.
1963 Ligonodina levis Branson and Mehl. Rexroad and Collinson Plate 2 figs 24-25, page 11.
1969 Ligonodina levis Branson and Mehl. Rhodes et al. Plate 26 figs 15, 17, page 134.
1973 Ligonodina levis Branson and Mehl. Austin and Aldridge Plate 1 fig 14.
1974 Ligonodina levis Branson and Mehl. Varker and Austin Plate 6 fig 12.
p1975 Ligonodina levis Branson and Mehl. Nicoll and Rexroad Plate 6 fig 14 (only).
?1981 Ligonodina levis Branson and Mehl. Metcalfe Plate 15 fig 10 (illustration does not clearly show lateral process)
1981 Kladognathus tenuis (Branson and Mehl) Sc element ß morphotype. Rexroad Plate 2 fig 21, page 13.

Interpretive sketch 2.2.32 Kladognathus aff. levis Sd element (sample CM 2).



Description:

Bipennate ligonodinan element with a large elongate posteriorly curved cusp, a strongly developed lateral process and a relatively small and weak posterior process. The unit is distinguished from the Idioprioniodus Sd element in side view by the anterior lateral process being angled posteriorly out of line of the cusp.

The massive, elongate cusp curves toward the posterior such that the sharply pointed distal portion is at approximately 45° to the posterior process. In mature specimens a shallow groove extends down the posterior side of the cusp in its proximal portion.

The anterior lateral process is of roughly the same thickness as the cusp at its proximal end but tapers rapidly to a flattened, adenticulate spatulate termination. The lateral process projects downwards and outwards at approximately 45°. It is approximately one fifth the length of the cusp, is curved posteriorly and may be slightly flexured either inwards or outwards. There are usually three small but elongate discrete denticles on the lateral process, and these denticles are often angled anteriorly but curved in symmetry with the cusp. In inner side profile there is characteristically little or no development anterior

of the cusp.

The posterior process is shorter than the cusp, quadrate in section and bears three or four well-separated, stump-like denticles.

Discussion:

A continuous evolutionary sequence can be traced from Ligonodina levis s.f. to L. tenuis s.f to Kladognathus primus s.f. to K. mehli s.f. (Rexroad 1981, Horowitz and Rexroad 1982). This is reflected by a progressive increase in development of the lateral process anterior of the cusp.

Although Rexroad (1981) designated this unit as an Sc element, it is here termed Sd due to its marked similarity to the Sd element of Idioprioniodus cf. healdi (see above); which suggests that the two elements occupied analogous positions within their respective apparatuses (see section 1.2b for an explanation of the terminology).

Sample range: CM 2 to CM 30.
Distribution: outer ramp.
Material: 3 specimens.

2.2h Genus: Lochriea Scott 1942
Type species: Spathognathodus commutatus Branson and Mehl 1941
Synonymy: 1942 Lochriea Scott.
1970 Paragnathodus Meischner (nom. nud.).

Lochriea commutata (Branson and Mehl 1941)

Plate 7 figs 1-6.

Pa element

Synonymy:

1941 Spathognathodus commutatus Branson and Mehl Plate 19 figs 1-4, page 98.
1942 Lochriea montanaensis Scott spathognath component; Plate 37 figs 1-7, Plate 38 figs 2-4, 6-7, 12, Plate 40 figs 13, 15, 19, text-fig 1 (c), page 298.
1949 Spathognathodus pellaensis Youngquist and Miller Plate 101 fig 6, page 622.
1953 Gnathodus inornatus Hass Plate 14 figs 9-11, page 80.
1956 Spathognathodus inornatus Hass. Elias Plate 3 figs 37-39, page 119.
1957 Gnathodus commutatus commutatus (Branson and Mehl). Bischoff Plate 4 figs 2-6, 15, page 23.
1957 Spathognathodus cf. S. commutatus Branson and Mehl. Rexroad Plate 3 figs 23-24, page 38.
1960 Spathognathodus commutatus Branson and Mehl. Clarke Plate 3 figs

4-5, page 19.

1961 Gnathodus commutatus (Branson and Mehl) var. commutatus Bischoff. Higgins Plate 10 fig 6, text-fig 1a, page 212.

1961 Gnathodus commutatus (Branson and Mehl). Rexroad and Burton Plate 139 figs 1-3, page 1153.

1964 Gnathodus commutatus pellaensis Rexroad and Furnish Plate 111 fig 3, page 671.

1965 Gnathodus commutatus (Branson and Mehl) nagatoensis Igo and Koike Plate 9 figs 9-13, page 89.

1967 Gnathodus scotiaensis Globensky Plate 58 figs 2-7, 10, 12, page 441.

1968 Gnathodus commutatus (Branson and Mehl). Higgins and Bouckaert Plate 2 fig 5, page 30.

1969 Gnathodus commutatus (Branson and Mehl). Rhodes et al. Plate 19 figs 9-12, page 95.

1970 Paragnathodus commutatus (Branson and Mehl). Meischner text-figs 2-3, page 1173.

1973 Gnathodus commutatus pellaensis (Youngquist and Miller). Merrill, Plate 3 figs 58-59, page 310.

1974 Gnathodus commutatus commutatus (Branson and Mehl). Austin and Husri Plate 3 figs 1-3, 12.

1974 Gnathodus commutatus (Branson and Mehl). Varker and Austin Plate 6 fig 21.

1975 Paragnathodus commutatus (Branson and Mehl). Higgins Plate 7 figs 7-9, 11, 13, 16, 20-21, page 70.

1976 Lochriea commutatus (Branson and Mehl) P element; Norby Plate 11 figs 1-10, 12-14, 16, page 146.

1981 Gnathodus commutatus (Branson and Mehl). Metcalfe Plate 7 figs 6-7, page 21.

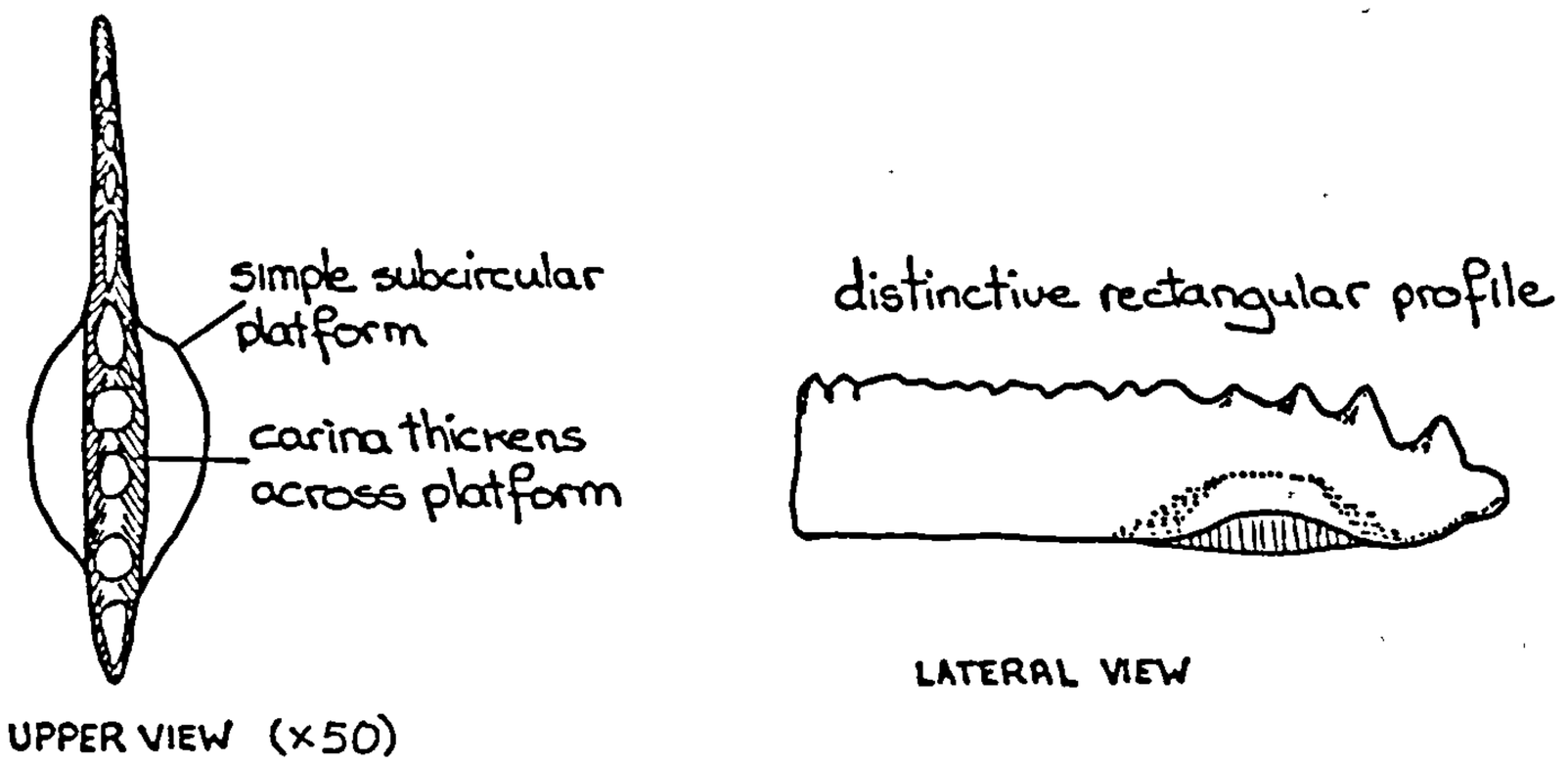
1984 Paragnathodus commutatus (Branson and Mehl). Austin and Davies Plate 3 figs 26, 31.

1985 Lochriea commutata (Branson and Mehl). Varker and Sevastopulo Plate 5.5 figs 11-12, page 200.

1985 Lochriea commutata (Branson and Mehl). Higgins Plate 6.1 fig 10, page 222 (due to a printing error the caption is listed under Plate 6.3).

1988 Lochriea commutatus (Branson and Mehl) Pa element; Sweet text-fig 5.51 (lower-left illustration), page 111.

Interpretive sketch: 2.2.33 Lochreia commutata Pa element (sample CM 24).



Description:

carminiscaphate platform element with anterior free blade comprising half to two-thirds the total length of the unit. In lateral view the upper and lower margins of the free blade are essentially straight and parallel (unlike Gnathodus), giving a distinctively rectangular profile. It is often hard to distinguish individual blade denticles due to their degree of fusion.

In upper view the blade thickens posteriorly and forms a high carina above a simple subsymmetrical platform which lacks ornamentation. In upper view the platform outline is highly variable, ranging from sub-circular to subelliptical; in detail the platform is always asymmetrical.

The distinctive, thickened carina may extend beyond the posterior margin of the platform, and usually thins toward its posterior termination.

Discussion:

Metcalfe (1981) describes this unit as highly variable, and reports some strongly curved specimens (not recovered in this study).

Sample range: CM 15 to CM 43, T5, PE 1.
Distribution: outer and mid-ramp.
Material: 23 specimens.

Pb element

Synonymy:

1957 Ozarkodina recta Rexroad Plate 2 figs 5-6, page 36.

?1957 Subbryantodus stipans Rexroad Plate 4 fig 1, page 39.

1961 Subbryantodus subaequalis Higgins Plate 12 fig 15, text-fig 6, page 218.

1968 Subbryantodus subaequalis Higgins. Higgins and Bouckaert Plate 3 figs 1-2, page 47.

?1969 Prioniodina stipans (Rexroad). Rhodes et al. Plate 28 figs 7- 10, page 198.

1969 Prioniodina subaequalis (Higgins). Rhodes et al. Plate 28 figs 1-4, page 198.

?1974 Prioniodina stipans (Rexroad). Austin and Husri Plate 12 figs 4, 7-8.

?1975 Subbryantodus stipans Rexroad. Higgins Plate 5 figs 14-15, page 74.

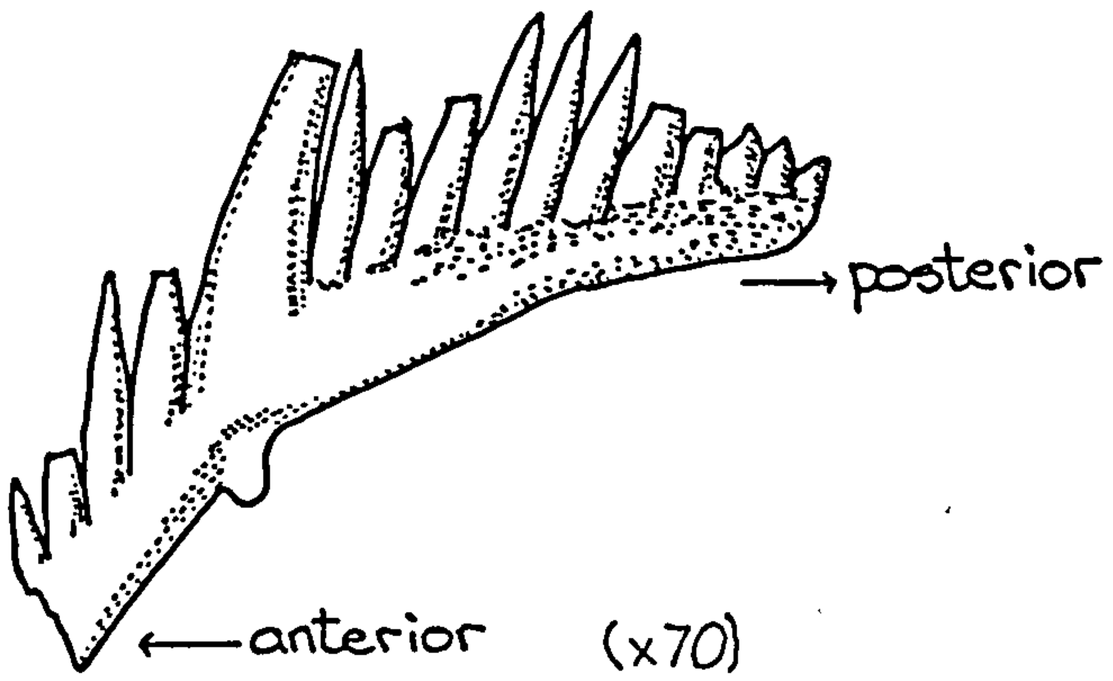
1975 Subbryantodus subaequalis Higgins. Higgins Plate 5 fig 17, page 74.

1976 Lochreia commutatus (Branson and Mehl) O element; Norby Plate 11 fig 11, Plate 12 figs 9-13, page 150.

1981 Subbryantodus subaequalis Higgins. Metcalfe Plate 19 fig 17.

1988 Lochreia commutatus (Branson and Mehl) Pb element; Sweet text-fig 5.51 (second from left), page 111.

Interpretive sketch 2.2.34 Lochreia commutata Pb element (sample CM 7, see discussion below).



Description:

Rather variable ozarkodinan angulate element. The unit is relatively elongate, thin and laterally compressed; with a straight but downwardly deflected anterior process and a curved and slightly arched posterior process. The cusp is two to three times wider than any of the denticles and slightly taller. It is nearly erect but leans toward the posterior, and at its base there may be a slight lateral flaring to form a flange on the edge of the basal cavity (particularly on the inner side). The denticles of both bars tend to be discrete (except in mature or gerontic specimens), especially on the posterior process. In one of the four recovered specimens the denticles of the posterior process alternate in size, and in another the posterior bar is markedly curved in upper view. The denticles of both processes are inclined slightly posteriorly.

Discussion:

Norby (1976) remarks on the high degree of variation exhibited by this element and suggests the form genus Ozarkodina recta Rexroad s.f. may represent the Pb elements of gerontic individuals. Norby (1976) also comments on the difficulties in recovering this element, probably due to its delicate nature.

On the basis of the material recovered in this study, a broad definition for this element has had to be adopted. In light of the anomolously early occurrence of the strongly curved Pb element in sample CM 7 (interpretive sketch 2.2.34 and Plate 7 fig 4), future studies may show it to be part of a different species (e.g. one of the homopunctatus group, see section 2.2d), which has been wrongly included in synonymy here.

Sample range: CM 7?, CM 31, PE 1.
Distribution: outer and mid-ramp.
Material: 4 specimens.

M element

Synonymy:

1942 Lochriea montanaensis Scott prioniod component; Plate 39 fig 9, Plate 40 fig 12, page 299.
1953 Prioniodus singularis Hass Plate 16 fig 4, page 88.
1956 Prioniodus cf. singularis Hass. Elias Plate 2 fig 45, page 112.
1956 Prioniodus roundyi var. dividen Elias Plate 2 figs 39-41, page 110.
1956 Prioniodus roundyi var. parviden Elias Plate 2 figs 42-43, page 112.
1958 Neoprioniodus singularis (Hass). Stanley Plate 66 figs 2-3, page 471.
1958 Neoprioniodus sp. A Stanley Plate 66 figs 4-5, page 472.
1964 Neoprioniodus singularis (Hass). Rexroad and Furnish Plate 111 fig 32 (listed as fig 33), page 674.
1969 Neoprioniodus montanaensis (Scott). Rhodes et al. Plate 22 figs 5-8,

page 160.

1974 Neoprioniodus montanaensis (Scott). Austin and Husri Plate 12 figs 11, 16, 18.

1975 Neoprioniodus singularis (Hass). Higgins Plate 3 fig 11, page 68.

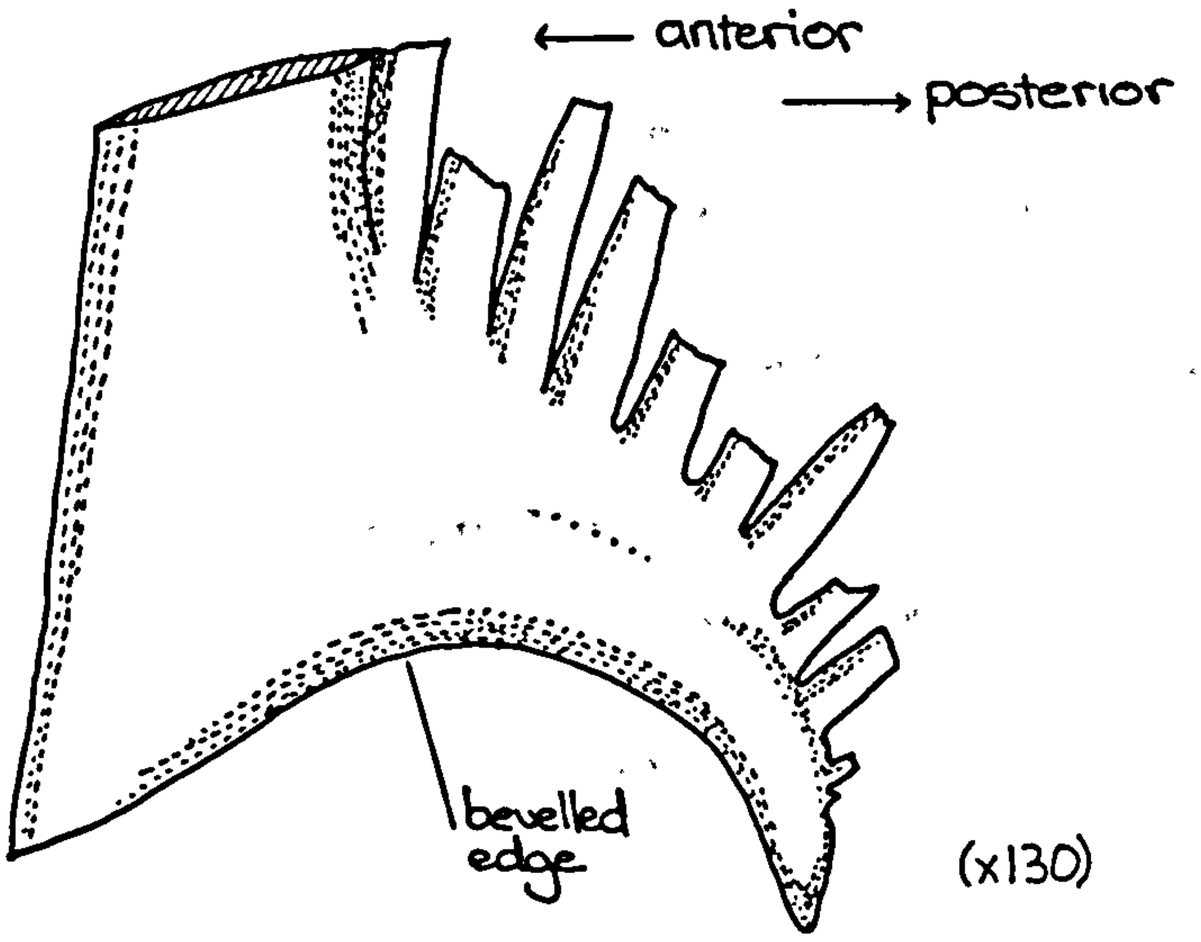
1981 Neoprioniodus singularis (Hass). Metcalfe Plate 18 figs 1-3.

1984 Neoprioniodus singularis (Hass). Austin and Davies Plate 3 fig 27.

1985 Neoprioniodus singularis (Hass). Varker and Sevastopulo Plate 5.6 fig 13, page 202.

1988 Lochriea commutatus (Branson and Mehl) M element; Sweet text-fig 5.51 (third from left), page 111.

Interpretive sketch 2.2.35 Lochriea commutata M element (sample CM 22)



Description:

Markedly arched and flexed neoprioniodontan dolabrate element. The whole unit is comparatively thin and laterally compressed. The large cusp is elongate, sharply pointed and, although straight in lateral view, is flexed inwards. In cross-section the cusp is fin-like with the inner side thicker than the outer. The anterior margin of the cusp is particularly sharp. A short, triangular, pointed anticusp is developed. The basal cavity is small and the inner lateral margins of the unit often display inwardly bevelled edges (see interpretive sketch 2.2.35).

The posterior process is shorter than the cusp, arched in lateral view and flexed inwards. The process gets progressively shallower towards its posterior and eventually tapers to a point. The ten-or-so bar-denticles gradually decrease in size toward the posterior and these denticles are closely set discrete, and may be curved inwards. The proximal one or two denticles are often almost entirely incorporated into the cusp.

Discussion:

The specimens recovered in this study accord well with the original description of Hass (1953). Norby (1976) comments that the variability in this element includes differences in denticle spacing, angle of the posterior bar and length of anticusp; however this is probably the most easily recognised element within this multielement species.

Sample range: CM 22 to CM 43, PE 1.
Distribution: outer and mid-ramp.
Material: 12 specimens.

Sa element

(Not recovered in this study)

Synonymy:

1961 Hibbardella pennata Higgins Plate 12 figs 5-6, page 213.
1969 Hibbardella (Hibbardella) parva Rhodes et al. Plate 25 fig 21, page 114.
1974 Hibbardella (Hibbardella) parva Rhodes et al. Austin and Husri Plate 13 figs 1-2.
p1975 Hibbardella pennata Higgins. Higgins Plate 1 fig 6 (only), page 36.
1976 Lochriea commutatus (Branson and Mehl) A_3 element; Norby Plate 11 figs 15, 17, page 157.
1981 Hibbardella pennata Higgins. Metcalfe Plate 14 figs 1, 4.

Discussion:

Norby (1976) comments that this element is very similar to the Sc element in lateral view. It can be distinguished from the Gnathodus Sa element by its wider more laterally compressed cusp, more widely diverging lateral processes which are attached to the main cusp over a greater vertical area and the straighter longer posterior process. The Sa element of Cavusgnathus has a more triangular, nearly straight cusp.

Sc_1 element

Synonymy:

p1956 Hindeodella bigeniculata Elias Plate 1 figs 20-21 (not fig 16), page 106.
1956 Hindeodella mehli Elias Plate 1 figs 22-24, page 108.
p1957 Hindeodella germana Holmes. Bischoff Plate 6 fig 32 (not fig 34), page 27.
1961 Hindeodella germana Holmes. Higgins Plate 10 fig 12.
1968 Hindeodella germana Holmes. Higgins and Bouckaert Plate 1 fig 12,

page 36.

1969 Hindeodella montanaensis (Scott). Rhodes et al. Plate 28 figs 21-26, page 123.

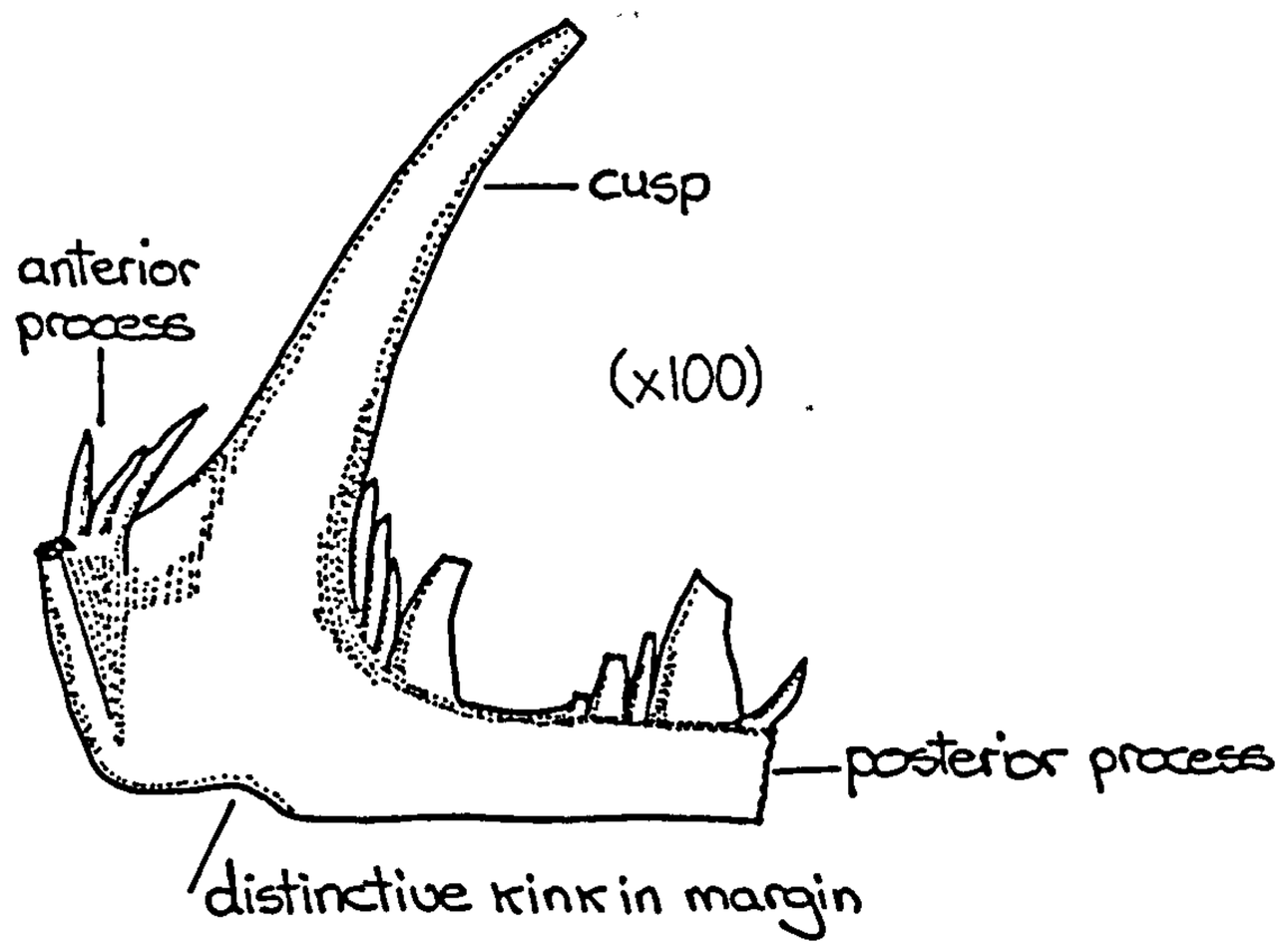
1974 Hindeodella montanaensis (Scott). Austin and Husri Plate 15 fig 16.

1975 Hindeodella germana Holmes. Higgins Plate 5 fig 6, page 38.

1976 Lochreia commutatus (Branson and Mehl) A_{1a} element; Norby Plate 12 figs 1-3, 6, page 155.

1981 Hindeodella mehli Elias. Metcalfe Plate 15 fig 3.

Interpretive sketch 2.2.36 Lochreia commutata Sc1 element (sample CM 31).



Description:

Bipennate hindeodellan element with a large cusp and distinctively upswept anterior process (in lateral view). The cusp is at least three times wider than any of the bar denticles and approximately four times as long, and curves posteriorly at approximately 35° to 40°. The posterior and anterior margins of the cusp may have two or three fine denticles attached (see interpretive sketch 2.2.36).

The posterior process is typically hindeodellan with three or four smaller denticles alternating with a series of larger denticles. In the only recovered specimen the larger denticles curve posteriorly toward their tips.

The anterior process is comparatively short and blade-like, and is bent at 90° to the posterior process and cusp. It bears several rather delicate, discrete denticles and its distal margin is upswept almost to the vertical. The anterior process is at least twice as deep as the posterior process and in lateral view joins the cusp considerably higher up. The lower margin of the anterior process has a distinct upward kink just below the cusp (see interpretive sketch 2.2.36).

Discussion:

In his examination of natural apparatuses Norby (1976) was unable to determine the presence of any Sb type elements, and suggested the S element complement to comprise: six Sc_1 elements, two Sc_2 elements and one Sa element.

Sample range: CM 31.
Distribution: outer ramp.
Material: 1 element.

Sc_2 element
(Not recovered in this study)

Synonymy:

p1942 Lochriea montanaensis Scott hindeodell component; Plate 39 fig 1 (horizontal element only).

1976 Lochriea commutatus (Branson and Mehl) A_{1c} element; Norby Plate 12 fig 5, page 156.

Discussion:

This element is rarely recovered (or at least rarely recognised) and can be distinguished from the nearly identical Sd element of Gnathodus by the upswept termination of its anterior process (Norby 1976). The cusp is of a similar size to the main bar denticles, and the anterior process is bent inwards at approximately 90° and bears ten-or-so denticles which are increasingly angled away from the cusp towards the distal tip of the process.

2.2i Genus: Mestognathus Bischoff 1957
Type species: Mestognathus beckmanni Bischoff 1957

Remarks:

In a monograph on the genus Mestognathus, von Bitter et al. (1986) recognised just five species (entirely on the basis of Pa elements), which show a phylogenetic sequence:
harmalai -> groessensi -> praebeckmanni -> beckmanni -> bipluti
The species M. dhuensis and M. neddensis were synonymised with those above.

Although some authors have suggested that Mestognathus may have had unpaired Pa elements (Higgins 1961, Druce 1973, Belka 1983); von Bitter et al. (1986) were able to distinguish sinistral and dextral elements on the basis of curvature of the left margin. They thus concluded that the Pa elements occurred as right and left pairs in a single animal and therefore belong to symmetry Class IIIa of Lane (1968).

Whether the Mestognathus apparatus included any other elements apart from the Pa component is uncertain. von Bitter et al. (1986) suggest that from the available data it is probable that the animal only bore one or more pairs of Pa elements. However, Armstrong and Purnell (1987) illustrate Mestognathus beckmanni Pb and M elements but give no information on the reason for their designation. Merrill and von Bitter (1984) and von Bitter et al. (1986) suggest that in light of the ramiform component known to occur in other, coeval cavusgnathoids, Mestognathus may have had other elements in its apparatus under optimal conditions and that their loss was a reaction to environmental stress.

Mestognathus beckmanni Bischoff 1957

Plate 7 figs 7-8.

Pa element

Synonymy:

1957 Mestognathus beckmanni Bischoff Plate 2 figs 4-6, 8-9, page 37.

p1967 Mestognathus dhuensis Globensky Plate 57 fig 22 (only).

1969 Mestognathus beckmanni Bischoff. Rhodes et al. Plate 15 fig 7, page 150.

p?1969 Mestognathus neddensis Rhodes et al. Plate 15 figs 4-5 (fig 6 = M. ?bipluti), page 153.

1974 Mestognathus beckmanni Bischoff. Austin and Husri Plate 5 fig 8.

p1974 Mestognathus neddensis Rhodes et al. Austin and Husri Plate 5 fig 2 (only).

1981 Mestognathus beckmanni Bischoff. Metcalfe Plate 8 figs 1-2.

p1983 Mestognathus beckmanni Bischoff. Belka Plate 1 figs 3-4, Plate 2 fig 5 (only, figs 3-4 transitional with M. bipluti), page 76.

p1983 Mestognathus bipluti Higgins. Belka Plate 2 fig 7 (only).

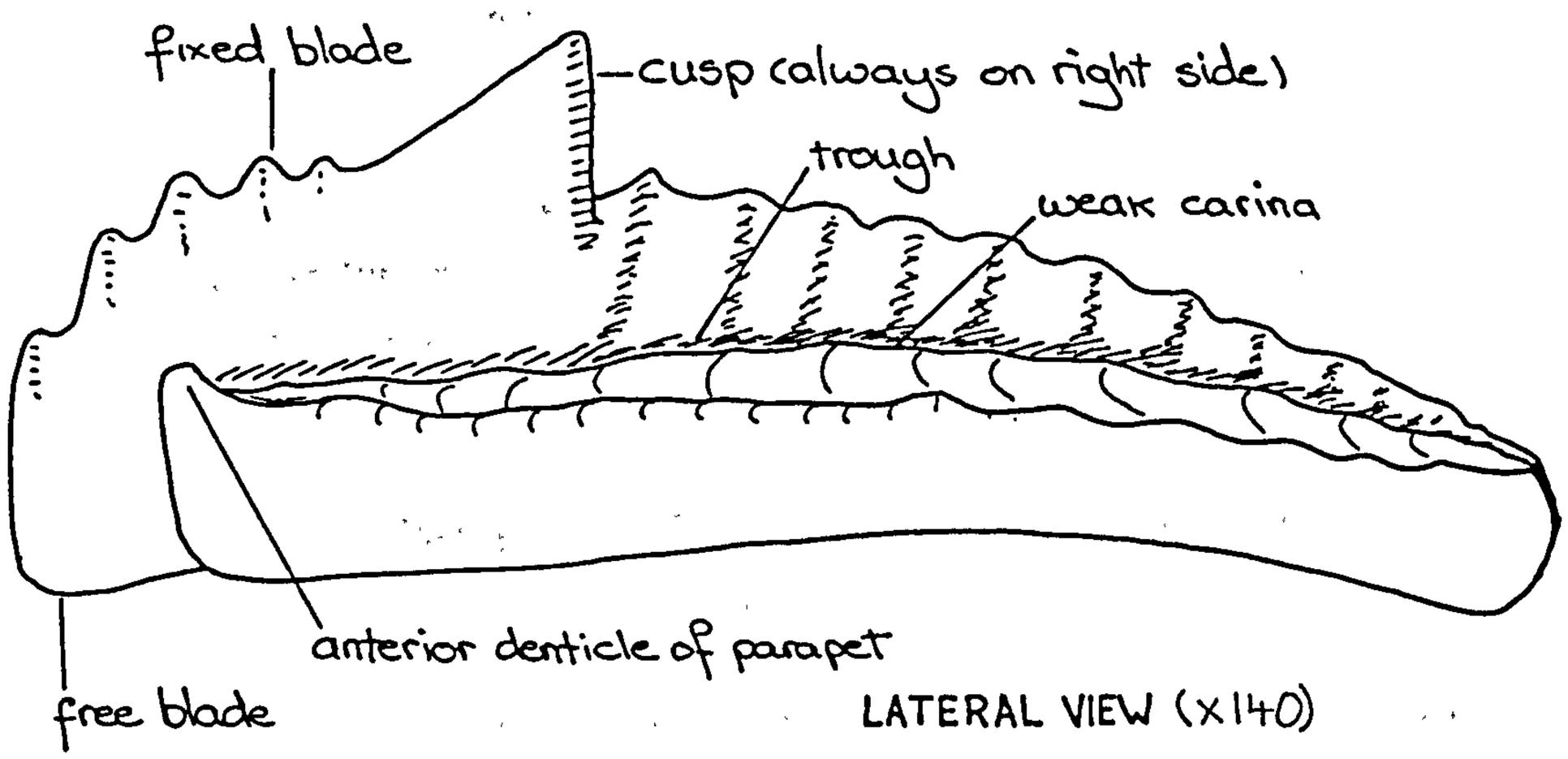
1985 Mestognathus beckmanni Bischoff. Varker and Sevastopulo Plate 5.5 figs 1, 3, 5, page 200.

1986 Mestognathus beckmanni Bischoff. von Bitter et al. Plate 1 figs 1-8, 23, Plate 2 figs 1-5, 9, Plate 3 figs 1-5, 9, Plate 4 figs 1-5, 9, Plate 12 figs 1-6, Plate 13 figs 1-9, Plate 14 figs 1-12, Plate 15 figs 1-12, Plate 16 figs 1-12, Plate 17 figs 1-13, Plate 19 figs 1-5, Plate 20 figs 3, 6, 10, 12, Plate 23 figs 1-3, Plate 25 figs 7-9, Plate 26 fig 4, Plate 27 figs 3-4, 7, page 35 (with extended synonymy).

?1987 Mestognathus beckmanni Bischoff. Austin Plate 13.4 fig 1.

1987 Mestognathus beckmanni Bischoff. Armstrong and Purnell Plate 3 figs 4, 6.

Interpretive sketch 2.2.37 Mestognathus beckmanni Pa element (sample T 5).



Description:

Asymmetrical carminiplanate cavusgnathan element with a right-sided anterior blade and a posterior v-shaped platform. The blade is continuous with the right margin of the unit and has a distinctive, large triangular cusp posteriorly. Anterior of the cusp there are five or more bluntly-triangular smaller denticles; and the anterior two or three of these (which comprise the free blade) are progressively lower such that in side view the blade curves downwards to meet its vertical anterior termination. The parapet (on the left margin, opposite the fixed blade) characteristically has a single pillar-like anterior denticle with a verticle or near-verticle anterior margin. The blade and parapet are separated by a deep trough.

The posterior platform is weakly arched in lateral view and has rounded and bulbous lateral margins. On the upper surface cross-ribs run in towards a weak central carina which extends from the posterior tip of the platform to the anterior tip of the parapet. The basal cavity is greatly restricted and situated slightly anterior of the mid-point; a slight groove surrounded by recessive basal margin extends to the tip of the anterior blade, and to the posterior tip. In some specimens a secondary keel of recessive basal margin extends from the basal cavity to the anterior tip of the parapet.

Discussion:

In immature specimens the basal cavity is elongate and more open than in adult specimens (Belka 1983), and in some specimens the anterior denticle is more rectangular than pointed, and may bear a small denticle anterior of the

main denticle (von Bitter et al 1986).

Sample range: CM 40, LS 5, T5.
Distribution: outer and mid-ramp.
Material: 8 specimens.

non-platform elements

No unequivocally mestognathid non-platform elements have been recovered in this study (see comments above).

2.2j Genus: Patrognathus Rhodes Austin and Druce 1969
Type species: Patrognathus variabilis Rhodes Austin and Druce 1969

Remarks:

Patrognathus Pa elements are sub-symmetrical with a short, median anterior blade of five-or-so denticles, of which the posterior-most is markedly larger than the others. The platform is lanceolate and bears a double row of nodes separated by a shallow central trough. The basal cavity is large, extending almost the entire length of the platform, and is laterally flared (asymmetrically), particularly in mature specimens.

Patrognathus capricornis (Druce 1970)

Plate: 7 fig 9.

Pa element

Synonymy:

1969 Taphrognathus sp. Druce Plate 41 figs 1a-b.
1970 Taphrognathus capricornis Druce Plate 15 figs 3a-5d, page 102.
?1974 Patrognathus capricornis Druce. Jenkins page 916.
1975 Capricornognathus capricornis Druce. Austin and Mitchell Plate 2 figs 5-12, 14-19, 21, 23, 28, 30-33, pages 47-48.
1981 Patrognathus capricornis Druce. Metcalfe Plate 9 figs 1a-2b, page 39.
?1987 Patrognathus capricornis Druce. Armstrong and Purnell page 109.

Description:

None of the elements recovered are in pristine condition, and details are obscured on all but one specimen. In upper view the platform is lanceolate and bounded on both margins by rows of 5-7 rounded, blocky, elongate nodes. There is a shallow central trough which is most clearly formed in the anterior part of the platform. At the posterior is a weak median carina of three separated denticles. The basal cavity is incomplete in all specimens, but appears to flare out laterally. The anterior free blade makes up approximately one third

the total length of the unit and comprises five denticles.

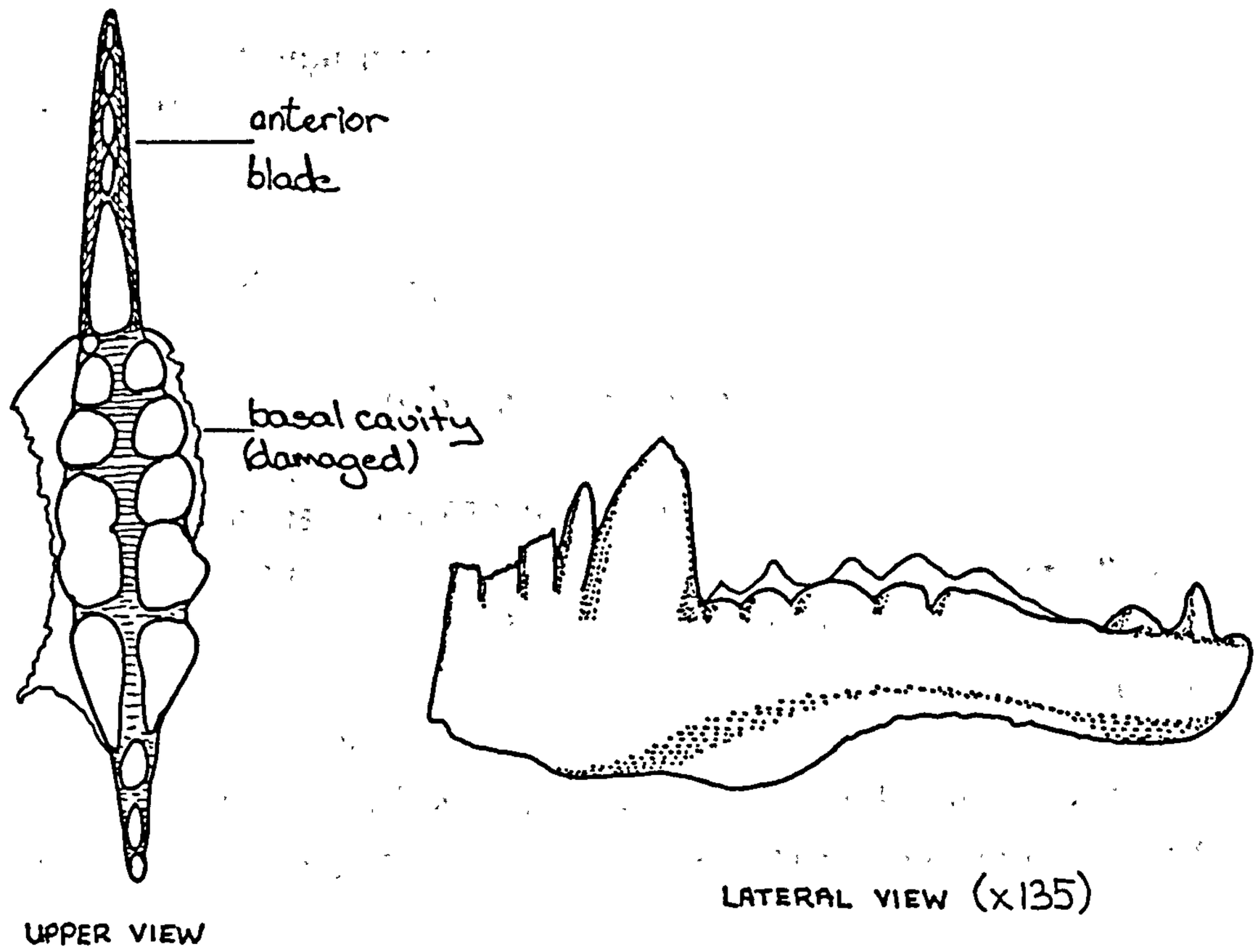
In lateral view, the posterior-most denticle of the blade is approximately twice the height and three times the width of the other four, in which there is a slight increase in size toward the posterior. The height of the platform is approximately half the height of the main denticle, and the platform nodes are crudely chevron tipped.

Discussion:

Three species of Patrognathus have been recognised: variabilis, andersoni and capricornis. The first two are generally considered to be lower Courceyan (Rhodes et al. 1969, Klapper 1971, Austin and Hill 1973, Varker and Sevastopulo 1985), and capricornis is considered as mid-Chadian to mid-Arundian (Druce 1970, Jenkins 1974, Austin and Mitchell 1975, Metcalfe 1981, Varker and Sevastopulo 1985). Differentiating between the two older species is often difficult; andersoni has a narrower basal cavity, and in some cases, a more distinct medial trough than variabilis (Klapper 1971). However Austin and Hill (1973) illustrate an ontogenetic succession within variabilis in which some of the less mature forms satisfy the criteria for andersoni. The authors implied that, while retaining the name andersoni, they would expect future N. American studies to show andersoni to be a juvenile form of variabilis.

Druce (1970) originally placed capricornis in the genus Taphrognathus, but Klapper (1971) suggested it should be removed to Patrognathus because Taphrognathus has an anterior blade in which the posterior denticles decrease in size, and possesses a short fixed blade. The plates of those authors illustrating capricornis (see synonymy list) show that within the populations there is a continuous variation between forms with the 'classic' triangular lateral profile of the blade, to forms which fit the diagnosis for variabilis (but for the stratigraphic separation). It is possible that future studies may result in the synonymising of capricornis with variabilis, although the material recovered in this study is too limited to provide any firm evidence. Support for this idea comes from the work of Austin and Mitchell (1975) who note that specimens which they have assigned to andersoni may in fact be immature forms of capricornis. These authors also picture transitional variabilis/capricornis forms (Plate 2 figures 5-7 and page 48) from the same sample as capricornis-proper. Further support comes from Armstrong and Purnell (1987) who list variabilis co-occurring with capricornis in the Chadian of the Northumberland Trough (but give no details of their diagnoses). A major stumbling block to the elucidation of the genus Patrognathus is the fact that it was an environmentally restricted, shallow water form with a patchy geographical and temporal distribution.

Interpretive sketch 2.2.38 Patrognathus capricornis Pa element (sample GL 7).



Sample range: LS 1, GL 5 to GL 7.
Distribution: distal mid-ramp.
Material: 4 specimens.

Non-platform elements

Discussion:

No complete apparatus reconstruction has been established for Patrognathus, but it is reasonable to assume a general similarity with the non-platform elements of other cavusgnathoid genera (see section 2.2b Cavusgnathus non-platform elements). This assumption is corroborated by the findings of Armstrong and Purnell (1987), who illustrate isolated M, Sa and Sc elements assigned to Patrognathus variabilis (Plate 3 figures 10-12), although no details or explanation are given for this designation.

2.2k Genus: Polygnathus Hinde 1879
Type species: Polygnathus dubia Hinde 1879
Synonymy: 1879 Polygnathus Hinde.
1925 Hindeodella Bassler 1925.
1957 Ctenopolygnathus Müller and Müller 1957.

Polygnathus bischoffi Rhodes Austin and Druce 1969

Plate: 7 fig 10.

Pa element

Synonymy:

1957 Polygnathus inornata Branson. Bischoff Plate 2 figs 17-18, 20-21, page 42.

p1959 Polygnathus cf. flabella Branson and Mehl. Voges Plate 34 fig 11 (only).

1969 Polygnathus bischoffi Rhodes et al. Plate 13 figs 8-11, page 184.

1974 Polygnathus bischoffi Rhodes et al. Austin and Husri Plate 9 fig 4.

1981 Polygnathus bischoffi Rhodes et al. Metcalfe Plate 9 figs 4, 7.

1985 Polygnathus bischoffi Rhodes et al. Varker and Sevastopulo Plate 5.2 figs 16-17, page 194.

1985 Polygnathus bischoffi Rhodes et al. Belka Plate 14 figs 6-8.

1987 Polygnathus bischoffi Rhodes et al. Armstrong and Purnell Plate 3 fig 13.

Description:

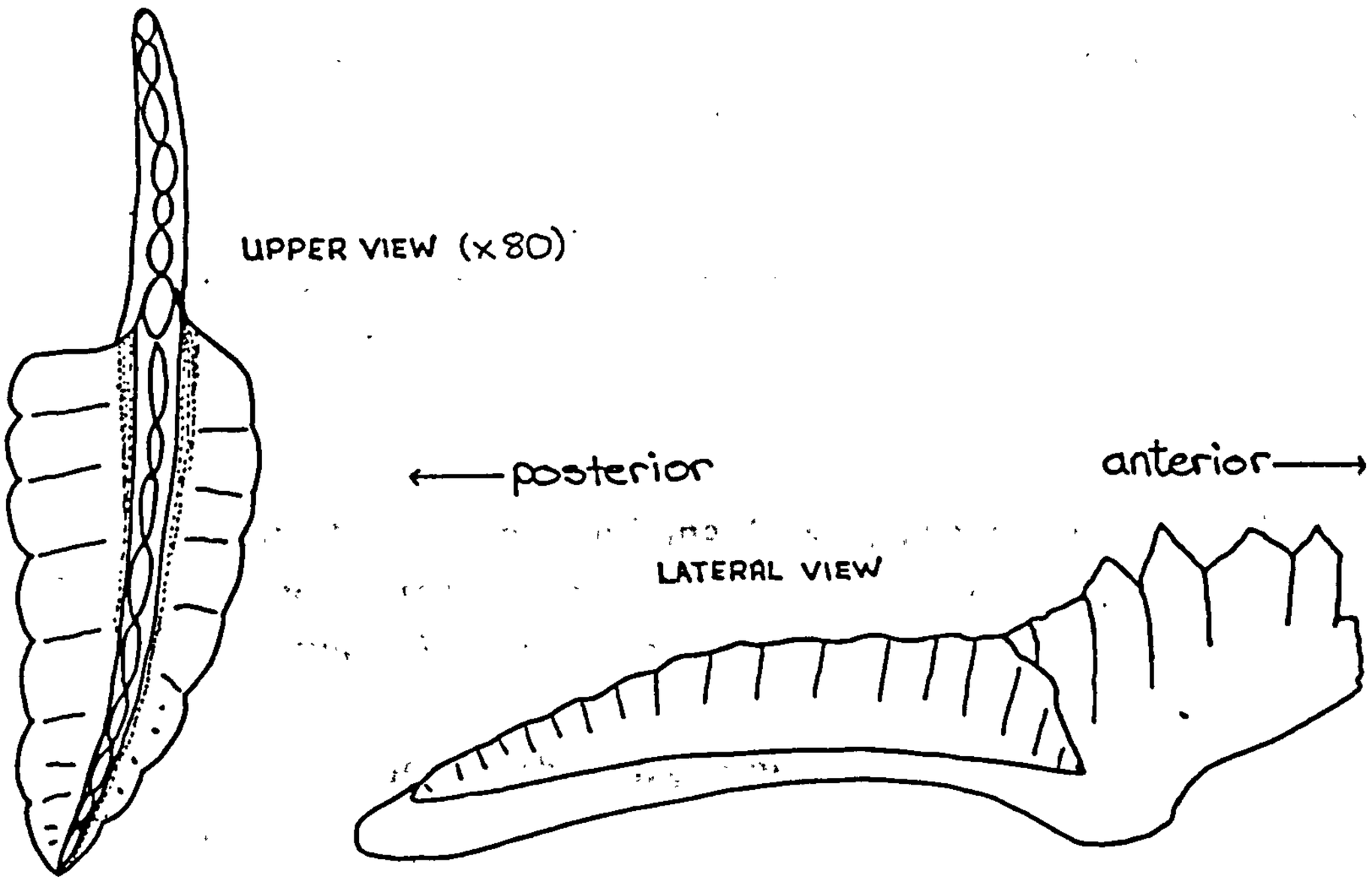
Carminiplanate polygnathan element with a sub-symmeterical platform which is triangular toward the posterior, but parallel sided anteriorly. The anterior blade is broken in the present specimens but is about one third the total length of the unit and bears at least 5 denticles. The denticles are fused to their chevron shaped tips and the posterior four are sub-equal in height. The anterior denticle is rather small.

In side view the blade is seen to be approximately one third higher than the characteristically arched platform, the margins of which are equal in height with the carina.

In upper view the long-axis of the unit is slightly curved, particularly in the posterior third. The platform is ornamented with delicate ribs which are most strongly developed on the platform margins; and there is a low, central carina of fused nodes extending from the blade to the posterior tip. Either side of the carina is an adcarinal trough which is increasingly more strongly developed toward the anterior where the troughs open.

The small, sub-symmetrical, elongate basal cavity is situated in the anterior part of the platform, and a grooved keel extends from it posteriorly. The underside of the free blade is missing or damaged in the present specimens.

Interpretive sketch 2.2.39 Polygnathus bischoffi Pa element (sample GL 5).



Discussion:

This form appears to be extremely similar to the Pa element of Polygnathus inornatus Branson and Mehl 1934, which ranges from the uppermost Famennian to the lower mid-Courceyan (Austin et al. 1985, Varker and Sevastopulo 1985). P. inornatus is therefore older than P. bischoffi, which ranges from the upper mid-Courceyan to the mid-Arundian. According to Rhodes et al. (1969) the two forms can be differentiated on the basis of P. inornatus having less accentuated adcarinal grooves and a more elongate platform.

While there may be a real and quantifiable difference between the two species, the differentiation between them often appears to be based stratigraphically rather than biologically. Rexroad and Scott (1964) noted how remarkably varied a species P. inornatus is, and although the present fauna is too limited to allow further elucidation, future studies of mid-Courceyan conodonts may show inornatus and bischoffi to be a single continuous lineage, in which case it would be difficult to "draw the line" between the two species presently recognised.

Sample range: GL 5 to GL 13, T 1.
Distribution: mid-ramp.
Material: 3 specimens.

non-platform elements

Not recovered in this study, but see Chauff (1981 plate 2) and Nicoll (1985 plates 1 and 2) for illustrations of the non-Pa component of Polygnathus communis Branson and Mehl 1934 and Polygnathus xylus xylus Stauffer 1940, which are probably similar to the non-Pa component of the above species.

2.21 Genus: Vogelgnathus Norby and Rexroad 1985

Type species: Spathognathodus campbelli Rexroad 1957

Remarks:

The use of cf. below in describing the single species recognised in this study reflects a degree of ambiguity regarding the nature of the Pb element recovered (see comments under Pb element below).

Vogelgnathus cf. campbelli (Rexroad 1957)

Plate 8 figs 1-3.

Pa element

Synonymy:

1957 Spathognathodus campbelli Rexroad Plate 3 figs 13-15, page 37.

1960 Spathognathodus pusillus Clarke Plate 3 figs 10-11, page 20.

1961 Spathognathodus campbelli Rexroad. Rexroad and Burton Plate 141 fig 15, page 1156.

1969 Spathognathodus cf. campbelli Rexroad. Rhodes et al. Plate 8 figs 1-4, page 233.

.?1969 Gnathodus simplicatus Rhodes et al. Plate 8 fig 5, Plate 18 figs 2-5, page 107.

.?1974 Gnathodus simplicatus Rhodes et al. Austin Plate 1 fig 20.

1974 Spathognathodus campbelli Rexroad. Austin and Husri Plate 9 figs 1, 5-6.

?1974 Spathognathodus postcampbelli Austin and Husri Plate 5 figs 1, 3-4, page 57.

.?1974 Gnathodus simplicatus Rhodes et al. Austin and Husri Plate 4 figs 5, 13-14.

1975 Spathognathodus campbelli Rexroad. Higgins Plate 10 fig 11, page 73.

1976 Pandorinellina campbelli (Rexroad) P element; Norby Plate 17, Plate 18, Plate 19 fig 1, page 170.

1981 Spathognathodus campbelli Rexroad. Metcalfe Plate 8 fig 5, page 41.

1984 Spathognathodus campbelli Rexroad. Austin and Davies Plate 3 fig 35.

1985 Vogelgnathus campbelli (Rexroad) Pa element; Norby and Rexroad Plate 2 figs 3-10, pages 3, 9.

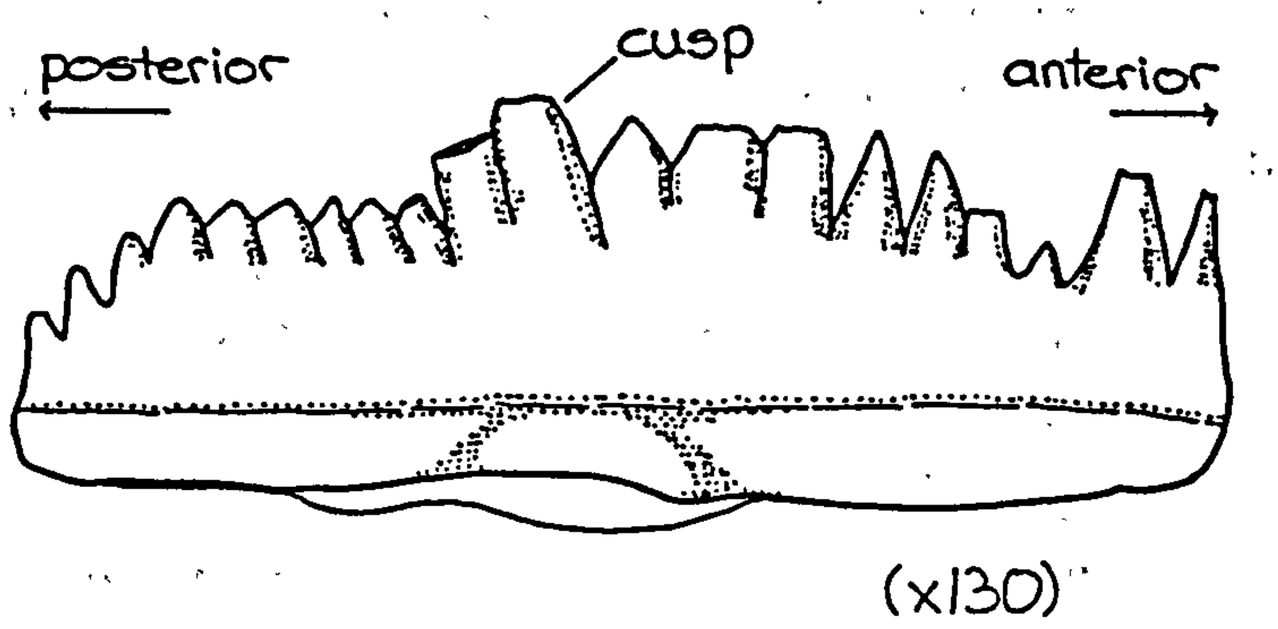
1985 'Spathognathodus' campbelli Rexroad. Higgins Plate 6.1 fig 6, page

218.

.?1985 "Spathognathodus" sp. A Belka Plate 15 fig 1.

1988 Vogelgnathus Pa element. Sweet text-fig 5.51 (top left), page 111.

Interpretive sketch 2.2.40 Vogelgnathus cf. campbelli Pa element (sample GL 15).



Description:

Carminiscaphate, blade-like spathognathodontan element two to three times as long as high, with a simple, unornamented posterior cup. In side view the lower margin may be horizontal or slightly arched (particularly toward the posterior), and the upper margin is slightly convex. The twenty-or-so denticles of the upper margin can often be divided into three groups. In the posterior third the denticles (approximately nine) are relatively small, crowded, inclined posteriorly and chevron tipped. There are often five larger and taller denticles in the central part of the unit, including the cusp which lies immediately above the anterior part of the basal cavity. The cusp and one major denticle posterior to it are posteriorly angled and the three major denticles anterior of the cusp are sub-vertical. The anterior-most six-or-so denticles of the unit are slightly shorter than the central denticles, they are angled vertically or slightly anteriorly, and are distinctively conical (see interpretive sketch 2.2.40).

Running approximately parallel with the lower margin of the unit there is a line or indentation (just above the flare of the basal cavity), which separates a thinner and smoother lower portion of the unit from the darker, more granular, denticulate portion. This line is often marked by a darkening of the element immediately above.

In upper view the element is slightly bowed with the most marked flexure in the posterior third. The basal cavity flares out from low down on the blade, is sub-symmetrical and extends to the posterior tip. The whole unit appears thin and delicate.

In lower view the elongate, lachrymiform basal cavity occupies the posterior half of the unit, and has a distinct pit at the anterior end beneath the cusp. The cup is sub-symmetrical but slightly arcuate and extends to the

posterior tip. There is a slight bulbous flaring of the cup at its anterior end, particularly on the inner side. The cavity is widest at a point just anterior of its midlength and uniformly narrows toward the posterior tip. A narrow groove extends anteriorly from the basal cavity.

Discussion:

The denticulation, oral outline and bowing of this unit are highly variable (Metcalfe 1981), and Norby (1976) implies that in some specimens the denticle differentiation is much less apparent than that described above. In view of the variation known to occur in this element, Gnathodus simplicatus s.f. Rhodes Austin and Druce 1969, is tentatively included in the synonymy. Rhodes et al. (1969) delineate G. simplicatus on the basis of the larger denticles being toward the anterior of the unit. Although no actual specimens have been examined in this study, all the illustrated specimens of G. simplicatus (see above) appear to have incomplete anterior portions, and in the original description Rhodes et al (1969 page 108) note that "in a few specimens the highest denticles are developed above the anterior end of the basal cavity" (as in the Vogelgnathus Pa element). Consequently it would appear that further studies are required to ascertain whether G. simplicatus s.f. is the Pa element of a distinct genus or simply a variation within Vogelgnathus; or at the very least to investigate the proximity of the relationship between the two.

Sample range: ?CM 2, GL 15, LL 4.
Distribution: outer, mid, and inner ramp.
Material: 5 specimens.

Pb element

The Vogelgnathus campbelli Pb element cited by Norby and Rexroad (1985) has not been recovered in this study; however in one of the three samples containing V. campbelli Pa elements, a similar but distinctive Pb element has been recovered. This element does not appear to have been previously described. Pending further studies this element is considered as the Pb component for the Arundian apparatus in which the above Pa element occurred, and for this reason the species discussed here is termed V. cf. campbelli.

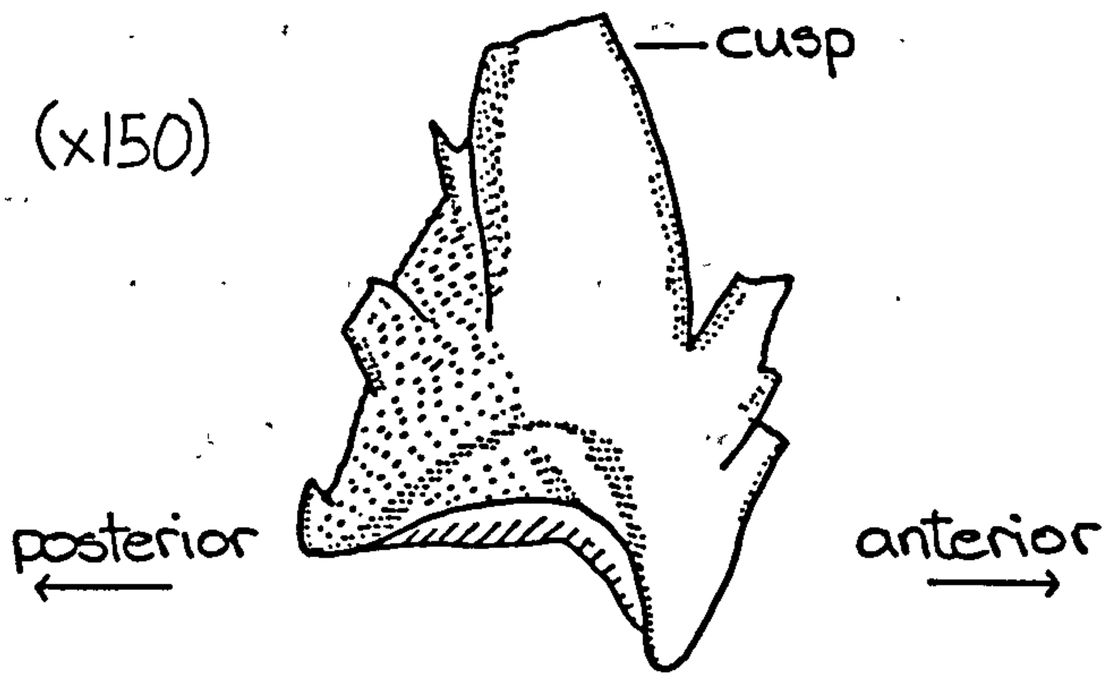
Description:

Small, delicate angulate element with a relatively large cusp and very short anterior and posterior processes which subtend an angle of approximately 150°. In side view the lower margin of the unit is arched, quite sharply, through an angle of approximately 70°. The basal cavity takes up most of the lower surface of the unit and extends to just short of the anterior and posterior tips. The cup is asymmetrically rounded with marked lateral flaring on both sides (see

interpretive sketch 2.2.41).

The cusp is massive and laterally flattened, with a sub-vertical posterior margin (except toward the distal tip) and a convex anterior margin; such that the cusp curves slightly posteriorly. The anterior process is short and downwardly pointed and bears two sub-circular denticles which are angled forward at approximately 45°. The distal tip of the process is adenticulate and bluntly pointed. The posterior process is equally short and bears four or five posteriorly angled, blocky, fused denticles which decrease in size toward the distal tip; which bears a small, conical, sub-vertical denticle. The proximal denticle of the posterior process is fused with the cusp for much of its length. Although the tips of all but the distal denticle are broken in the one recovered specimen, the regular decrease in denticle size appears to give a rather triangular outline to the process.

Interpretive sketch 2.2.41 Vogelgnathus cf. campbelli Pb element (sample GL 15).



Discussion:

The above description generally accords with that of Norby and Rexroad (1985) except for the larger bar-denticles of both processes, especially the posterior. None of the illustrated specimens appear to have a complete anterior process, and this may help to explain why none are as markedly arched in side view as the present specimen. All of the Pb elements illustrated by Norby and Rexroad (1985) appear to be more elongate than the present specimen, even though they are incomplete.

Only one specimen was recovered in the present study and further specimens are required to ascertain whether this is truly an older species of Vogelgnathus than V. campbelli or whether there is a degree of variation within the Pb element of multielement V. campbelli.

Sample range: GL 15.
Distribution: mid-ramp.
Material: 1 specimen.

non-P elements

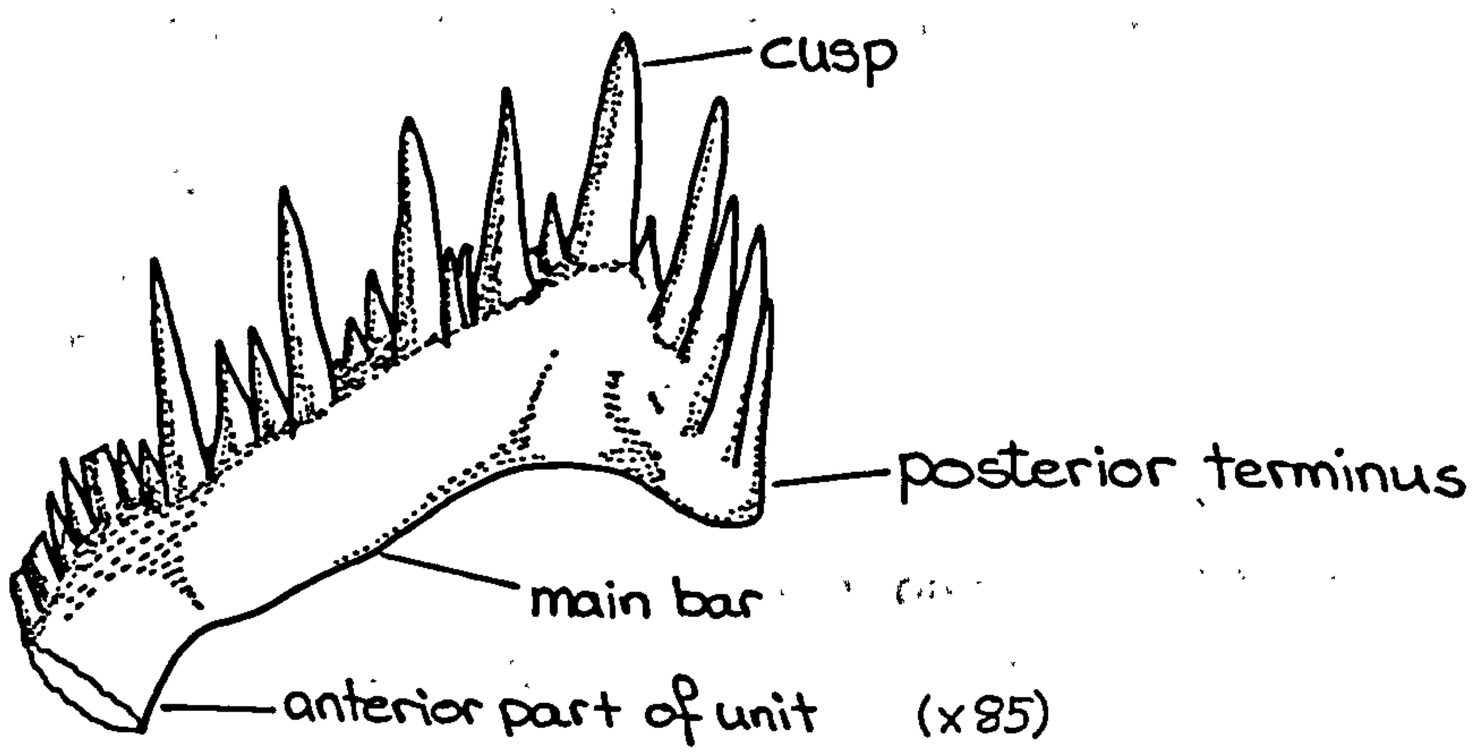
No Vogelgnathus M or S elements have been recovered in the present study, presumably due to the general paucity of this genus. See Norby and Rexroad (1985 Plate 3) for illustrations of the non-P elements of Vogelgnathus campbelli, which are presumably similar to those of the present species.

2.2m Elements not yet assigned to a multielement apparatus.

i) Genus: **Angulodus s.f.** Huddle 1934
Type species: Hindeodella walrathi Hibbard 1927

Angulodus cf. sp. nov. B s.f. Rhodes Austin and Druce 1969
Plate: 9 fig 2.
Synonymy:
?1969 Angulodus sp. nov. B Rhodes et al. Plate 29 fig 5, page 67.

Interpretive sketch 2.2.42 Angulodus sp. nov. B Rhodes et al s.f. (sample CM 4).



Description:

Angulodontan element with a robust bar which has rather rounded lateral faces. The recurved posterior terminus of the unit (sensu Rhodes et al. 1969) is curved round at approximately 100° to the main bar, and is deflected downwards. The anterior part of the unit is flexured inwards and downwards through approximately 45°. The cusp is roughly equal in size to the main bar-

denticles, and the denticulation has a distinctively spiky and needle-like appearance.

The anterior part of the specimen is broken but the denticles appear to be smaller than those of the main bar. The main bar bears alternating large and small (x2) needle-like denticles, and in upper view the large denticles curve inwards. On the main bar the small and large denticles appear to be misaligned, with the small denticles further toward the outer side of the unit. The recurved posterior terminus bears three large denticles of roughly equal size, which are stepped down towards the distal tip. At the angle between the main bar and the posterior terminus a larger denticle, taken to be the cusp, is angled outwards; and beneath this is the small basal cavity.

Discussion:

The general appearance of the denticulation of the single recorded specimen is the same as that of the other unusual specimen recovered from this sample (see gen. et sp. nov. below), and it is probable that both occured in the same apparatus. In multielement terms, the gross morphology of these two units is closest to that of the Sc and M elements of Aethotaxis (sensu Sweet 1988).

At present Aethotaxis advena is the only species to have been recognised (Baesemann 1973), and in the U.S.A. has been reported from throughout the Pennsylvanian (upper Namurian to Stephanian), and from the earliest Permian (Merrill and von Bitter 1976). Dean (1987) reports A. advena from Arnsbergian (lower Namurian) rocks of the Midland Valley of Scotland.

It is anticipated that future studies, involving bulk resampling of the bed from which this specimen was recovered, will lead to the elucidation of this apparatus; and an assessment of whether it is ancestral to A. advena.

Sample range: CM 4.
Distribution: outer ramp.
Material: 1 specimen.

ii) Genus: **'Apatognathus' s.f.** Branson and Mehl 1934
Type species: Apatognathus varians Branson and Mehl 1934

'Apatognathus' cuspidatus s.f. Varker 1967

Plate: 8 figs 4-5.
Synonymy:

p?1963 Apatognathus? porcata (Hinde). Rexroad and Collinson Plate 1 figs 10-11 (only).
1967 Apatognathus? cuspidata Varker Plate 17 figs 4, 6-10, page 131.
1974 Apatognathus cuspidatus Varker. Austin and Husri Plate 10 figs 4, 8,

15.

p?1974 Apatognathus geminus (Hinde). Austin and Husri Plate 10 fig 17 (only).

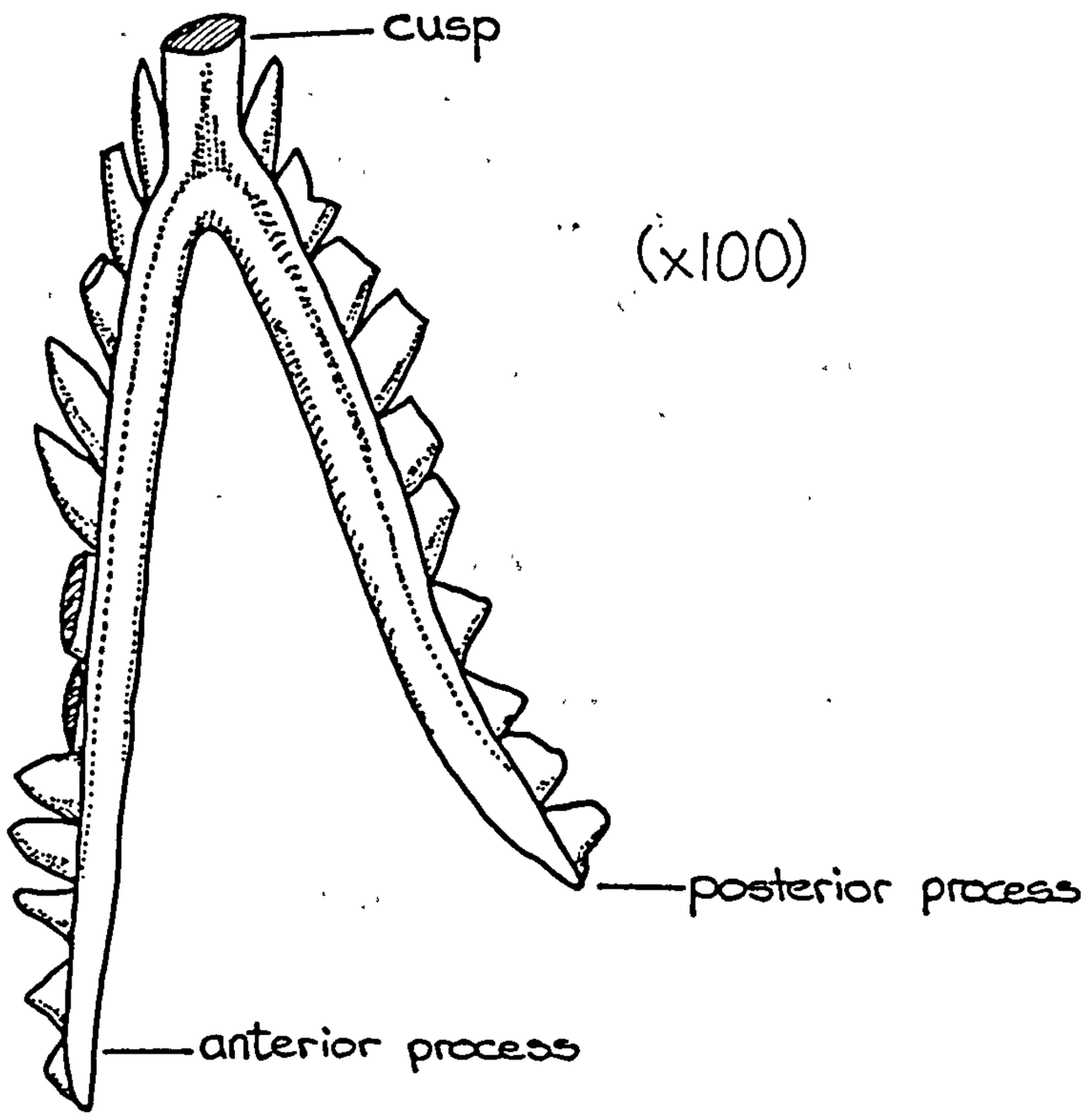
p1981 Apatognathus cuspidatus Varker. Metcalfe Plate 13 fig 8 (only).

?1984 Apatognathus libratus Varker. Austin and Davies Plate 3 fig 19.

1985 'Apatognathus' cuspidatus Varker. Varker and Sevastopulo Plate 5.4 figs 1-2.

1987 'Apatognathus' cuspidatus (Varker). Armstrong and Purnell Plate 1 fig 1.

Interpretive sketch 2.2.43 'Apatognathus' cuspidatus s.f. (sample CM 4)



Description:

Elongate and elegant bipennate apatognathan element with little or no thickening of the processes and a comparatively long cusp which appears continuous with the bars of the processes.

The anterior bar (sensu Varker 1967) is straight, slightly flattened and bears up to approximately twelve, subequal triangular denticles which become increasingly flattened toward the distal tip. These denticles are directed upwards and apically and are roughly confluent with the cusp. There is an angle of approximately 40° between the anterior process and the slightly shorter posterior process; and there is a twist or torsion between them so that the ten denticles (approximately) of the posterior process point outwards in a plane

approaching 90° to those of the anterior process. The denticles of the posterior process may be slightly larger than those of the anterior process. The distal tips of the processes are bluntly pointed, and there is a slight backwardly directed kink toward the tip of the posterior process.

The cusp appears to be a continuation of the processes, and is of similar thickness. It is about three times wider than the neighbouring denticles and at least three times longer. The cusp is angled up from the plane of the two processes, is curved upwards and may curve slightly toward the posterior. At the inner apex of the unit where the two processes meet, the bar is approximately as deep as the longest bar-denticle.

Discussion:

Varker (1967) recorded forms with a more acute angle between the processes, and included the need for the cusp to be more than half the bar length in his definition of A? cuspidata s.f.; however in the present study there is a continuous gradation to mature specimens in which the cusp may be only about one third of the bar length. Varker (1967) distinguished A? cuspidata by its large apical cusp, regular denticulation and the torsion between the two processes. In the present study some forms intermediate between the above and the ?Hindeodus scitulus M element were recovered, the main distinction being the lack of thickening of the posterior bar in A. cuspidatus.

Some of the apatognathan fragments recovered from the mid-ramp localities (Lydstep, Giltar and Tenby) are probably referable to this species, but often a definitive designation is not possible.

Sample range: CM 4 to CM 23, SQ 2 to SQ 3, GL 15, LL 3.
Distribution: outer to inner ramp.
Material: 26 specimens

'Apatognathus' libratus s.f. Varker 1967

Plate: 8 fig 6.
Synonymy:

1967 Apatognathus? librata Varker Plate 18 figs 3, 6, 8-9, 12-13, page 134.

1969 Apatognathus c.f. libratus Varker. Rhodes et al. Plate 20 fig 8, page 75.

non1974 Apatognathus libratus Varker. Austin and Husri Plate 10 fig 6 (specimen transitional between ?H. scitulus M element and 'A.' petilus of this study ?).

?1981 Apatognathus libratus Varker. Metcalfe Plate 13 figs 1-2.

non1984 Apatognathus libratus Varker. Austin and Davies Plate 3 fig 19 (see 'A.' cuspidata above).

1985 'Apatognathus' libratus Varker. Varker and Sevastopulo Plate 5.4 figs 8-11, page 198.
1987 Apatognathus libratus Varker. Austin Plate 13.4 fig 7.
1987 'Apatognathus' libratus (Varker). Armstrong and Purnell Plate 1 fig 2.

Description:

Apatognathan unit distinguished by its symmetrical nature, and a cusp of subequal size to the surrounding denticles. The processes subtend a comparatively wide angle of approximately 45° and there is little or no torsion between them so that the bar-denticles of the two processes tend to mirror each other. The denticles are stubby, subequal and are fused for their lower two thirds. In inner view (sensu Varker 1967) the processes become more flattened and blade-like distally, but are never asymmetrically thickened.

Discussion:

The symmetrical nature of this unit might suggest it to be the Sa element of ?Hindeodus scitulus, however the present study provides insufficient evidence to ratify this. Also Sweet (1988) includes a symmetrical apatognathan form, which does not meet the description above, in his reconstruction of H. scitulus (text-fig 5.54), although he does not cite his references.

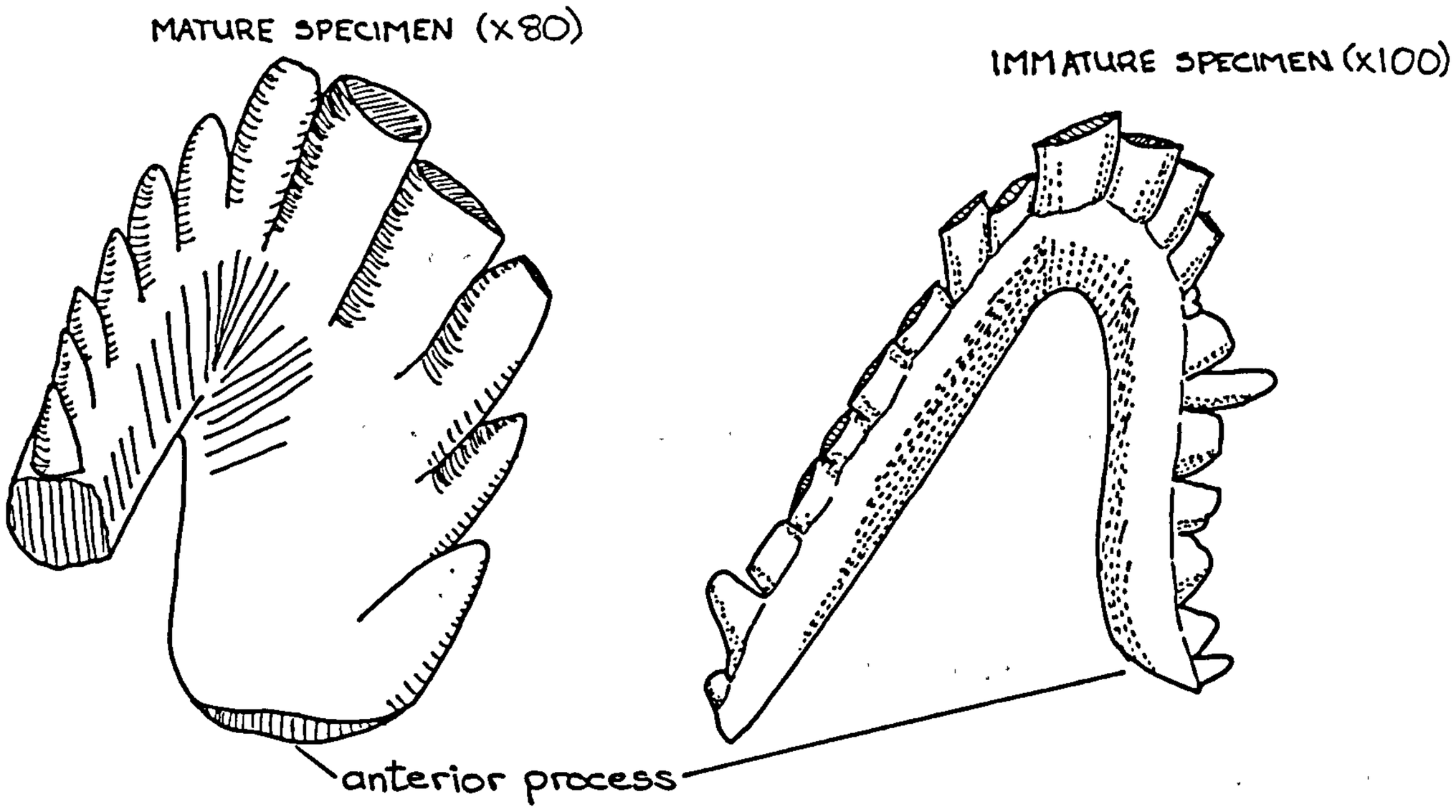
Sample range: CM 9? to CM 24, GL 14.
Distribution: outer and mid-ramp.
Material: 4 specimens.

'Apatognathus' petilus s.f. Varker 1967

Plate: 8 fig 7.
Synonymy:

1967 Apatognathus petila Varker Plate 17 fig 11, Plate 18 figs 7, 10-11, page 135.
1969 Apatognathus petilus Varker. Rhodes et al. Plate 20 figs 12-14, 17, page 72.
1974 Apatognathus petilus Varker. Austin and Husri Plate 10 fig 7.
?1981 Apatognathus petilus Varker. Metcalfe Plate 13 figs 4-7.
1984 Apatognathus petilus Varker. Austin and Davies Plate 3 fig 20.
1985 'Apatognathus' petilus Varker. Varker and Sevastopulo Plate 5.4 figs 3-5, page 198.
?1987 'Apatognathus' aff 'A.' libratus (Varker). Armstrong and Purnell Plate 1 fig 4.

Interpretive sketch 2.2.44 'Apatognathus' petilus s.f. (samples CM 27 and CM 32).



Description:

Stocky and robust, asymmetrical apatognathan unit with marked thickening of the anterior process, a cusp of subequal size to the surrounding denticles and torsion between the two processes.

The thinner posterior process (sensu Varker 1967) bears about nine comparatively small, conical denticles directed upwards and slightly apically. The bar is roundedly quadrate in section, relatively straight, and has a steep inner lateral side. All the denticles are of subequal size.

The anterior process is twisted around to lie in a plane at approximately 90° to the posterior process. The inner lateral face is markedly flattened and blade-like in mature specimens. The denticles of the anterior process are larger than those of the posterior process, and increase in size towards the apex of the unit.

The cusp is often not clearly distinguishable, and is of similar size to the two neighbouring denticles of the anterior process. This development of three subequal, larger denticles at the apex of the unit is distinctive. The inner face of the unit beneath the cusp is steep, and wall-like.

Discussion:

There is considerable variation in this element, particularly with respect to the degree of thickening and flattening of the anterior bar, and the length of the processes. At least some of this variation can probably be attributed to

ontogeny (see interpretive sketch 2.2.44).

Sample range: CM 15 to CM 32, SQ 1 to SQ 2, GL 9 to GL 14, T 5, CB 5.
Distribution: outer to proximal mid-ramp.
Material: 17 specimens.

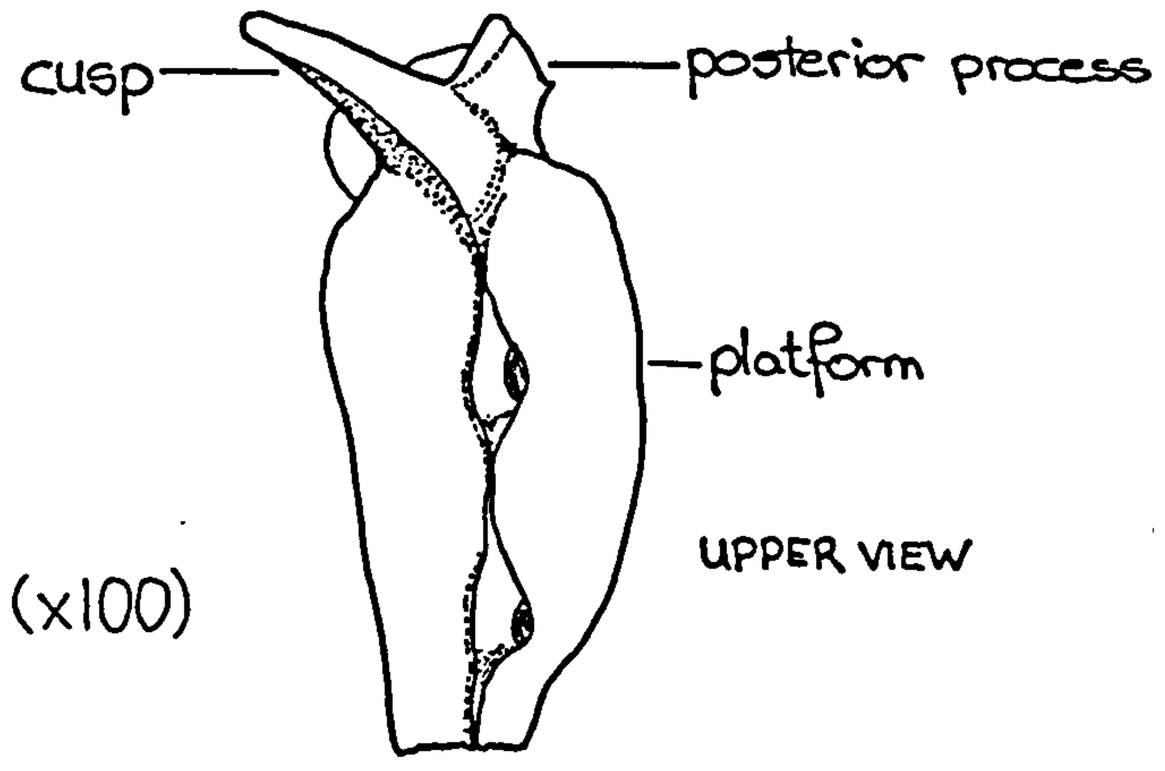
iii) Genus: Geniculatus s.f. Hass 1953
Type species: Polygnathus? claviger Roundy 1926

Geniculatus cf. claviger s.f. (Roundy 1926)

Plate: 9 fig 1.
Synonymy:

p?1953 Geniculatus claviger (Roundy). Hass Plate 15 figs 10, 15-16, 18 (figs 11, 12, 17 and 19 are indeterminate), page 77.
?1953 Prioniodus inclinatus Hass Plate 16 figs 10-14, page 87.
1974 Geniculatus claviger (Roundy). Matthews and Thomas Plate 50, 1, 4.
1975 Geniculatus claviger (Roundy). Higgins Plate 2 fig 5, page 27.
p1981 Geniculatus claviger (Roundy). Metcalfe Plate 12 figs 3-6.

Interpretive sketch 2.2.45 Geniculatus cf. claviger s.f. (sample CM 9).



Description:

Element with wide, tapering, shield-like platform which bears two feeble node-like denticles. The cusp is long (over half the length of the platform) and is directed outwards and posteriorly. The posterior process is blade-like and twisted at approximately 100° to the platform, and is also deflected downwards. The basal cavity is small asymmetrical and roughly oval. A thin slit bounded by

a zone of recessive margin extends along the underside of the platform from the cavity.

Discussion:

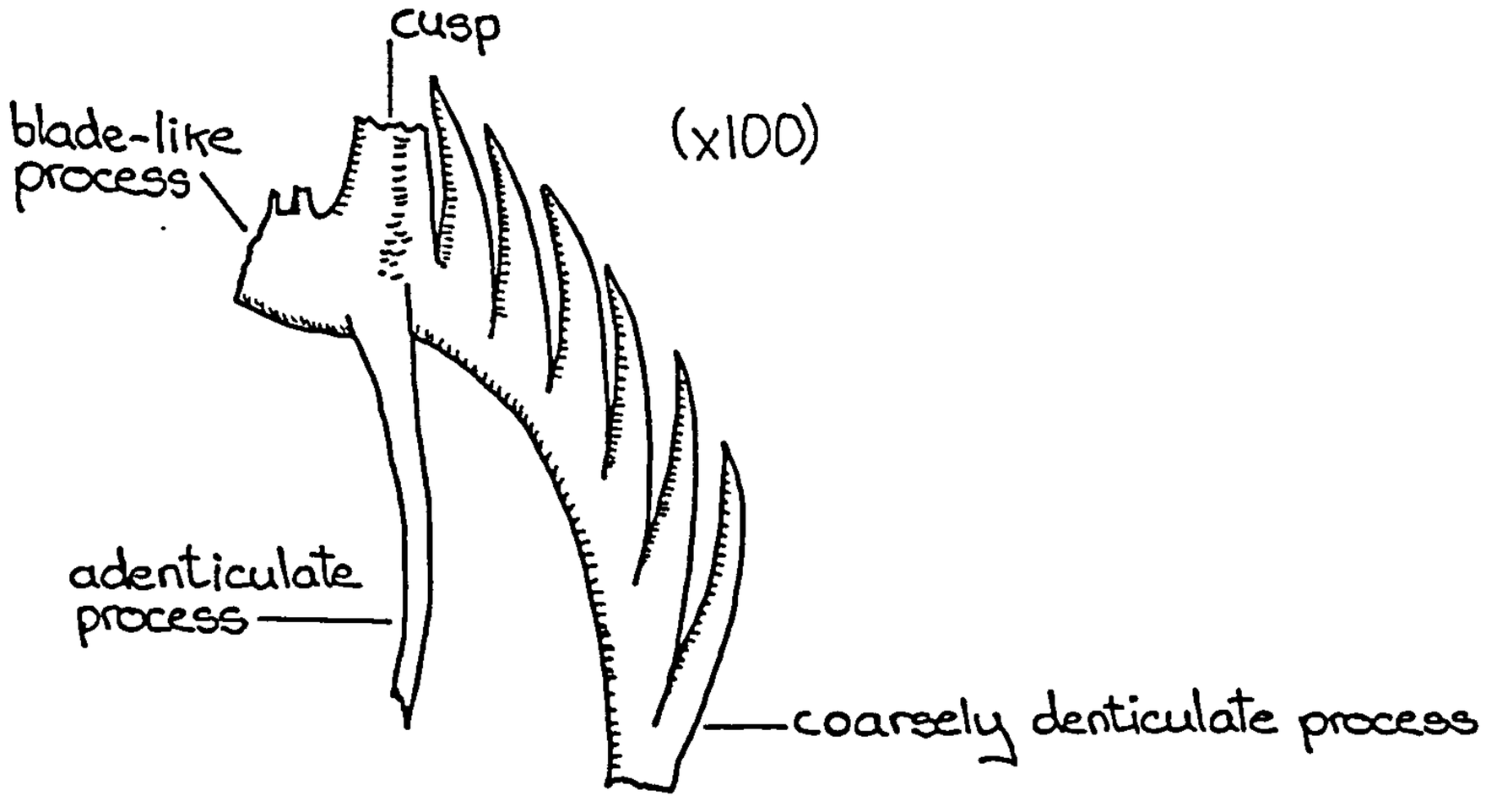
The single element recovered in this study is incomplete, but the extremely weak nodes suggest it to be a juvenile. The closest specimen to the present example which has been previously described was tentatively suggested to be "a ?young specimen" by Higgins (1975).

Sample range: CM 9.
Distribution: outer ramp.
Material: 1 specimen.

iv) Gen. et sp. nov. s.f.

Plate: 9 fig 3.

Interpretive sketch 2.2.46 Gen. et sp. nov. s.f. (sample CM 4).



Description:

An unusual tertiopedate (?) element with an arched, coarsely denticulate process angled downwards from the cusp, a thin elongate adenticulate process in the position of an anticusp, and a denticulate blade-like process in the horizontal plane (see interpretive sketch 2.2.46).

The arched process is angled downwards at approximately 45° from the cusp and curves down so that the distal tip is subparallel with the cusp. At least six large, subequal, discrete coarsely conical denticles are borne on the process,

and towards their distal tips the denticles are recurved toward the cusp. The more distal denticles are slightly more elongate than the more proximal ones. In the present specimen the distal tip of the process is missing. The lower portion of the process, beneath the denticles, is comparatively shallow.

The cusp is broken in the present specimen, but is at least twice as thick as the bar denticles described above; and in its distal portion may be recurved toward the posterior part of the unit. Projecting downwards from the base of the cusp there is a long, delicate, slightly curved, needle-like adenticulate process, which is approximately twice as long as the proximal denticles described above.

The third (posterior ?) process is broken in the present specimen but appears to be blade-like and to bear at least two rather feeble, well-spaced denticles.

Discussion:

As noted above, this element probably occurred in the same apparatus as Angulodus cf. sp. nov. B s.f. (see discussion section), which in multielement terms is similar to the Sc element of Aethotaxis advena. Apart from the unusual adenticulate process, the present unit is similar to the X element of A. advena (sensu Baesemann 1973). It is anticipated that future studies will enable the possibility of a relationship to be investigated.

Sample range: CM 4.
Distribution: outer ramp.
Material: 1 specimen.

CURATION OF SPECIMENS

For each of the processed samples, all recovered conodont elements are stored on a single cavity slide. The slides are deposited in the Department of Geology at the University of Southampton under the curatorship of Dr. R.L. Austin. Each slide bears its sample number (see figs 2.1.4, 2.1.5, 2.1.6 and 2.3.6), and a five figure departmental catalogue number. Each of the specimens figured in the following plates has its own catalogue number, and is stored on one of six scanning electron microscope stubs.

To locate any of the specimens on a stub, the stub should be orientated such that the number written on the upper surface appears the correct way up. The specimens are numbered sequentially going down each column - starting on the left. Details of each cavity slide and each illustrated specimen are recorded in the Department of Geology Fossil Specimen Catalogue (26694-26935), at the University of Southampton.

PLATE 1

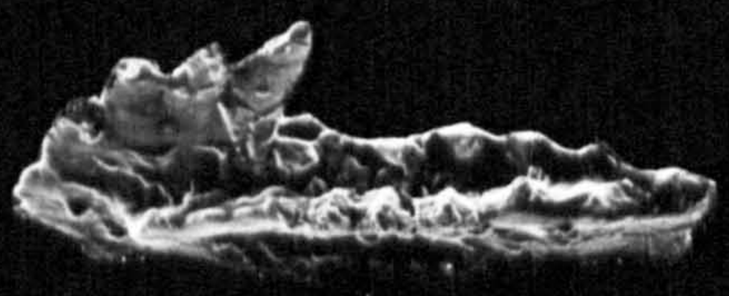
1-4 *Cavusgnathus altus*

1. Pa element, immature specimen, lateral view, sample GL 14, 26878 (x 130).
2. Pa element, mature specimen, upper view, sample GL 5, specimen lost (x 160).
3. M element (of cavusgnathoid type), lateral view, sample CM 5, 26879 (x 165).
4. Sc element (of cavusgnathoid type), inner lateral view, sample GL 9, 26881, (x 30).

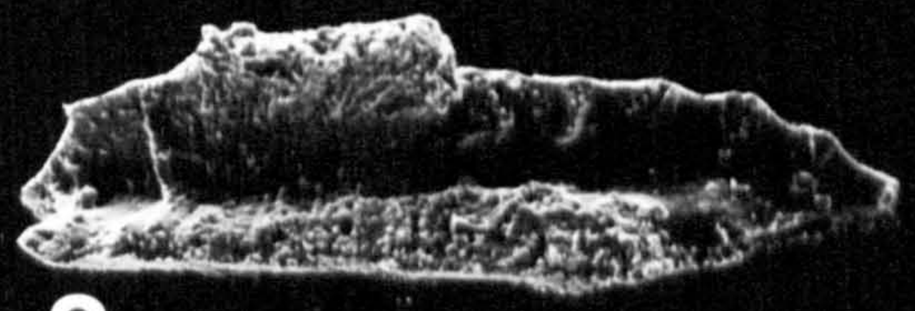
5 *Clydagnathus gilwernensis*

5a. Pa element, lateral view, sample LL 1, 26882 (x 100).
5b. -oblique upper view.
5c. -oblique lower view.

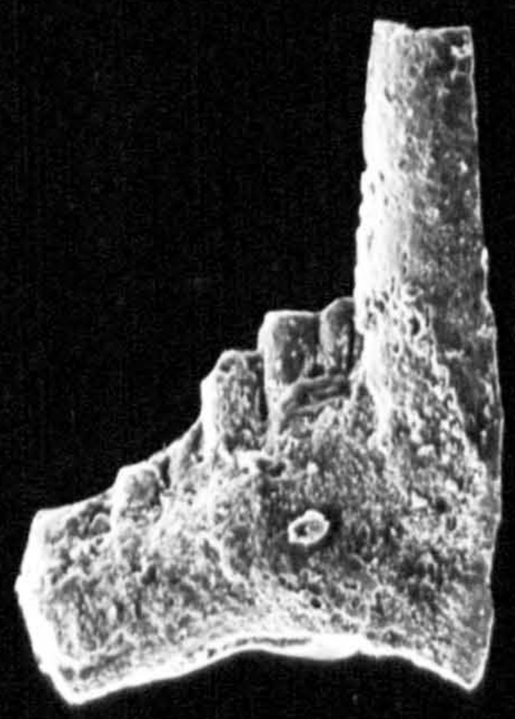
Plate 1



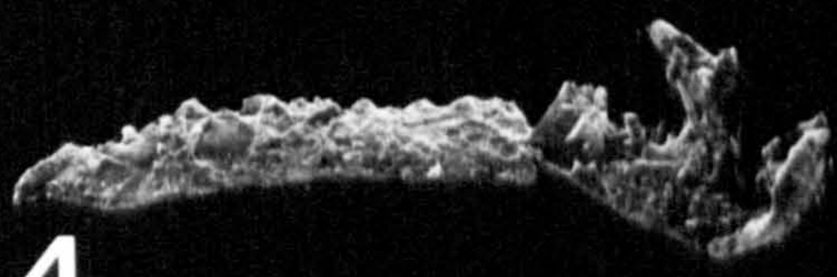
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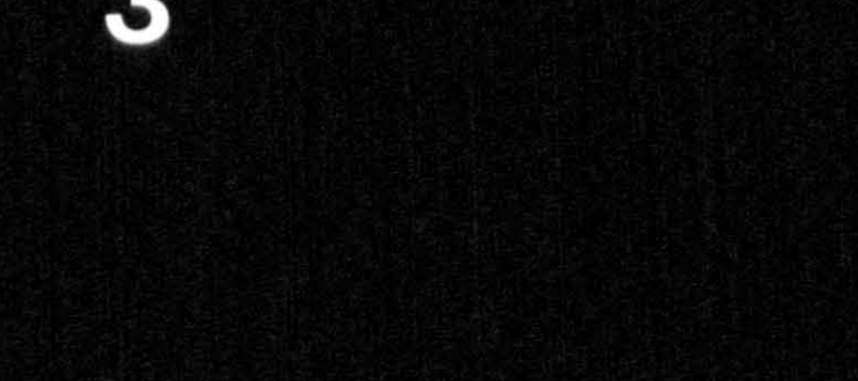
2



3



4



5a



5b

5c

PLATE 2

1-2 *Gnathodus cuneiformis*

1a. Pa element, mature specimen, upper view, sample CM 2, 26860 (x 70).

1b. -oblique posterior view showing relative height of parapets.

1c. -upper view X50 (for size comparison with immature specimen).

2a. Pa element, immature specimen, upper view, sample CM 2, 26861 (x 100).

2b. -oblique posterior view showing detail of parapets.

2c. -upper view X50 (for size comparison with mature specimen).

3-6 *Gnathodus* aff. *girtyi*

3a. Pa element, mature specimen, upper view, sample CM 22, 26862 (x 45).

3b. -oblique posterior view showing detail of parapet area.

4a. Pa element, less mature specimen than 3, upper view, sample CM 23, 26864 (x 50).

4b. -oblique posterior view showing detail of parapet area.

5. Pa element, immature specimen, upper view - showing features transitional between specimen 3 and *G. girtyi sensu stricto*, sample CM 30, 26843 (x 70).

6. Pa element, immature specimen, upper view - with parapet disposition approaching that of *G. girtyi sensu stricto*, sample CM 42, 26875 (x 50).

Plate 2


1a


1b


1c


2a


2b


2c


3a

3b


4a

4b


5

6

PLATE 3

1-5 *Gnathodus texanus*
- a series of upper views illustrating the range of platform ornamentation included within the *texanus* plexus herein.

1. Pa element, with single pillar-like node on outer platform, sample CM 6, 26883 (x 50).
2. Pa element, with weak shoulder-like parapet and one or two scattered nodes, sample SQ 1, 26698 (x 35).
3. Pa element, with single elongate node in place of an outer parapet, sample CM 11, 26885 (x 60).
4. Pa element, with reduced outer platform and a short weak lineation parallel to the carina in place of an outer parapet, sample CM17, 26876 (x 50).
5. Pa element, with reduced and and unornamented outer platform, sample CM 17, 26844 (x 40).

In all of the above (which are dextral specimens) note the range of morphology of inner parapet, posterior tip and platform shape included here within the *texanus* concept.

6-9 *Gnathodus homopunctatus*

6. Pa element, mature specimen showing characteristic lateral view with high carina, flat lower profile and gently convex upper profile, sample, CM 2, 26866 (x 70).

7-9. Series of Pa elements illustrating ontogenetic progression.

7a. Pa element, very immature specimen, upper view showing relatively elongate platform outline and weak ornamentation, sample CM 2, 26869 (x 150).

7b. -oblique posterior view showing rounded node-like nature of early ornamentation.

8a. Pa element, immature specimen, upper view showing incipient development of ridges on both platforms, sample CM 2, 26868 (x 100).

8b. -oblique posterior view showing early development of platform ornamentation.

9a. Pa element, mature specimen, upper view showing lachrymiform platform outline, sample CM 2, 26865 (x 90).

9b. -oblique posterior view showing strongly developed platform ornamentation.

Plate 3

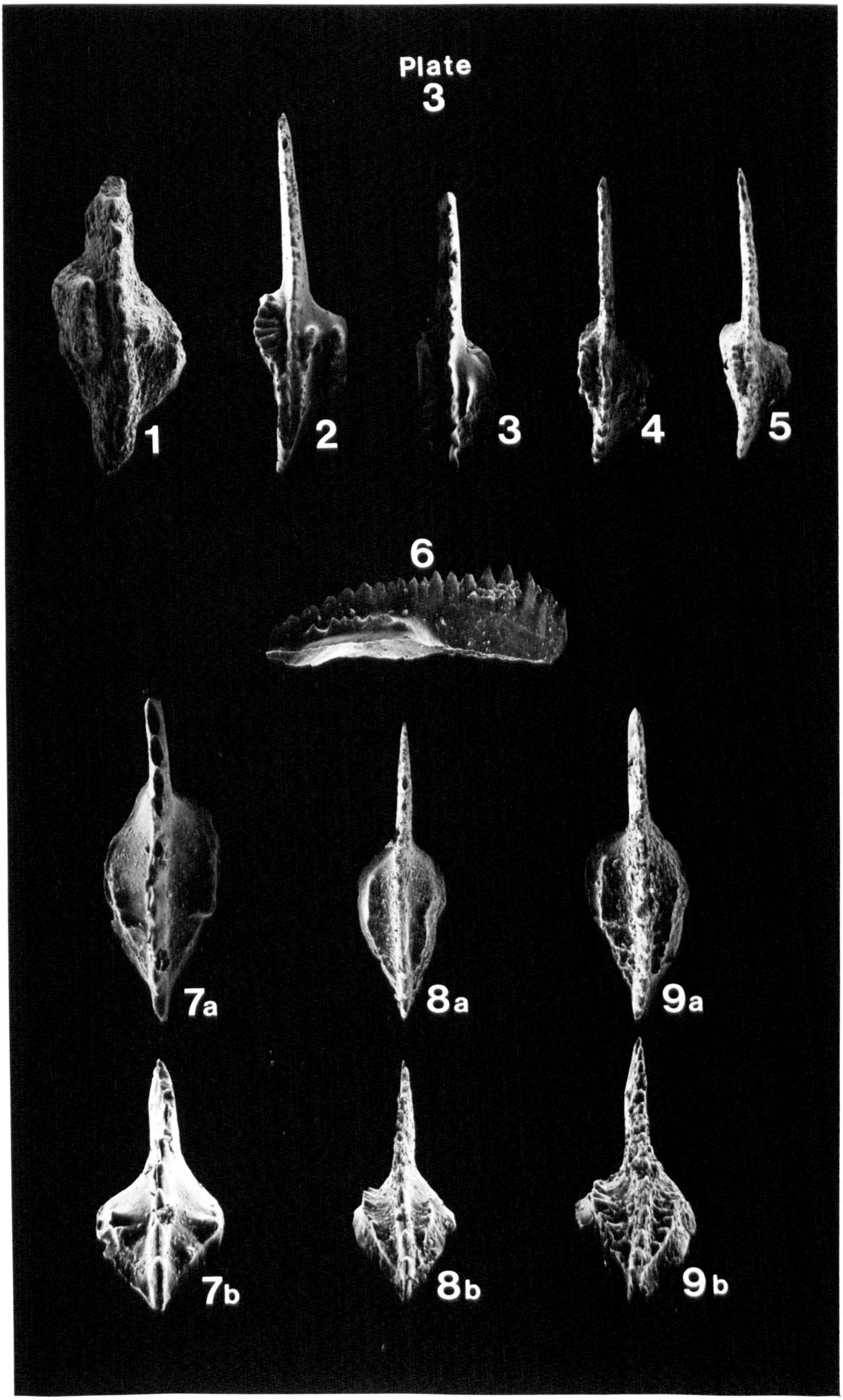


PLATE 4

1-2 *Gnathodus mermaidus*

1. Pa element, mature specimen upper view, sample CM 43, 26886 (x 60).

2a. Pa element, mature specimen oblique lateral view showing node-like nature of platform ornamentation sample CM 42, 26887 (x 45).

2b. -upper view.

3-5 *Gnathodus symmutatus*

3. Pa element, upper view showing weak development of carina and lack of any platform shoulders as seen on *G. homopunctatus* and *G. mermaidus*, sample T 5, 26891 (x 100).

4. Pa element, upper view showing lanceolate outline of platform, sample CM 2, 26889 (x 100).

5. Pa element, lateral view, sample CM 2, 26888 (x 90).

6-12 *Gnathodus* non-platform elements

6. Pb element, lateral view, sample CM 2, 26841 (x 35).

7. M element, lateral view, sample CM 2, 26893 (x 70).

8. Sa element, lateral view, sample CM 20, 26894 (x 90).

9. Sb element, lateral view of anterior part, sample CM 15, 26895 (x 45).

10. Sc_1 element, lateral view of anterior part, sample CM 4, 26896 (x 75).

11. Sc_2 element, lateral view of anterior part, sample CM 4, 26897 (x 65).

12. Sd element, upper view, sample CM 23, 26898 (x 45).

Plate 4



1



2a



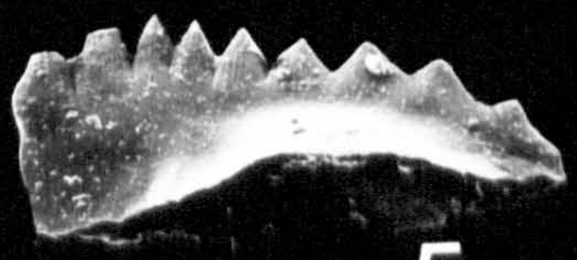
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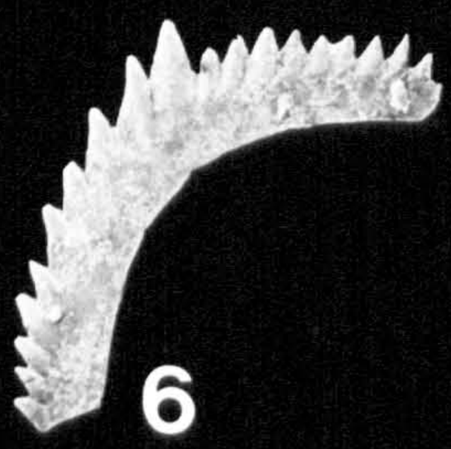
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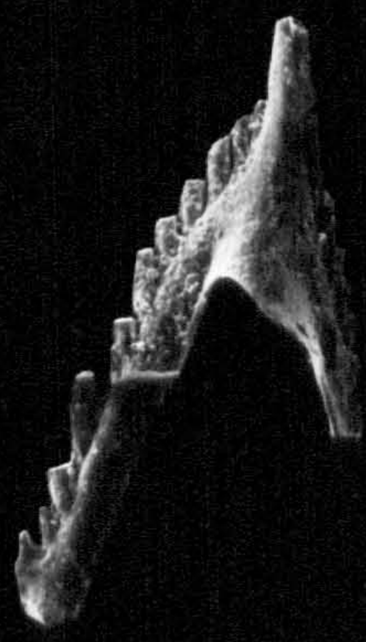
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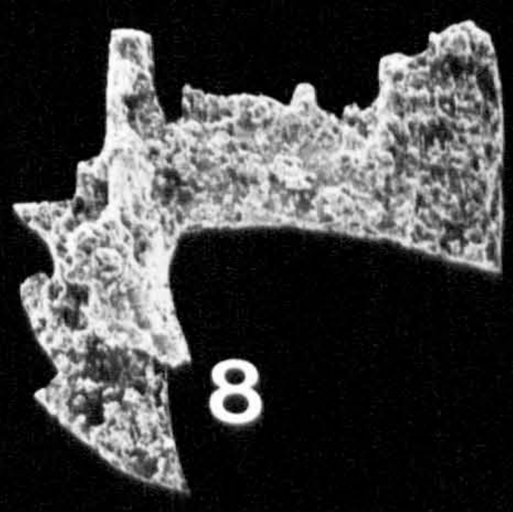
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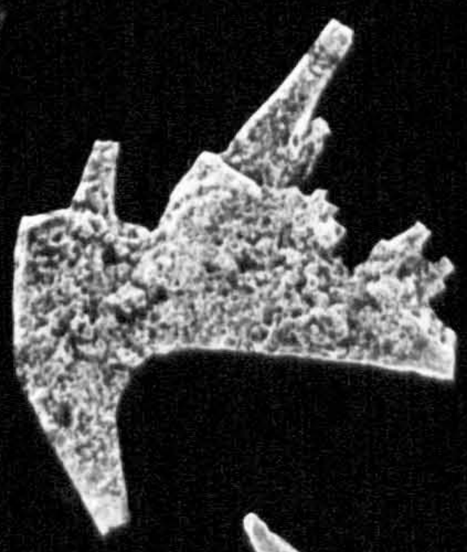
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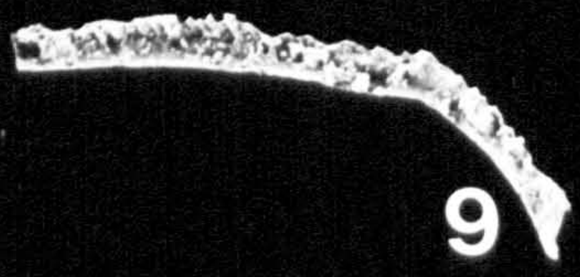
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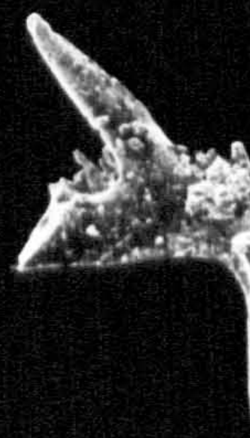
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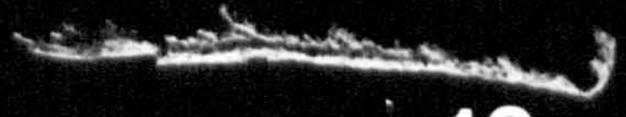
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PLATE 5

1-4 *Hindeodus cristulus*

1. Pa element, upper view, sample CM B4, 26899 (x 60).
2. Pa element, lateral view, sample B 4, 26900 (x 50).
3. Pb element, inner lateral view, sample CM 29, 26901 (x 120).
4. Sa element, posterior view, sample PE 1, 26902 (x 120).

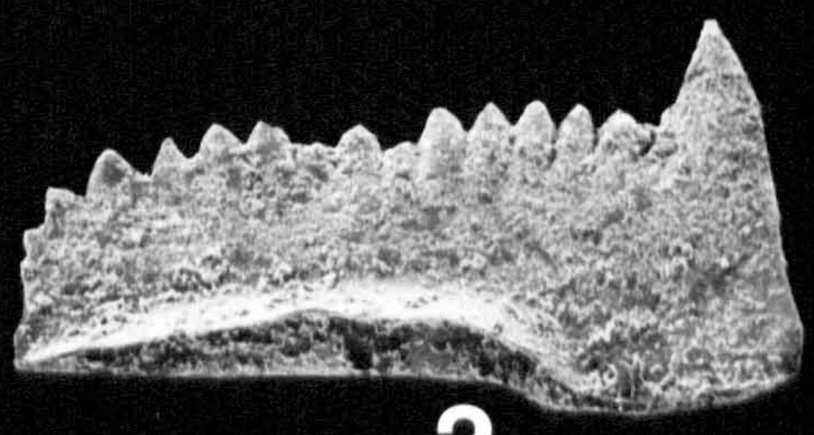
5-8 *?Hindeodus scitulus*

5. Pa element, lateral view, sample CM 9, 26694 (x 35).
6. Pb element, inner lateral view, sample SQ 1, 26903 (x 55).
7. M element, sample CM 38, 26695 (x 35).
8. Sc element, sample CM 43, 26905 (x 70).

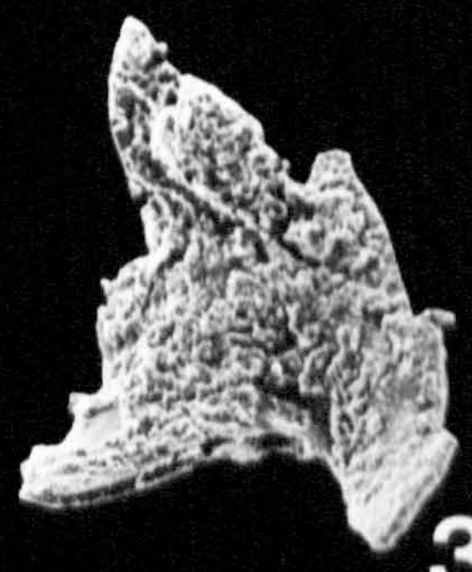
Plate 5



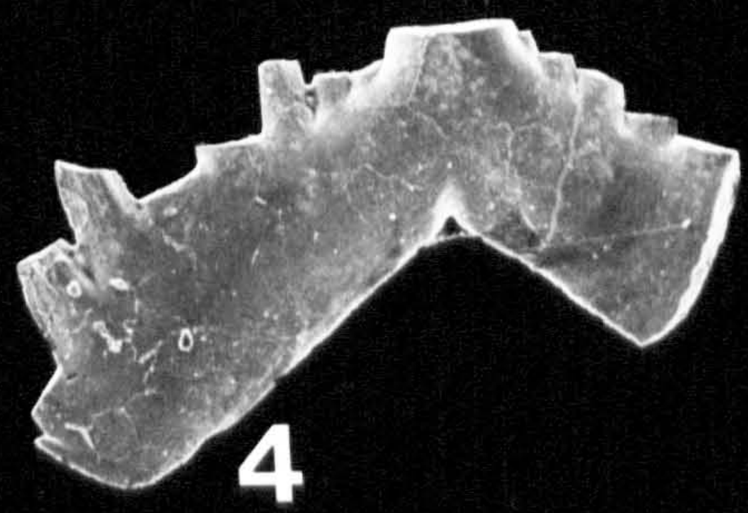
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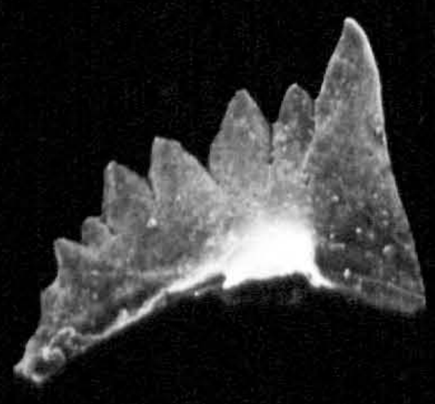
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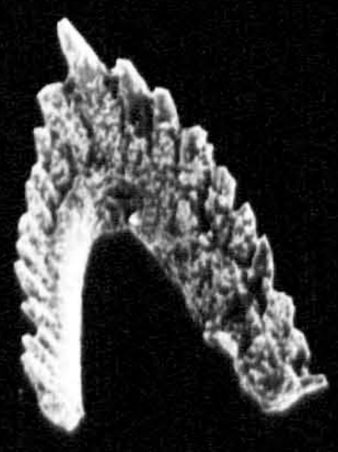
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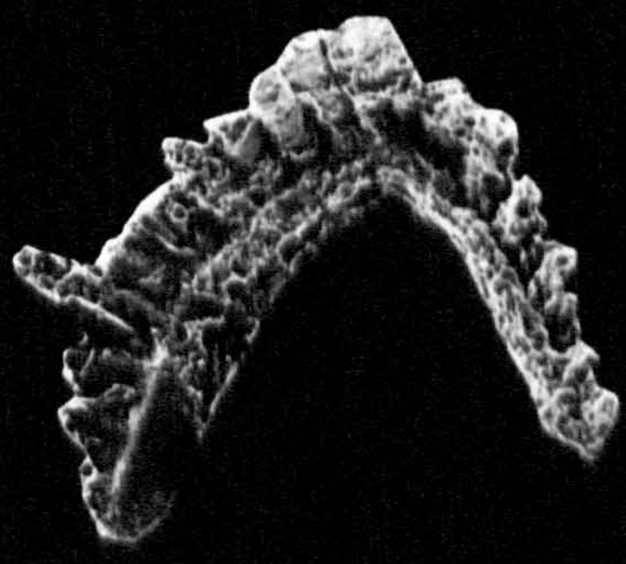
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PLATE 6

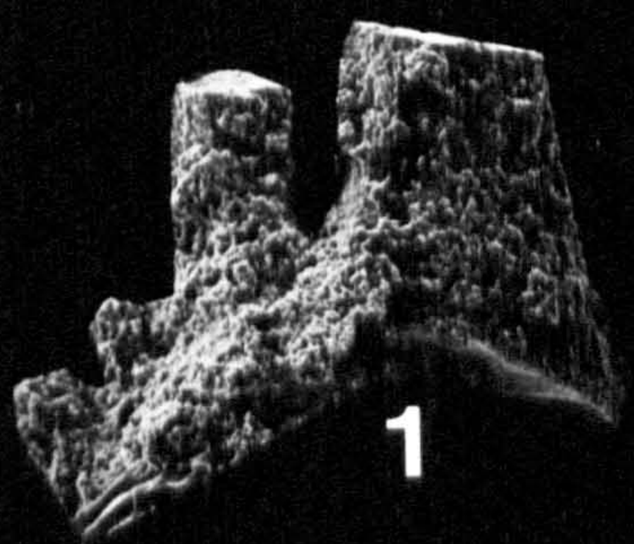
1-5 *Idioprioniodus* cf. *healdi*

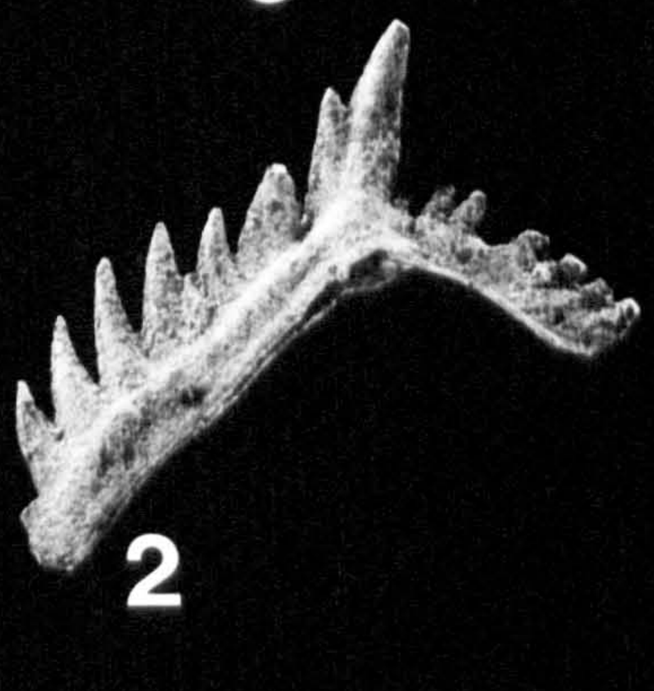
1. Pb element, lateral view, sample CM 14, 26906 (x 80).
2. Sb element, lateral view, sample SQ 2, 26907 (x 35).
3. Sc_1 element, posterior view, sample CM 24, 26908 (x 35).
4. Sc_2 element, lateral view, sample SQ 1, 26909 (x 45).
5. Sd element, inner lateral view, sample CM 37, 26910 (x 70).

6-11 *Kladognathus* aff. *levis*

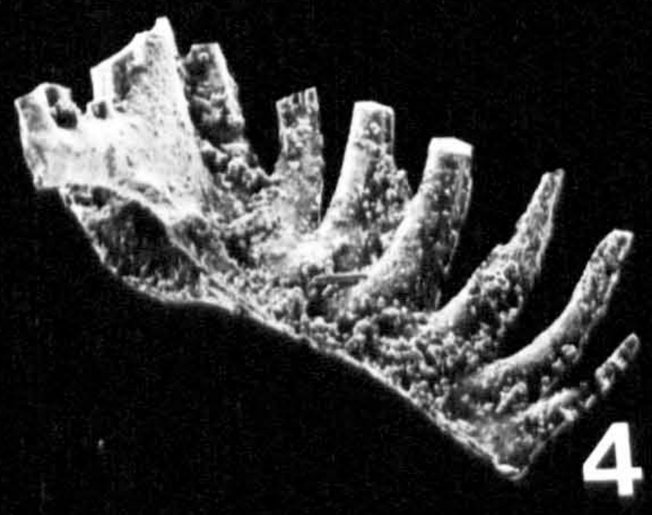
6. M element, lateral view (most of cusp missing), sample SQ 3, 26912 (x 50).
7. M element, lateral view, sample CM 27, 26853 (x 50).
8. Sa element, anterior view, sample PE 1, 26916 (x 65).
9. Sa element, lateral view, sample CM 23, 26915 (x 55).
10. Sb element, posterior view, sample CM 7, 26911 (x 65).
11. Sd element, inner lateral view, sample CM 2, 26917 (x 45).

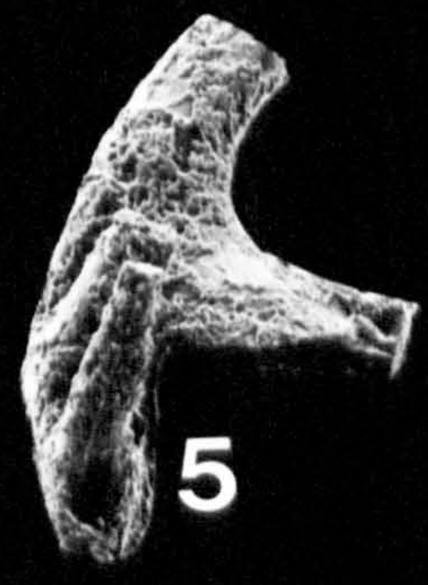
Plate 6

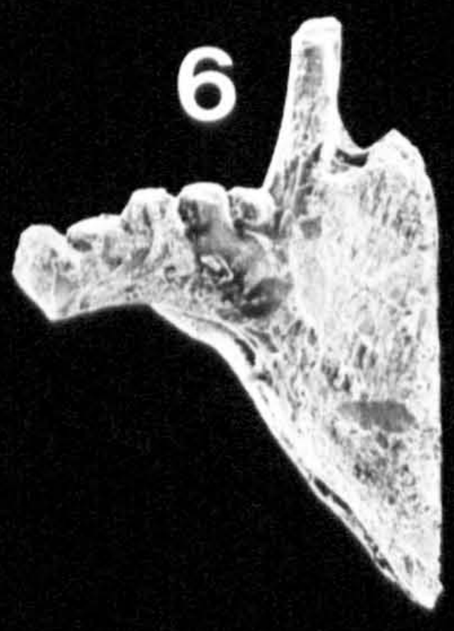

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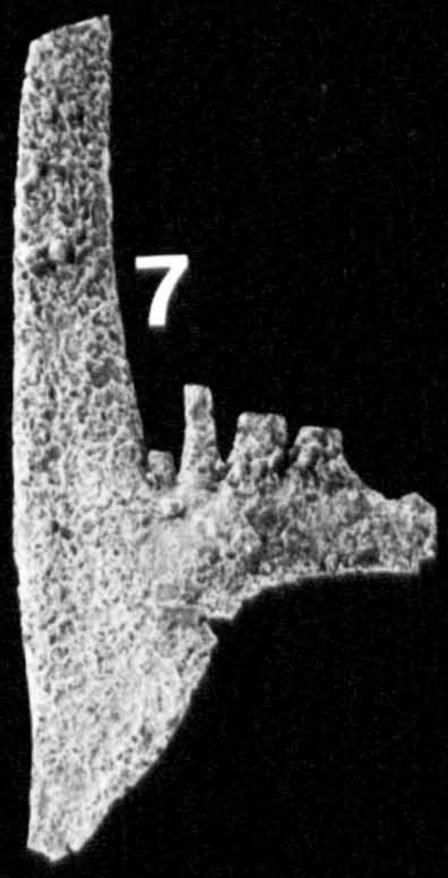

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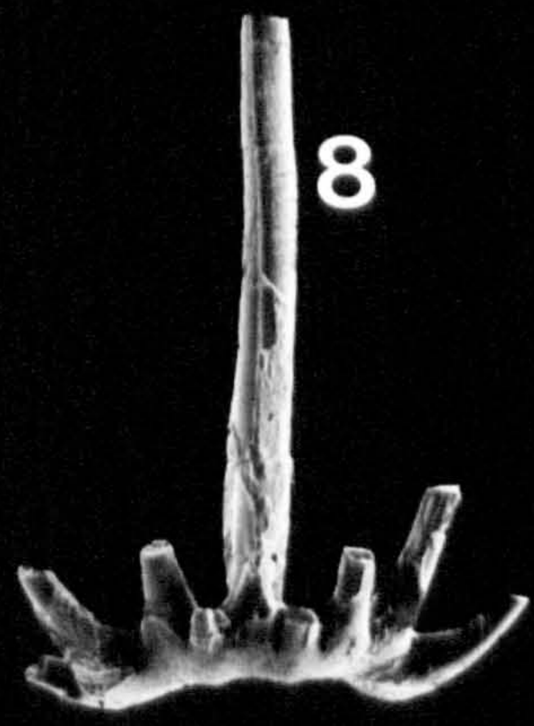

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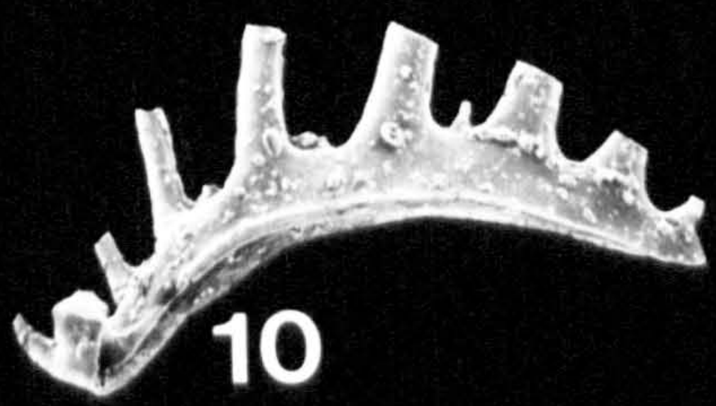

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PLATE 7

1-6 *Lochriea commutata*

1. Pa element, upper view, sample T 5, 26919 (x 60).
2. Pa element, lateral view, sample CM 43, 26918 (x 70).
3. Pb element, inner lateral view, sample CM 31, 26921 (x 60).
4. Pb element, inner lateral view, sample CM 7, 26920; see discussion of this unit under *L. commutata* Pb element in section 2.2h (x 70).
5. M element, inner lateral view (most of cusp missing) sample CM 22, 26922 (x 90).
6. Sc_1 element, inner lateral view, sample CM 31, 26924 (x 80).

7-8 *Mestognathus beckmanni*

7. Pa element, upper view, sample T 5, specimen lost (x 40).
8. Pa element, upper view, sample CM 40, 26696 (x 40).

9 *Patrognathus capricornis*

9a. Pa element, upper view, sample GL 7, 26925 (x 90).
9b. -lateral view.

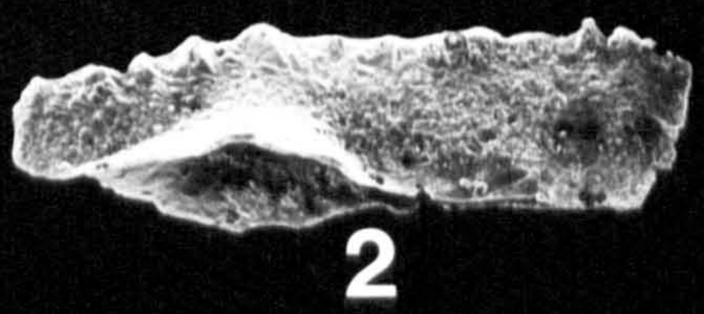
10 *Polygnathus bischoffi*

10a. Pa element, lateral view, sample GL 5, 26926 (x 100).
10b. -upper view.

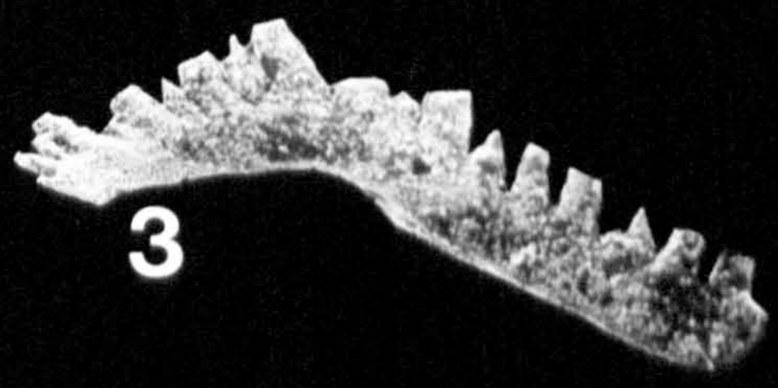
Plate 7



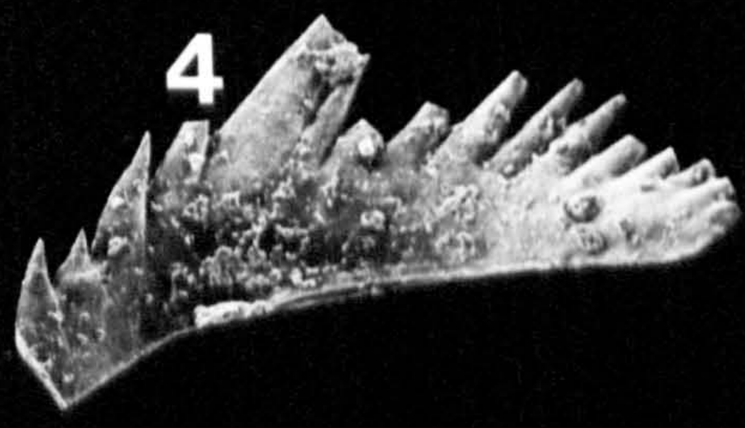
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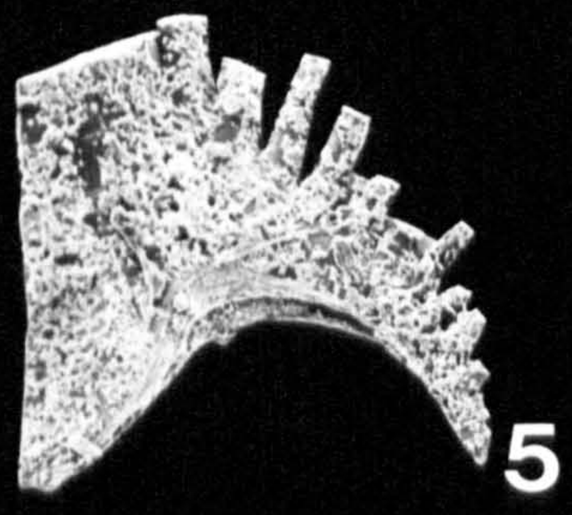
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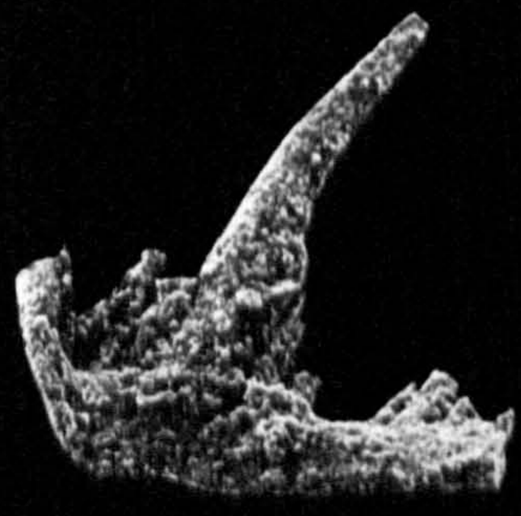
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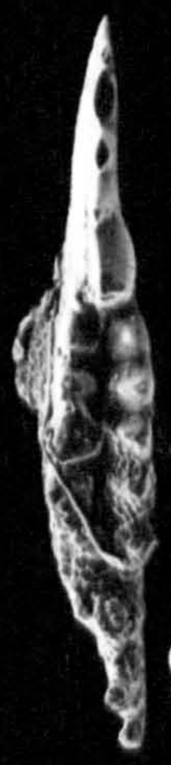
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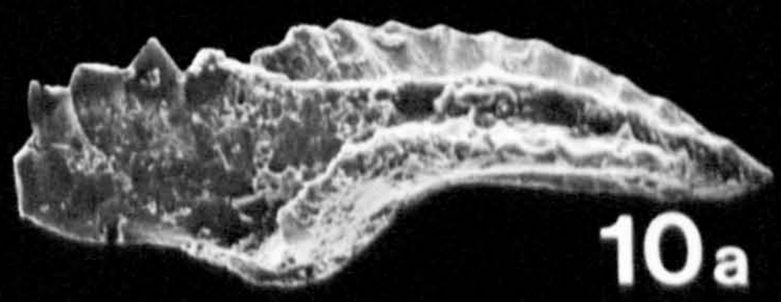
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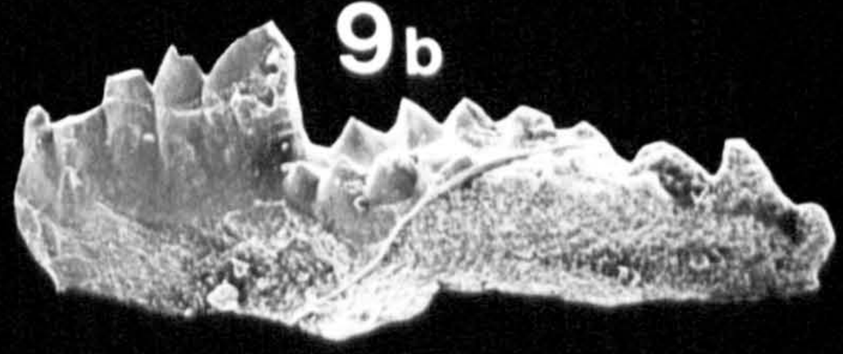
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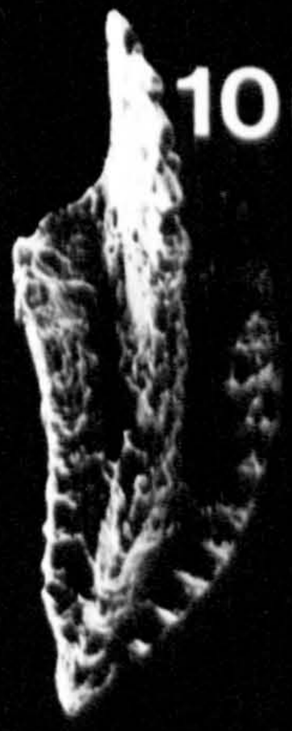
10a



8



9b



10b

PLATE 8

1-3 *Vogelgnathus* cf. *campbelli*

1. Pa element, upper view, sample GL 15, 26928 (x 100).
2. Pa element, lateral view, sample GL 15, 26927 (x 100).
3. Pb element, inner lateral view, sample GL 15, 26929 (x 100).

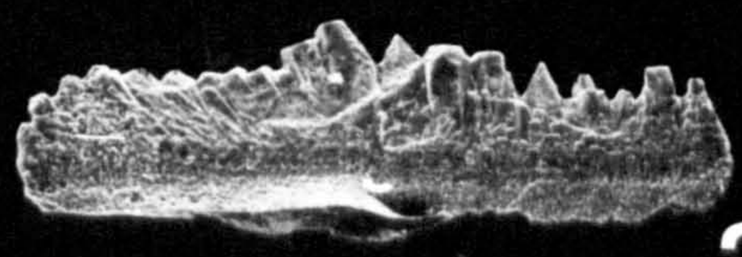
4-7 *'Apatognathus'* s.f.

4. *'Apatognathus' cuspidatus* s.f., sample CM 4, 26932 (x 50).
5. *'Apatognathus' cuspidatus* s.f., sample LL 3, 26874 (x 35).
6. *'Apatognathus' libratus* s.f., sample GL 14, 26933 (x 100).
7. *'Apatognathus' petilus* s.f., sample CM 27, specimen lost (x 80).

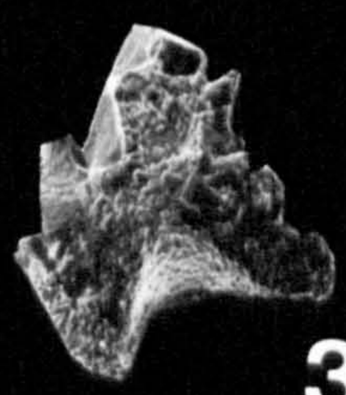
Plate 8



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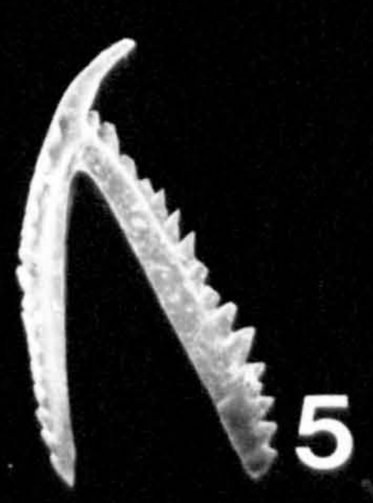
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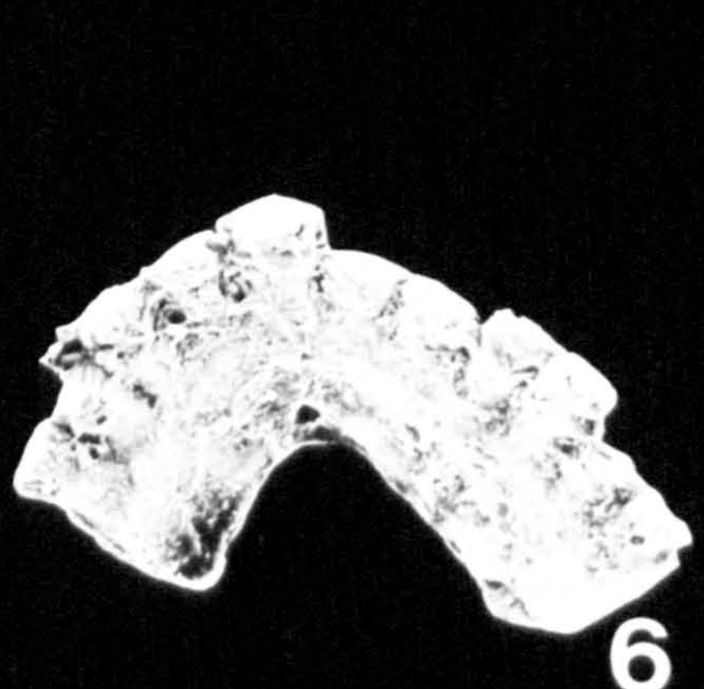
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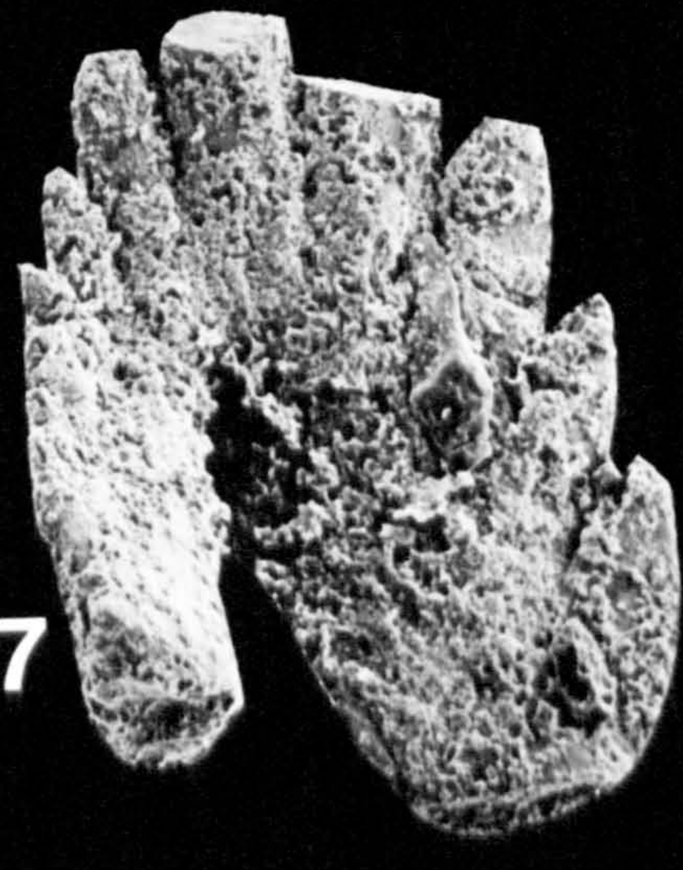
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7

PLATE 9

1. *Geniculatus claviger* s.f.
   1a. upper view, sample CM 9, 26935 (x 110).
   1b. -upper lateral view.
   1c. -lower lateral view.

2. *Angulodus* s.f. cf. sp. nov. B Rhodes *et al.* 1969.
   - inner lateral view, sample CM 4, 26930 (x 85).

3. Gen. et sp. nov. s.f. (orientation uncertain).
   3a. sample CM 4, 26931 (x 100).
   3b. -as above, with rotation of specimen.

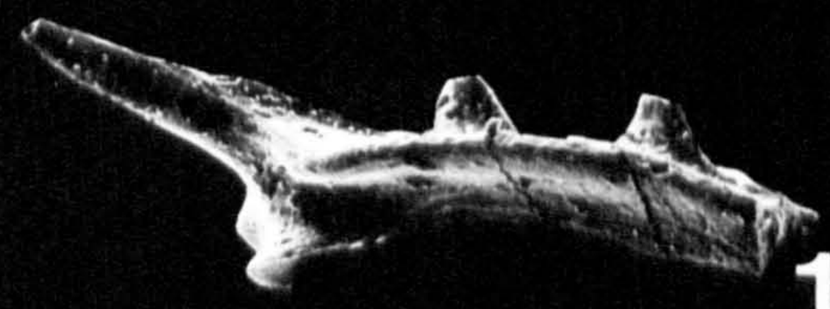
Plate 9



1a

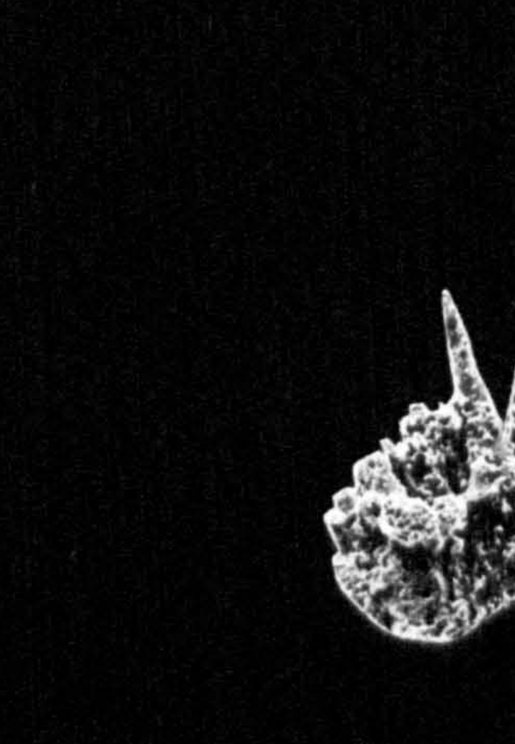


1b

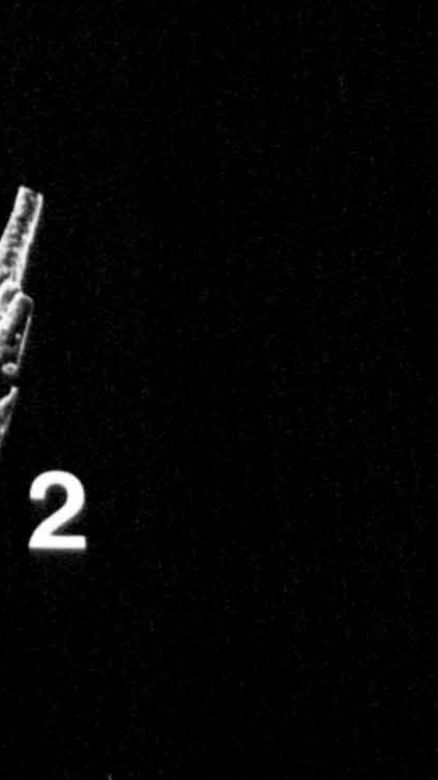


1c

2



3a



3b

2.3 RESULTS, DISCUSSION AND CONCLUSIONS.

2.3a Introduction.

The numbers of each conodont element recognised in the present study are tabulated in appendix C (tables C1-C4); and the following discussion is based on these findings. The outer and mid-ramp faunas are discussed under three main headings:

- environmental controls on conodont distribution.
- stratigraphical aspects of the findings.
- implications for conodont phylogeny.

The Llanelly Quarry fauna is discussed separately (2.3e). It should be borne in mind that the following discussion is offered with the caveat that the limited number of specimens recovered precludes statistically valid conclusions in many cases.

2.3b Environmental controls on the conodont distribution.

The results under discussion in this section are those from the precisely sampled outer ramp and mid-ramp localities on the south coast of Dyfed, details of which are shown in figs 2.1.4 and 2.1.5. Broadscale differences can be seen between the generalised outer ramp and mid-ramp faunas obtained from combining the Castlemartin and Stackpole Quay results (outer ramp), and the Lydstep Haven, Giltar Point and Tenby results (mid-ramp).

Within the outer ramp Pen-y-Holt facies there is a relatively rich conodont fauna, giving an average yield of 10.7 elements per kilogram. Elements of the genus Gnathodus dominate, and make up approximately 70% of the fauna. In order of abundance, the other genera recovered are: Idioprioniodus, Lochriea, ?Hindeodus, Kladognathus, Hindeodus, Vogelgnathus and Mestognathus. Discrete elements of 'Apatognathus' s.f. make up 4.4% of the fauna, and various other discrete elements make up the remainder (see table C.1 of appendix C).

The mid-ramp fauna shows greater generic diversity (with the addition of Cavusgnathus, Patrognathus, and Polygnathus); but the overall abundance of 1.9 elements per kilogram is markedly lower than that of the outer shelf. Gnathodus, although still the most abundant, accounts for just 20% of the fauna and the order of abundance of the other genera is slightly altered to read: Lochriea, ?Hindeodus, Mestognathus, Idioprioniodus, Kladognathus, Cavusgnathus, Patrognathus, Vogelgnathus, Polygnathus and Hindeodus. Discrete elements of 'Apatognathus' s.f. make up 16% of the total.

Purely in terms of relative abundance, the important components of the outer and mid-ramp faunas can be divided into four groups:

Group 1 includes only Gnathodus, which is by far the most abundant genus.

Group 2 contains Idioprioniodus, Kladognathus, Lochriea and ?Hindeodus, which together form an appreciable component of the fauna throughout, accounting for approximately 60% and 40% of the non-Gnathodus outer and mid-ramp faunas respectively.

Group 3 comprises Hindeodus and Vogelgnathus which are scarce, but present throughout. These genera account for approximately 2% and 8% of the non-Gnathodus outer and mid-ramp faunas respectively.

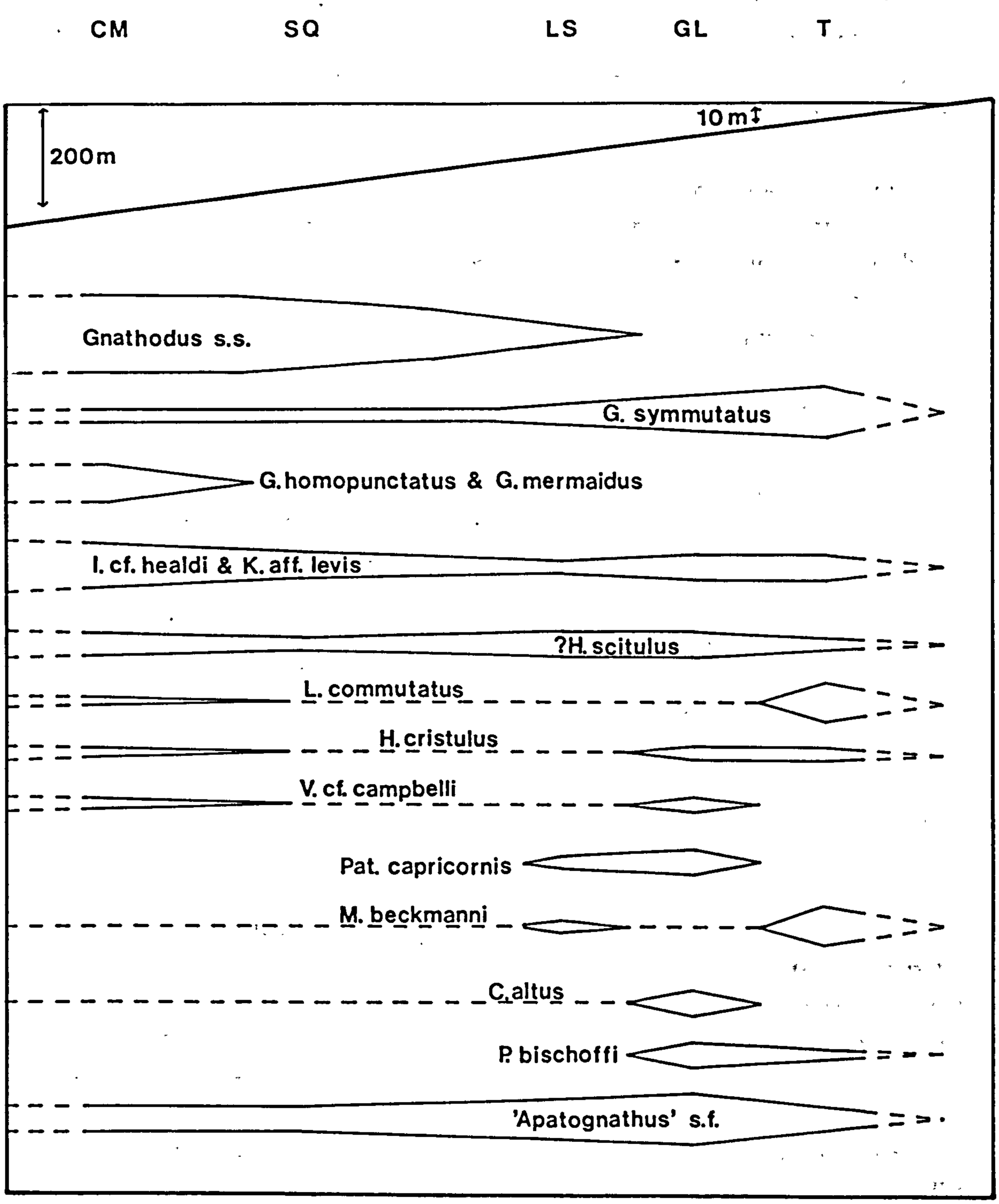
Group 4 consists of Polygnathus, Mestognathus, Cavusgnathus and Patrognathus. These genera form an appreciable part of the mid-ramp fauna, and account for approximately 25% of the non-Gnathodus component; whereas in the outer ramp they account for less than 1%.

Relating the pattern of relative abundance (elements/kg) to the sedimentological facies sequences represented by the Dixon groups does not reveal an unequivocal correlation (see table C4 of appendix C). The comparable Dixon groups of Castlemartin and Stackpole Quay show the same relative pattern, decreasing from a markedly high abundance in group 7 times to low abundance in group 9 times, although collections from Stackpole Quay are always less rich. In the mid-ramp the Lydstep Haven and Tenby figures do seem to follow the same general trend, with highest abundances during group 3 times and second highest during group 1 times. Giltar Point, however shows a completely different pattern; but too much should not be made of this in light of the low number of specimens on which many of these observations are based.

Moving away from relative abundances to an analysis of patterns of occurrence on a simple presence/absence basis, it is interesting to note that although different species show different (coeval) patterns these do not appear to tie in with the Dixon groups. It would seem that whatever the environmental factors are which control the distribution of conodont species, they are more subtle than those controlling the sequence of sedimentological "packages".

A number of favoured ecological associations can be deduced from the data, although these are by no means binding or mutually exclusive. As abundance and distribution patterns are closely related in a low frequency fauna such as that of the present study, the ecological associations can best be elucidated by examining, in turn, each of the relative-abundance groupings of the previous page (and fig. 2.3.1).

figure 2.3.1 Cross-ramp section for mid-Arundian times, showing the presumed relative positions of the sample sites and the interpreted conodont distribution-patterns. The thickness of the horizontal bars at any point is proportional to the relative percentage of that species' total population at that point. (the vertical scale used for each group is not constant). CM = Castlemartin, SQ = Stackpole Quay, LS = Lydstep Haven, GL = Giltar Point and T = Tenby.



Group 1 (Gnathodus).

Species of "Gnathodus sensu stricto" show a different distribution pattern from the species of "the homopunctatus group" (see remarks in section 2.2d for an explanation of these divisions). In the outer ramp, the former tend to occur throughout successive samples (to a varying extent), but their distribution appears to show a marked stratigraphical control (fig. 2.3.4). There is no apparent correlation with the occurrence pattern of any of the other groups. Species of "Gnathodus sensu stricto" have only been recovered from Lydstep Haven in the mid-ramp, and in each case there are no co-occurring species. These elements recovered from the mid-ramp are all Pa elements, and are generally only approximately two thirds the size of their counterparts from the outer ramp.

The distribution pattern of G. mermaidus (of "the homopunctatus group") probably has a degree of stratigraphical control (only occurring in upper Arundian rocks), but it can be noted that G. mermaidus has only been recovered from samples which also contain G. aff. girtyi. G. homopunctatus ranges throughout most of the outer ramp section but has a patchy distribution - which suggests a high degree of facies control. Although it is only seen in seven of the fifty outer ramp samples, where it does occur it can make up a high proportion of the fauna (e.g. samples CM 2 and CM 9). G. homopunctatus has not been recorded from the mid-ramp sites. G. symmutatus has a similarly patchy distribution to that of G. homopunctatus, but is generally less abundant in the outer ramp, and is found in the mid-ramp sites.

Group 2 (Idioprioniodus, Kladognathus, Lochriea and ?Hindeodus).

I. cf. healdi and K. aff. levis have a similar distribution pattern, and commonly occur in the same samples. L. commutata often co-occurs with the above, but shows a stratigraphical overprint on its distribution - increasing in abundance toward the end of the Arundian Stage. ?H. scitulus also does not occur in early Arundian times but often co-occurs with other members of this group.

Group 3 (Hindeodus and Vogelgnathus).

Both members of this group share a similar overall distribution pattern, although they have not been recovered together in the same sample in this study. This mutual exclusion can be more easily explained by their general rarity than by invoking any ecological control.

Group 4 (Polygnathus, Mestognathus, Cavusgnathus and Patrognathus).

P. bischoffi has only been recovered from Giltar Point and Tenby (probably the most nearshore sites), and in sample GL 5 co-occurs with the cavusgnathoid species P. capricornis and C. altus. The latter two species show a

close association with each other but do not co-occur with M. beckmanni. This is highlighted in sample T 5, from which P. capricornis and C. altus are absent but an unusually high number of M. beckmanni elements co-occur with an unusually high number of L. commutata and G. symmutatus elements. Dixon's group 9 of the Pen-y- Holt Limestone was probably a time of relatively shallow conditions, which occurred as the late-Arundian sea regressed southwards, and it is notable that this is the only time when Mestognathus occurs in the outer ramp (albeit a single specimen). This suggests that species recovered from the outer ramp during group 9 times were tolerant of relatively shallow conditions (e.g. L. commutata, G. aff. girtyi and G. mermaidus). However the evidence for this is only circumstantial, although Higgins (1981) lists L. commutata and G. girtyi as minor components of nearshore biofacies, as well as occurring in deeper water environments.

In a broad sense the above observations are in accordance with what might have been predicted by the various biofacies models reviewed in section 1.2g. That is to say that the most abundant mid-Viséan faunas are to be found in distal shelf settings, and are dominated by Gnathodus. More proximal shelf faunas contain a higher proportion of cavusgnathoid forms and elements of 'Apatognathus' s.f. However, in a more detailed comparison with the present fauna, several discrepancies with the above models are highlighted.

Two major shortcomings of the three-phase model of Druce (1973) are that it is oversimplified, particularly with respect to elements of his I and II biofacies; and that it does not account for species without Pa elements. Similarly although the relative distribution pattern of Austin (1976) essentially agrees with that of the present study (fig. 2.3.1), Austin's sedimentological framework is too generalised to be of practical application in specific areas. Also the observation that scaphate Pa elements tend to be restricted to shallow water and planate elements to deeper water is not borne out, and the designation of Polygnathus as a deeper water group than Gnathodus in the Viséan is presumably only true of pre-Arundian times.

von Bitter (1976) and Austin and Davies (1984) discriminate between a more offshore Gnathodus dominated biofacies; and a more onshore biofacies association of Cavusgnathus, Mestognathus and 'Apatognathus' s.f. Austin and Davies (1984) suggest that within the latter biofacies, Mestognathus and 'Apatognathus' s.f. are less tolerant of fluctuating salinity conditions than Cavusgnathus. If this is true, it is probable (due to its high level of association in the present study) that Patrognathus should be included with Cavusgnathus as being a more euryhaline genus. A drawback with the dual shelf/basin scheme of conodont biozones proposed by Austin and Davies (1984) is that Taphrognathus is cited as being the form typical of lower Arundian shelf faunas (fig. 1.4.1), but has not been recovered at all in the present study. In dealing

specifically with a conodont fauna from the Arundian Pen-y-Holt Limestone of Stackpole Quay, Austin and Davies (1984) suggest that Gnathodus inhabited a quiet, shallow, stenohaline environment, of no more than a few metres depth. In light of the sedimentological argument favoured herein, it is more likely that the Pen-y-Holt Limestone was not deposited in shallow water conditions; and that the depth stratified, shelf-edge (approximately 100m - 200 m water depth) life habit for Gnathodus suggested by Sandberg is correct (in: Lane et al 1980). However the possibility that different Gnathodus species exhibited different life-habits should not be overlooked. The observation that Lochriea commutata probably lived further offshore than Gnathodus (Austin and Davies 1984) is not supported by the findings of the present study.

The most comprehensive attempt to establish a series of coeval conodont biofacies for Dinantian times is that of Sandberg and Gutschick (1984 - see fig. 1.2.6), as reviewed by Dreesen et al. (1986). In this scheme a standardised cross-shelf profile is divided into seven biofacies which occupy linear belts paralleling the coastline (of which biofacies III to VII are relevant to this discussion). The findings of the present study support the proposed life habit of Gnathodus (see above) and, to a lesser extent, Hindeodus (distal mid-ramp) and Mestognathus (harsh, nearshore, hypersaline lagoons). It should be noted that in von Bitter et al. (1986), Sandberg's interpretation of the Mestognathus habitat is slightly expanded, such that Mestognathus is considered to have been euryhaline, but to have become more widespread through time.

The South Wales Arundian conodont fauna can be divided into two major biofacies:

1. A distal-shelf biofacies association, dominated by mature elements of Gnathodus sensu stricto with G. homopunctatus, but lacking a sizeable cavusgnathoid component.
2. A proximal-shelf biofacies in which Gnathodus sensu stricto is comparatively rare, G. symmutatus accounts for a high proportion of the Gnathodus elements recovered and cavusgnathoid species and Polygnathus bischoffi occur.

With a larger data base than that of the present study, there is the potential for further subdivision of these two major biofacies - particularly in the proximal shelf (e.g. separate M. beckmanni - L. commutata and C. altus - Pat. capricornis biofacies). The results are not sufficient to elucidate the palaeoenvironmental parameters involved in the distribution of the conodonts recovered.

In light of the present study, criticisms of the Sandberg and Gutschik (1984) model are that it contains more subdivisions than are actually seen, and appears to be over restrictive in delineating ecological limits for given genera. Some of these discrepancies may be explained by Sandberg and Gutschik's use of a rimmed-platform sedimentological model, and the fact that their biofacies

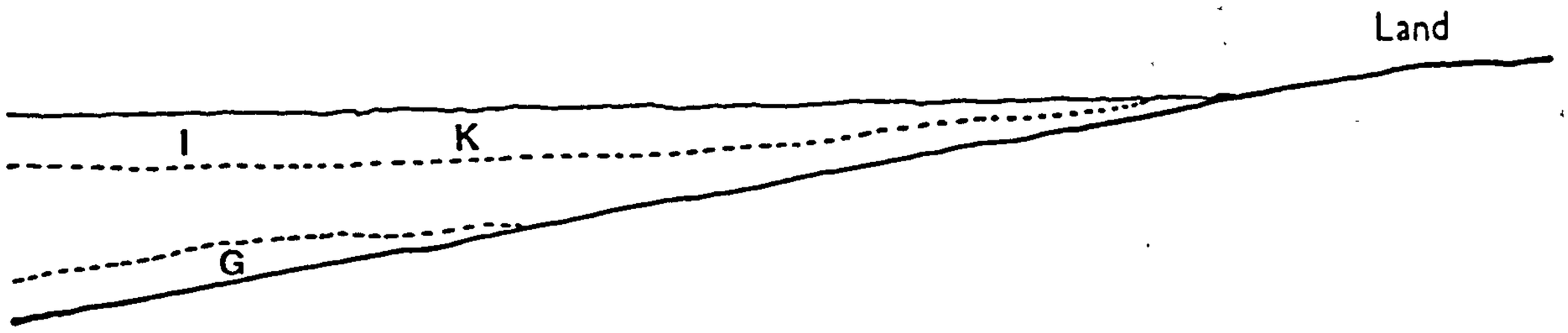
are derived from the more diverse faunas of the anchoralis-latus Zone (late Courceyan). Dreesen et al. (1986) suggest that mixing of their proposed biofacies, as occurs herein, may be explained by processes such as tidal currents and storm surges. While these play a part, it seems likely that the range of life habits exhibited by the different species within a particular fauna was more varied than Dreesen et al. (1986) suggest (see fig. 1.2.6).

An important point to arise from the distribution of Gnathodus across the South Wales ramp is that biofacies associations at a generic level may be misleading, and studies should be made at the specific level where possible.

The cross-shelf associations discussed above are mainly based on empirical, sedimentological observations, and are not necessarily to be viewed as palaeoecological models linked to aspects of life habit. The work of Klapper and Barrick (1978) has shown that the results of an element distribution study (as presented here), rarely provides conclusive evidence in support of a specific palaeoecological model of conodont life habit (e.g. Seddon and Sweet 1971, Barnes and Fåhræus 1975). However, possibly the most elegant explanation of the distribution seen across the South Wales Arundian ramp, is to invoke a combination of planktic and nektobenthic life habits (Barnes 1976). Elements of Gnathodus sensu stricto dominate the deeper water outer ramp environment, and stunted or juvenile elements are occasionally recovered from slightly more onshore. This suggests a depth stratified habitat, with mature individuals living preferentially at a depth greater than that of the mid-ramp sea floor (well below normal wave base). In contrast, mature elements of Idioprioniodus and Kladognathus occur, without morphological or size differences, right across the shelf - suggesting a more planktic, free-swimming life habit (fig. 2.3.2).

It is tempting to speculate one stage further and link the differences in the apparatus plans of the above to the differing requirements of their life-habits, however without further knowledge of the function of the conodont apparatus it is not possible to be more specific.

figure 2.3.2 Suggested preferred life-habits of Gnathodus s.s. and Idioprioniodus & Kladognathus, during Arundian times.



G = Gnathodus habitat.
IK = Idioprioniodus and Kladognathus habitat.

2.3c Stratigraphical aspects of the findings.

The outer ramp, Pen-y-Holt Limestone of South Wales can be subdivided into a sequence of three conodont biozones, based on the first occurrences of species of Gnathodus s.s. (fig. 2.3.3). This biozonation is broadly applicable to distal parts of the mid-ramp, High Tor Limestone, but the comparatively low conodont abundance, and the lack of mature specimens of Gnathodus s.s. mean that stratigraphical precision is lost. The stratigraphical range of each species, throughout the sampled intervals, is shown in figures 2.3.4 and 2.3.5. The species ranges have been plotted on composite sections, which are derived from correlating the bases of each Dixon group between relevant sample sites (for an explanation of these groups see section 2.1d parts i and ii).

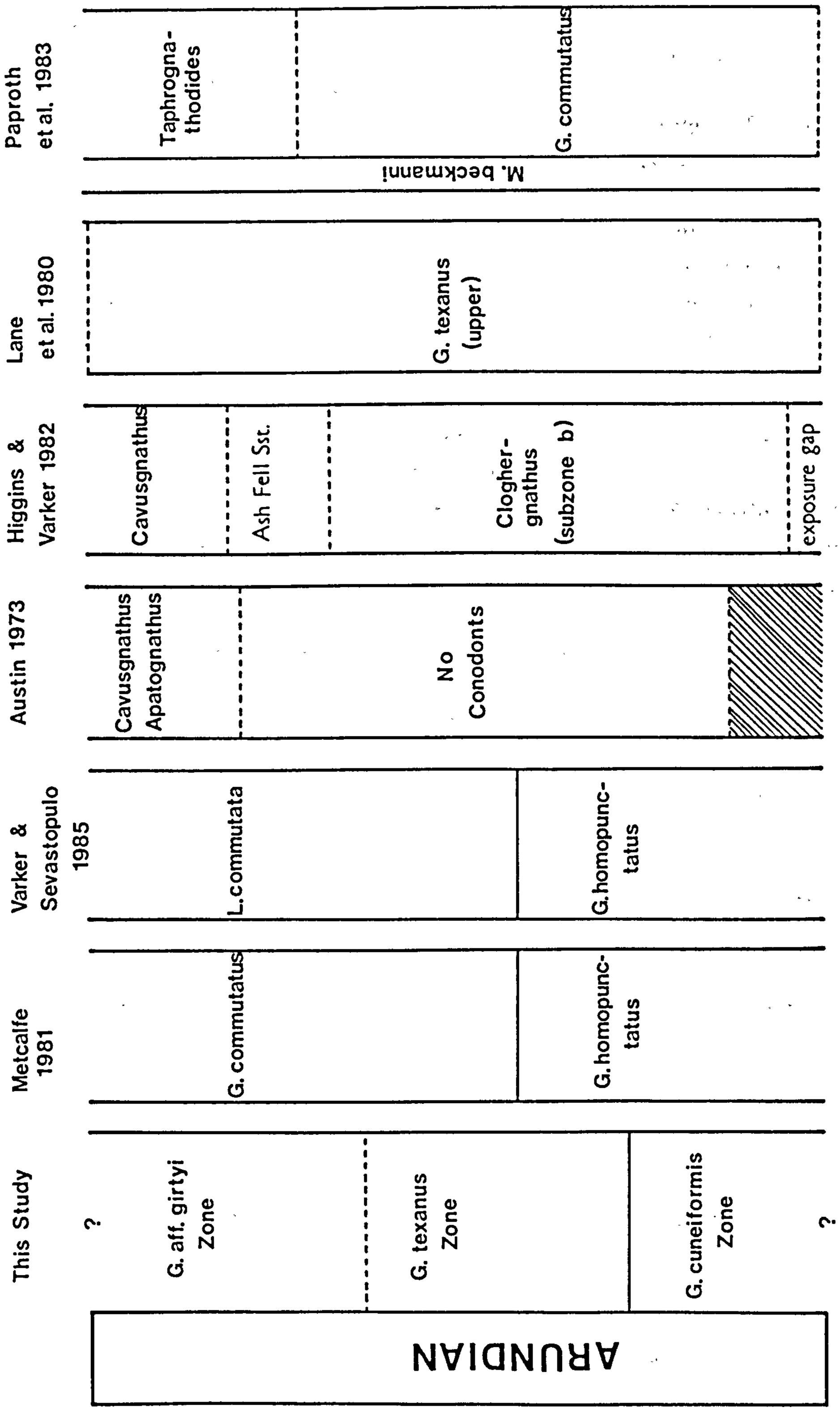
The following series of stratigraphical biozones (fig. 2.3.3) pertain to the outer ramp Pen-y-Holt Limestone, sampled at Castlemartin and Stackpole Quay, and the Dixon groups referred to are not correlatable with those for the mid-ramp sites.

i) Gnathodus cuneiformis Zone.

This zone covers the lowest part of the Arundian succession sampled, and extends upwards into Dixon's group 5 (fig. 2.1.4). The position of the base of the G. cuneiformis Zone has not been established in the present study. In a report on the conodont fauna recovered from the Chadian/Arundian boundary at Castlemartin, Austin (1987) records G. typicus (here synonymised with G. cuneiformis) as ranging from at least 16 m below the base of the Arundian section. This might suggest that the cuneiformis Zone can be assumed to stretch down at least as far as the lower part of the Hobbyhorse Bay Limestone (Chadian). However two complications arise in incorporating the information of Austin (1987) into the present scheme.

Firstly, correlation of the horizons sampled is difficult; the base of Austin's sample AR 23 is the base of the distinctive mudstone from which sample CM 1 was taken in the present study (Ramsbottom 1981). Therefore figure 13.2 of Austin (1987) places the base of the Arundian Stage approximately 5 m above the point taken herein (Simpson 1985). The figure on page 14.4 of Ramsbottom (1981), places the base of the Arundian Stage 17 m below Austin's sample AR 23, (approximately 2.5 m above the point taken herein). A further complication in attempting to correlate the base of the Arundian Stage between the different studies is that in the photographs of the stratotype section on page 14.3 of Ramsbottom (1981), the base of the Arundian Stage is shown at a level several metres below that of the present study. Much of the confusion outlined above probably results from the fact that Ramsbottom (1981) stated the basal Arundian units to be inaccessible, and had to estimate thicknesses.

figure 2.3.3 The Pen-y-Holt conodont zonation scheme compared with various established schemes for the same time interval (dotted lines imply an inferred correlation).



Austin (pers. comm. 1984) was only able to sample the basal Arundian beds through the use of an army abseil team. Simpson (1985) found the basal Arundian part of the Castlemartin section to be accessible through a narrow clifftop gully to the east of Hobbyhorse Bay, and was thus able to log the section accurately. For this reason the measurements of Simpson (pers. comm. 1985) are used in the present study.

The second complication with incorporating the data of Austin (1987) into the present study is one of species definition. As well as G. typicus (= G. cuneiformis), Austin (1987) reports numerous specimens of G. pseudosemiglaber from the Chadian/Arundian boundary beds. The majority of the specimens illustrated have well-developed outer parapets and appear synonymous with G. cuneiformis herein. However, in upper view it is often difficult to distinguish between G. cuneiformis and G. texanus as defined in the present study; and some of Austin's specimens appear closer to the latter (e.g. Austin 1987, Plate 13.1 figs 15, 25 and 26). Because of this, G. pseudosemiglaber of Austin (1987) is not formally synonymised with G. cuneiformis in section 2.2d of this study.

If all specimens of G. pseudosemiglaber of Austin (1987) can be synonymised with G. cuneiformis, the G. cuneiformis Zone of the present study can be said to range at least 11 m below the base of the Arundian Stage (as understood herein). However, if some of the Chadian and lower Arundian specimens of G. pseudosemiglaber of Austin (1987) are synonymous with G. texanus of the present study, the G. cuneiformis Zone does not exist, and the occurrence of G. cuneiformis without G. texanus in samples CM B1 to CM 5 must either reflect localised facies control on the distribution of G. texanus, or result from statistically invalid sampling. In this case the G. texanus Zone would extend throughout the G. cuneiformis Zone of this study.

Pending further investigation, it is considered most likely that all G. pseudosemiglaber specimens of Austin (1987) are synonymous with G. cuneiformis, and the G. cuneiformis Zone is therefore considered to be valid. This Zone probably correlates, at least in part with the Gnathodus cuneiformis Assemblage Zone of Austin and Husri (1974), which was reported from the Durnish Limestone of County Limerick, where the Zone immediately underlies the first occurrence of L. commutata (see discussion below on use of inception of L. commutata for correlation).

ii) Gnathodus texanus Zone.

This zone covers the upper two thirds of Dixon's group 5, his group 6 (from which no conodonts were recovered), and most of his group 7 (fig. 2.1.4). The upper limit of the G. cuneiformis Zone is defined by the lower limit of the succeeding zone, which is marked by the first occurrence of G. texanus. In the present study this occurs in sample CM 6 towards the base of Dixon's group 5

figure 2.3.4 Species range chart for the outer ramp sites.

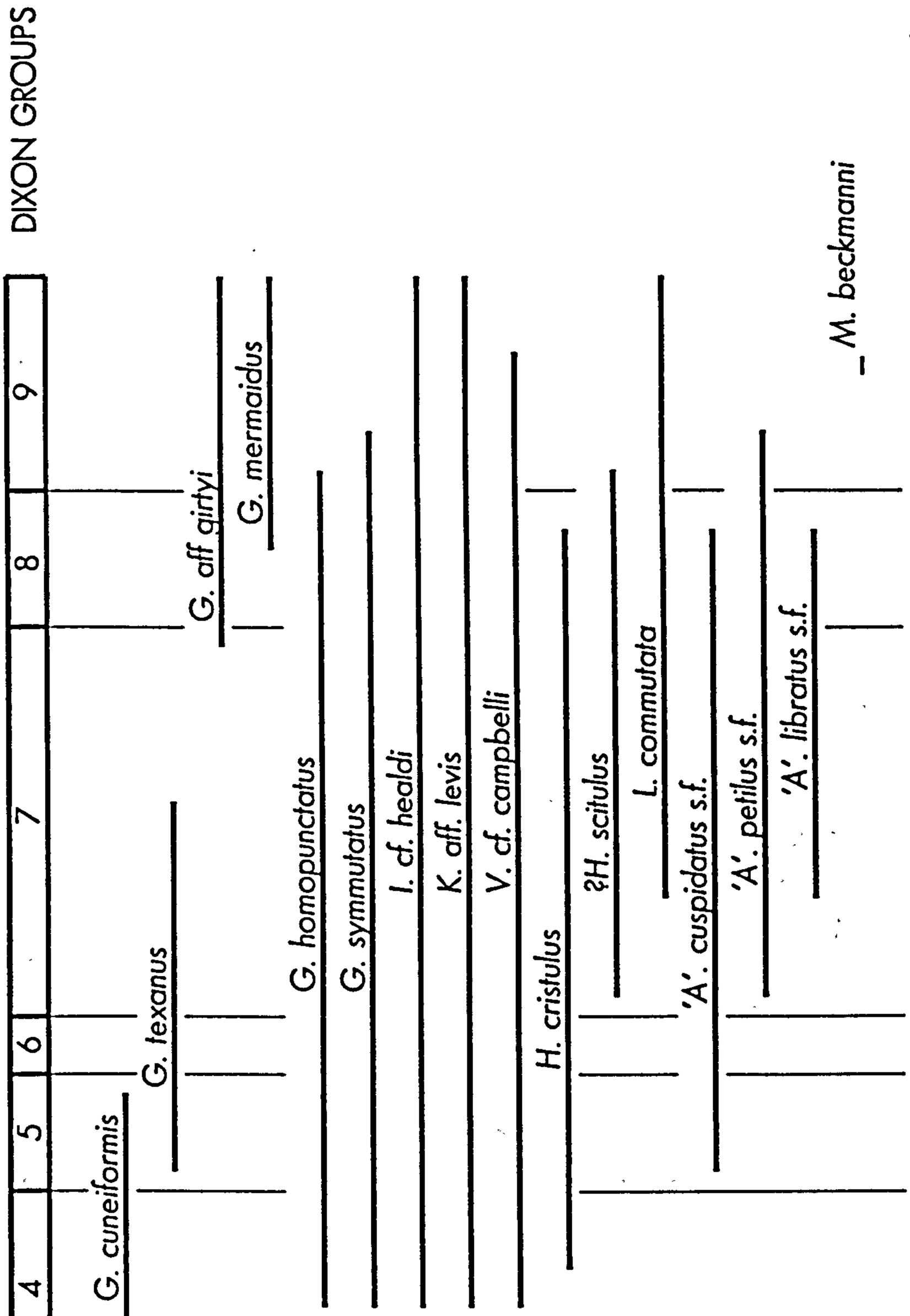
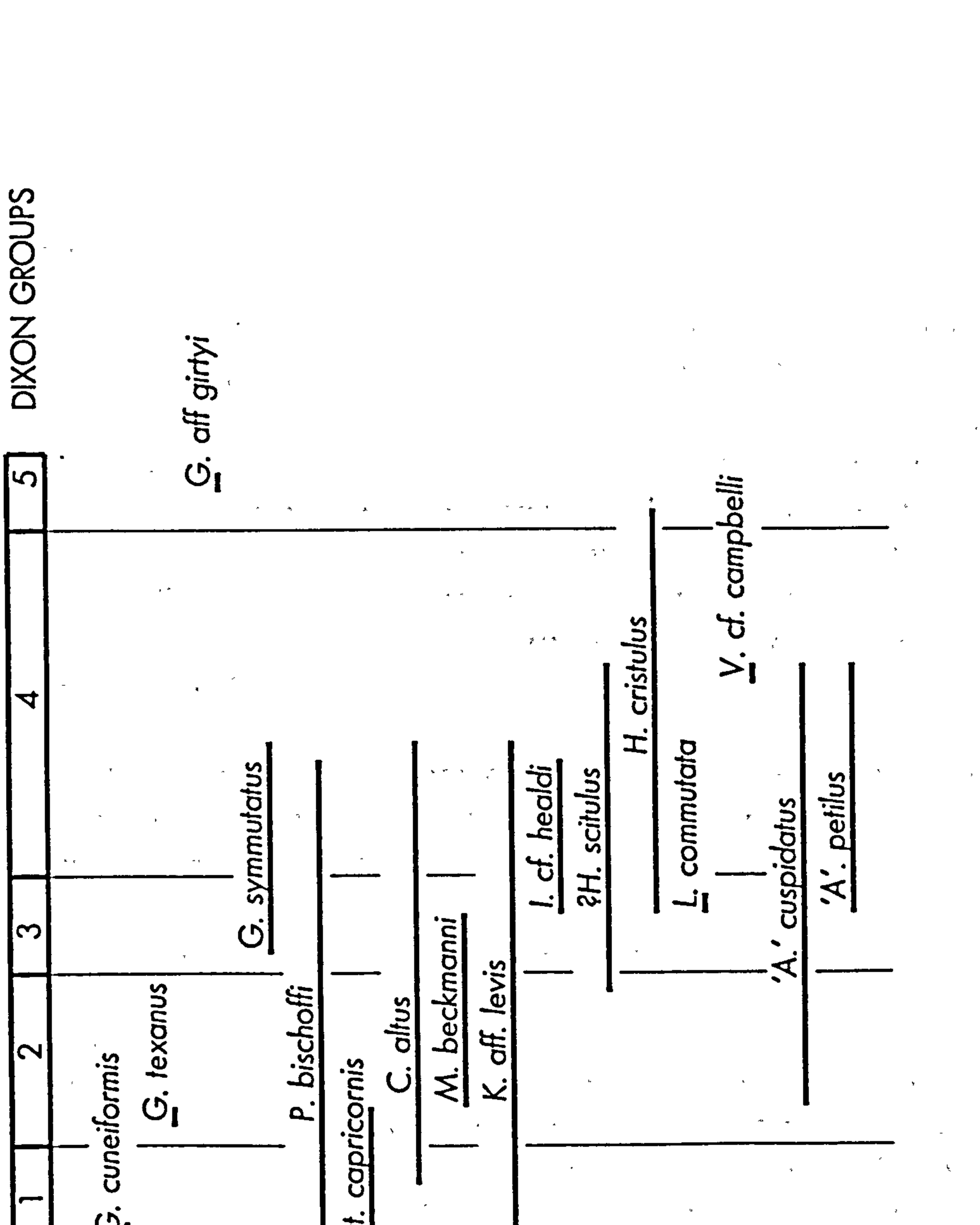


figure 2.3.5 Species range chart for the mid-ramp sites.



(fig. 2.1.4), but see the comments above on the findings of Austin (1987). The stratigraphical ranges of G. texanus and G. cuneiformis overlap over the lower part of the G. texanus Zone, throughout most of Dixon's group 5 (fig. 2.3.4). However, throughout the lower two thirds of Dixon's group 7, G. texanus is present in all samples, whilst G. cuneiformis is absent; and this interval shows the highest overall conodont abundances seen in the present study. The first unequivocal occurrence of L. commutata, in the present study, occurs in the middle part of Dixon's group 7, towards the upper part of the G. texanus Zone. Although elements of L. commutata are not abundant until the succeeding G. aff. girtyi Zone, its co-occurrence with G. texanus may be used to indicate the upper part of the G. texanus Zone.

iii) G. aff. girtyi Zone.

This zone extends throughout Dixon's groups 8 and 9. The exact boundary between the G. texanus and G. aff. girtyi Zones has not been sampled, but is known to occur towards the top of Dixon's group 7. Thirteen Pa elements of G. texanus were recovered from sample SQ 2, approximately in the middle of Dixon's group 7; and just below the top of group 7 one Pa element of G. aff. girtyi was recovered from sample SQ 3 - which lacks G. texanus (fig. 2.1.4). The top of the G. aff. girtyi Zone has not been established, but the range of G. aff. girtyi is known to extend upwards into rocks of Holkerian age because 12 Pa elements were recovered from sample CM 43, 20 m above the Arundian/ Holkerian boundary at Castlemartin, and 13 elements were recovered from sample PE 1 (fig. 2.1.6). Holkerian conodont faunas have not been sufficiently investigated in the present study to allow recognition of the Arundian/Holkerian Stage boundary.

The species which co-occur with the above eponymous species in each biozone can be seen from figure 2.3.4. Two major limitations with the above zonation are that it is only fully applicable to the Pen-y- Holt Formation (outer ramp), and that it is based on a small number of specimens. Further studies are needed to determine how fully the zonation can be accepted. Of the proximal shelf species (Group 4 of section 2.3b), P. bischoffi and Pat. capricornis appear to be at the upper end of their stratigraphical range in mid-Arundian times (Varker and Sevastopulo 1985), and their recovery in rocks of the High Tor Limestone Formation may be indicative of lower Arundian times (Dixon's mid-ramp group 1 to mid-group 4). However because both of these species are restricted to the more varied shallow shelf environment, and their distribution is known to be facies controlled, their use as stratigraphical markers is limited.

Representative conodont zonations which cover the Arundian time interval are shown in figure 2.3.3. These zonations can be divided into two categories: those derived from studies of more proximal shelf faunas (Austin 1973, Higgins

and Varker 1982, Paproth et al. 1983), and those derived from deeper water settings. Although there is little correlation between the Pen-y-Holt conodont zonation as defined herein and any of the other conodont zonations shown; detailed comparisons reveal similarities with the deeper water faunas of figure 2.3.3.

The first occurrence of Lochriea commutata appears to be a useful point of correlation between the Pen-y-Holt zonation and that of the Craven Lowlands (Metcalfe 1981), and is used as a datum level in figure 2.3.3. The earliest record of L. commutata in the Craven Lowlands is of 2 Pa elements from a 2 kg sample taken 10 m below the top of the Embsay Limestone at Embsay Beck. This point is at least 10 m above the first occurrence of archaediscid forams - which occur several metres above the base of the Arundian Stage in the Arundian stratotype section. In their study of forams from The Embsay Limestone, Fewtrell and Smith (1978) implied that there may also be a degree of facies control on the archaediscid first occurrence, which would imply that the base of the Arundian part of the Embsay Limestone may be up to twenty metres or so lower down the section. This ties in closely with the relative positions of the first occurrence of archaediscid forams and L. commutata in the Castlemartin section. In the Clitheroe Anticline (Metcalfe 1981), the first occurrence of G. texanus is above the base of the Arundian Stage but below the first occurrence of L. commutata, and this parallels the situation in the Pen-y-Holt Limestone.

The Craven Lowlands fauna was not investigated using multielement criteria, and this adds difficulty to making direct comparisons with the Pen-y-Holt fauna. However, all but one of the components of the Arundian conodont fauna of the Craven Lowlands (Metcalfe 1981), have also been recovered from the Pen-y-Holt Limestone; and several of the outer ramp species of the present study which were not recorded from the Arundian part of the Embsay Beck section have been found in older and younger rocks in the Craven Lowlands.

Apart from the occurrence in the Embsay Limestone of three specimens of Embsaygnathus asymmetricus - which was not recovered in the present study, the two major differences between the conodont faunas from the Craven Lowlands and the Pen-y-Holt Limestone are the lack of G. aff. girtyi and the greatly extended range of G. antetexanus (which is here synonymised with G. cuneiformis) in the Craven Lowlands. E. asymmetricus is extremely rare and has only been reported from a handful of localities (Metcalfe 1981, Swift in: Varker and Sevastopulo 1985, Llewellyn Jones pers. comm. 1987), and its absence in the present study may only reflect its overall low abundance. Metcalfe (1981) shows G. antetexanus (= G. cuneiformis) to range from Chadian to Brigantian rocks in the Craven Lowlands, hence the G. cuneiformis Zone of the Pen-y-Holt Limestone (herein) is seen to be of only extremely local significance, and presumably to be a reflection of changing environmental conditions rather than representative of an evolutionary lineage.

Similarly the lack of G. aff. girtyi in the Craven Lowlands may be the result of facies control on distribution. Alternatively specimens here referred to G. aff girtyi may be included within the broad interpretation of G. girtyi by Metcalfe (1981), although none of these are recorded by him from pre-Asbian times.

The distribution of the shallower water species of the present study (group 4 of section 3.3b) in the Craven Lowlands is interesting: Cavusgnathus is absent from pre-Asbian rocks; P. bischoffi and Pat. capricornis reach the upper limit of their range in late Chadian times, and M. beckmanni occurs throughout. From the presence of the latter, it can be inferred that although the Craven Lowlands Arundian conodonts and the Pen-y-Holt conodonts are both representative of outer shelf faunas, the Pen-y-Holt fauna appears to be slightly more distal-shelf in its nature. The similarity between the two environments is also reflected in the foram faunas, and Simpson and Kalvoda (1987) note that elsewhere, in the more high energy shallow water environments, Arundian rocks tend to contain a diverse archaediscid fauna including Glomodiscus and Uralodiscus whereas in both the Pen-y-Holt Limestone and the Embsay Limestone there is a poorly diversified assemblage with Ammarchaediscus - which is seen as typical of lower energy deeper water conditions.

The zonational scheme of Varker and Sevastopulo (1985) is largely based on the Metcalfe (1981) zonation discussed above; although the base of the L. commutata Assemblage Zone is said to be marked by the first appearance of C. charactus, C. unicornis and 'A.'. libratus, as well as the nominate species. C. cristatus and C. regularis are cited as occurring above the base of the L. commutata Zone. Of these forms only 'A.'. libratus has been recovered in the present study, and this correlates closely with the first occurrence of L. commutata.

The Pen-y-Holt fauna can be correlated with a horizon within the long ranging texanus Zone of Lane et al. (1980). This zonation is based on faunas from western Europe (essentially Germany and Belgium) and central and western parts of the U.S.A. Their texanus Zone covers the interval from the first occurrence of G. texanus to the first occurrence of G. bilineatus (or Cavusgnathus in the U.S.A.). In Europe Scaliognathus anchoralis is said to range as high as the base of the texanus Zone; and the upper limit of its range is placed in the early part of the Chadian Stage by Varker and Sevastopulo (1985). G. bilineatus is known to occur slightly earlier in Belgium than in the U.K., at a horizon correlated with the early part of the Asbian Stage by Varker and Sevastopulo (1985). Hence the texanus Zone of Lane et al. (1980) covers an interval which is equivalent to that from early Chadian to early Asbian times in the U.K. Conodonts found in the texanus Zone include G. texanus, P. bischoffi, M. beckmanni, G. semiglaber, G. pseudosemiglaber, P. communis communis, Cloghergnathus spp., Bispathodus spp., Eotaphrus burlingtonensis and in central and western North America Taphrognathus varians; and of these the first three

named have been recovered in the present study.

The other zonations shown in figure 2.3.3 are all derived from proximal shelf, shallow water faunas and are of extremely localised application. It is interesting to note that, even from the inner and mid-ramp areas, no specimens of Cloghergnathus or Taphrognathus were recovered in the present study; and these are the eponymous forms for Arundian zones in the schemes of Higgins and Varker (1982) and Paproth et al. (1983) respectively. The first occurrence of L. commutata in the shelf environments of the U.K. is typically somewhat later than in Belgium (Paproth et al. 1983, Varker and Sevastopulo 1985); although, according to the latter, Stewart (1981) indicates that in the Culm facies of Devon and Cornwall L. commutata may occur even earlier than in Belgium.

From the above it is clear that G. texanus, G. cuneiformis and L. commutata (of this study) have longer ranges elsewhere and that several species cited as typical of Arundian times in other studies have not been found in South Wales; hence the conodont stratigraphical scheme for the Pen-y-Holt Limestone Formation (fig. 2.3.3) is seen to be of local application only.

2.3d Implications for conodont phylogeny.

A series of extinctions around the Courceyan/Chadian boundary led to a marked decline in conodont species diversity (Sweet 1988), and this appears to be coupled with a relative decline in overall conodont abundance which lasted until Brigantian times (Paproth et al. 1983). Sweet (1988) suggests that this decline can be linked with a global reduction in the area of deeper shelf environments. Immediately prior to the end-Courceyan extinction episode, Ziegler and Lane (1987) report a peak in conodont species diversity, which involved the genera Siphonodella, Protognathodus, Pseudopolygnathus, Polygnathus and the distinctive but short-lived bactrognathids (Eotaphrus, Bactrognathus, Doliognathus, Dollymae and Staurognathus).

Broadly speaking, the mid-Viséan interval (Arundian-Asbian) can be viewed as a high-stress period in terms of conodont phylogeny, in which the group as a whole staged a general recovery which eventually led to the re-establishment of a relatively stable conodont fauna. This overview is corroborated by Higgins (1981) who alludes to the existence of a distinctive late Viséan conodont fauna which was established during mid-Viséan times. This fauna is characterised by the genera Gnathodus and Lochriea, and corresponds to the fauna of diversity cycle XI of Sweet (1988).

Viewing the South Wales Arundian conodont fauna within the overall context outlined above, the species present may be separated into a series of groups according to their phylogenetic history:

i) Survivors of the end-Courceyan reduction in species diversity, reaching the upward limit of their stratigraphical range in Arundian times.

Polygnathus bischoffi, which appears to reach the upper limit of its stratigraphical range in Arundian times, is the youngest species of the genus Polygnathus and ranges upwards from the late Courceyan (Varker and Sevastopulo 1985, Sweet 1988); and a similar form of Pa element is known from uppermost Famennian rocks (P. inornatus). The findings of the present study show that P. bischoffi was a component of the shallow water conodont fauna of South Wales during lower and mid-Arundian times. This broadly concurs with the stratigraphical range reported by Varker and Sevastopulo (1985), although the upper limit of the range is extended slightly. The ephemeral nature of shallow-shelf sub-environments means that the reported ranges of shallow water conodont species often reflect shifting facies rather than evolutionary changes, and the youngest occurrence reported here is not intended to be taken as a definitive upper limit on the range of P. bischoffi. The recovery of Clydagnathus gilwernensis from the Llanelly Formation suggests that it is another species which survived the end-Courceyan extinction event. This species has previously only been reported from uppermost Devonian and lowest Courceyan horizons, and the findings of the present study substantially extend its range upwards, at least to mid-Chadian times (see section 2.3e below).

The stratigraphical range of Gnathodus cuneiformis is not well established, and a major problem in its elucidation is the variation in form of this type of gnathodan Pa element, and the associated variety of definitions of G. cuneiformis used by different conodont workers (see sections 1.4b and 2.2d pages 81-83 and 86). Lane et al. (1980) comprehensively re-evaluated the criteria for definition of G. cuneiformis, and established a series of three morphotypes - the youngest of which ranges from Courceyan to early Chadian times. These authors did however suggest that an extension of the range may be possible in the light of further data. As the work of Lane et al. (1980) was used as a basis for the interpretations of the present study, it is proposed that the range of G. cuneiformis be extended upwards at least to lower Arundian times. Austin and Husri (1974) report G. cuneiformis from County Limerick and County Clare in Eire, in rocks stated to range in age from S_1 to D_2 (upper Arundian to Brigantian); however the criteria used to define the species are not given, and the associated conodont fauna suggests an older lower limit to the range.

ii) Survivors of the end-Courceyan reduction in species diversity, which range upwards to form part of the late Viséan conodont fauna.

Included in this group are Gnathodus symmutatus, Hindeodus cristulus and ?Hindeodus scitulus. Opinion differs on whether G. symmutatus can be consistently recognised as a species distinct from G. homopunctatus (e.g. Metcalfe 1981), and on the stratigraphical range of the species. The results of the present study suggest that G. symmutatus is a valid species, although differentiation between immature specimens of G. symmutatus and G. homopunctatus is not possible. Austin (1987) suggests that the first occurrence of G. symmutatus is important for recognition of the Chadian/Arundian boundary, but Sweet (1988) reports the inception of G. symmutatus in the equivalent of late Courceyan times.

Little can be added to the phylogenetic understanding of H. cristulus and ?H. scitulus from the results of the present study, as both of these species have established ranges from mid-Courceyan to post-Brigantian times (Varker and Sevastopulo 1985, Sweet 1988). The possibility of a change in the nature of some of the apatognathan components of ?H. scitulus through time is discussed in section 2.3f26.

iii) Species originating in Chadian times not forming part of the late Viséan conodont fauna.

Patrognathus capricornis is reported to range from mid-Chadian to lowest Arundian times (Varker and Sevastopulo 1985), although the similar form Pat. variabilis is known from lower Courceyan rocks (see discussion in section 2.2j). The recovery of Pat. capricornis from lower Arundian rocks at Lydstep Haven and Giltar Point corroborates the upper limit for the range of the species given by Varker and Sevastopulo (1985), although the limitations on stratigraphical range outlined above for shallow water forms apply to Pat. capricornis as well as P. bischoffi (see part i).

iv) Species originating in Chadian times which form part of the late Viséan conodont fauna.

Gnathodus texanus is known to be a long-ranging species elsewhere, and has been recovered from rocks ranging in age from early Chadian to early Asbian (Lane et al. 1980). In the present study G. texanus is restricted to mid-Arundian times (Dixon's Pen-y-Holt groups 5 to 7 of figure 2.1.4). This range in the Pen-y-Holt Limestone of South Dyfed is presumably the result of facies control on distribution, although it is difficult to isolate any environmental parameters which are specific to this interval.

Gnathodus homopunctatus, and Mestognathus beckmanni range widely throughout most of the Arundian Stage in the sampled sequences, and elsewhere both are known to range from earliest Chadian to post-Brigantian

times (Varker and Sevastopulo 1985, Sweet 1988).

Kladognathus levis was proposed to be the oldest member of an evolutionary sequence which was detected within the genus Kladognathus by Horowitz and Rexroad (1982), but the lower limit of its range has not been fully established. Aldridge (1988) suggests the first occurrence of the genus Kladognathus to be in Chadian times. Chauff (1983) records M, Sa and Sc elements of K. levis in lower Osagean rocks (late Courceyan), but because other elements of the apparatus were not recovered designates this multielement association as Arisemotaxis levis (this has not been included in synonymy in section 2.2g as the plates are unclear and no diagnoses are given). The erection of a separate genus for this association seems unwarranted as the findings of the present study indicate that the M, Sa and Sc elements of the apparatus were relatively stable through time while the Sb element was more changeable, and the other elements of the apparatus tend to be rarer and less distinctive anyway. In the South Wales Arundian fauna the M, Sa and Sc elements are found with the probable Sb element Magnilaterella clarkei s.f., and the association is termed K. aff. levis as it is assumed to be a previously undefined apparatus, but not sufficiently different from K. levis to justify assignment to a distinct genus. Chauff (1983) does record the presence of elements of Magnilaterella sp. s.f. but these are not described and it is not clear whether the illustrated specimens are referable to Mag. clarkei s.f. It may be that K. aff. levis of the present study is the same species as described by Chauff (1983) as Arisemotaxis levis - in which case this species ranges at least from late Courceyan to late Arundian time. Alternatively the Sb element reported by Chauff (1983) may be sufficiently different from Mag. clarkei s.f. to warrant designation as a species ancestral to K. aff. levis and the other Kladognathus species.

Idioprioniodus healdi ("I. conjunctus") was designated by Merrill and Merrill (1974) to be the older of the two species of Idioprioniodus then described. Aldridge (1988) implies the genus to be late Viséan and younger, and Sweet (1988) does not extend the range of I. healdi much below the top of the texanus Zone (early Asbian). However, elements of the apparatus have been reported from the Osagean (late Courceyan/Chadian) by Nicoll and Rexroad (1975) and Chauff (1983), under the names I. paraclaviger and I? conleyharpi respectively. Chauff (1983) states that the Osagean apparatus is distinguished by having a metalonchodinan element but no lonchodinan element in the symmetry transition series; but on examining the illustrated specimens, and the apparatus positional nomenclature used, the apparatus appears to be the same as that of I. healdi. Therefore the range of I. healdi can be assumed to extend from late Courceyan to post-Brigantian times.

The species of Idioprioniodus recovered in the present study is termed I. cf. healdi rather than I. healdi because the M element which is commonly cited in the apparatus reconstruction of the latter has not been recovered, although a

plexus of similar forms has (this situation is discussed under M element in sections 2.2f and 2.2g). The use of cf. implies that the species determination is provisional (Bengtson 1988). If the assumed range of I. healdi (above) is accepted, then I. cf. healdi of the present study can be placed toward the lower end of a continuous lineage (I. healdi) in which there is a degree of variation in the morphology of the M elements.

Examples of the Vogelgnathus campbelli Pa element have been recovered from rocks of late Chadian age (Metcalfe 1981), and the species has a stratigraphic range which extends into the Namurian (Sweet 1988). The early phylogenetic history of V. campbelli is not fully understood (Sweet 1988), and the species recovered in the present study is designated V. cf. campbelli because the single Pb element found differs from the form cited by Norby and Rexroad (1985) in their reconstruction of the Chesterian (Brigantian) V. campbelli apparatus. Further examples must be recovered to see whether the Arundian specimens represent a species ancestral to V. campbelli, which can be discerned by the nature of its Pb elements. The phylogenetic situation is made more complex by the report of an early species of Vogelgnathus by Armstrong and Purnell (1987), from Chadian and Arundian rocks in the Northumberland Basin. This species has a distinctive Pa element which is relatively foreshortened and plume-like, however the single (rather damaged) Pb element illustrated appears to be similar to that of the present study (although there is no written description). Further studies are required to establish whether the Arundian form described herein is distinct from V. campbelli sensu stricto, and to discover the relationship between it and V. sp. nov. of Armstrong and Purnell (1987).

v) Species originating in Arundian times which form part of the late Viséan conodont fauna.

Cavusgnathus altus (as C. cristatus) has been recovered from rocks equivalent in age to the late Arundian (Rhodes et al. 1969), and its occurrence in early Arundian rocks in the present study provides a slight downward extension to its reported range.

The range of Gnathodus mermaidus is not fully established, but its recovery from late Arundian rocks in the present study correlates broadly with the work of Austin and Husri (1974) and Belka (1985) who respectively reported it to range from the equivalent of early and mid-Arundian to Asbian times.

Lochriea commutata first occurs in mid-Arundian times in South Wales, which correlates with its inception in the Craven Lowlands (Metcalfe 1981); however L. commutata is thought to have occurred before this in Belgium and South West England (Varker and Sevastopulo 1985), and it may be conjectured that its co-ordinated appearance in shelf-seas north and south of St. George's Land is the result of a single migration event.

The specimens decribed in the present study as Gnathodus aff. girtyi are

here considered to be ancestral to G. girtyi sensu stricto. The phylogenetic history of G. girtyi has been much debated (Merrill 1972, Grayson et al. 1988), and further studies are needed to clarify the situation. The findings of the present study suggest (on purely morphological grounds) that there may be a continuous lineage from G. aff. girtyi in late Arundian times through G. girtyi in Asbian times to Neognathodus and Declinognathodus in Namurian times (see discussion under G. aff. girtyi in section 2.2d).

Rapidly evolving, relatively widespread and robust marine fossils (such as conodont elements) have the potential to provide information about evolutionary mechanisms. The present study is limited in this respect by being confined to a single Stage, which is a short span in terms of evolutionary time. However, when considered in the context of overall Lower Carboniferous conodont phylogenetic patterns, broad conclusions can be drawn.

The present study of the Arundian conodont fauna of South Wales highlights a window in terms of time and space, in which to consider the phylogenetic development of mid-Viséan conodonts as a whole. Although the early and late Arundian faunas are distinct, the extinctions and first occurrences which account for the changes do not appear to occur as a series of discrete events. Rather the overall picture is a complex mosaic of first and last occurrences, active evolution and seemingly unchanging lineages. This picture is partly accounted for by the effects of facies control on species migrations, as some forms are known to have longer ranges elsewhere (G. texanus for example), and the restricted spatial distribution of some species is highlighted by the present study (see section 2.3b above). Other occurrences and disappearances appear to be related more closely with actual extinctions and the evolution of new species (Pat. capricornis and G. mermaidus for example).

Two major conclusions can be drawn from the above; firstly that any study of a single area, even if it includes a variety of environments, is likely to reflect the effect of facies change and species migration as well as actual evolutionary events; and secondly that the nature of the change seen in the present fauna appears to be rather gradual and complex and does not support the over rigorous application of an event philosophy of conodont stratigraphy (see for example Sandberg et al. 1988).

This last point might be taken further to suggest that the evolutionary changes seen in the present fauna occur in a complexly interwoven and gradual way. In which case the South Wales Arundian conodont fauna does not provide support for a mode of evolutionary change involving punctuated equilibria - as proposed by Eldredge and Gould (1972); or it at least implies that the periods of punctuation are not particularly dynamic. However, although it is undoubtedly an interesting area for future speculation, the present study does not provide conclusive support for any single theory about the mode of evolutionary change.

2.3e The inner-ramp fauna and the age of the Llanelly Formation.

The Llanelly Formation is representative of an extremely nearshore depositional environment, and comprises a thin (20 m) peritidal and alluvial package which crops-out along the north-east part of the South Wales Coalfield in the Abergavenny and Merthyr Tydfil areas. The unit was named by George et al (1976), and is equivalent to the calcite mudstone group of George (1954).

Wright (1981) divided the Llanelly Formation into four members (fig. 2.3.6), and investigated its sedimentology in detail. The lowest and highest members (Clydach Halt and Gilwern Clay respectively) are interpreted as siliciclastic alluvial deposits with palaeosols. The lower limestone member (Cheltenham Limestone) generally makes up the bulk of the Llanelly Formation and consists of thin to medium bedded fine grey limestones with pale-green clay interbeds. Wright (1981) interprets the clays as palaeosols and notes a crude shallowing-up cyclicity throughout the sequence; such deposits suggest periodical transgression followed by progradation of the tidal flat zone. In an idealised case this would result in shallow water (<5 m) lagoonal conditions becoming increasingly more saline and more shallow, until prolonged periods of emergence resulted in the formation of a soil, some of which may have contained a volcanic component (Wright 1986). The Penllwyn Oolite Member, which immediately overlies the Cheltenham Limestone, has a sharp erosive base (Barclay 1989). It is equivalent to the Seminula Oolite of Robertson (1927), and the Linoproductus Oolite of George (1954). This unit is mainly an oolitic grainstone and has at its base a distinctive coarsely bioclastic and oncoidal horizon, termed the Uralloporella Bed (Wright 1982). This bed is tentatively suggested to represent schizohaline lagoonal conditions (Wright 1981, 1982), and the overlying oolite to have been deposited as a nearshore shoal, resulting from landward migration of shoreface sands (Wright 1986).

The age of the Llanelly Formation has not been firmly established, as it contains a rather restricted fauna and flora which is of little biostratigraphical use (Barclay 1989). It is generally agreed that the Llanelly Formation is pre-Holkerian, as the overlying Dowlais Limestone Formation has been accurately dated, on the basis of its relatively rich coral and brachiopod fauna (Barclay 1989). The Llanelly Formation overlies the Gilwern Oolite Formation in the Clydach Valley, and oversteps the older Blaen Onnen Oolite further north (Wright et al. 1987).

A conodont fauna recovered from the Gilwern Oolite is reported to include: Cavusgnathus sp., Cloghergnathus sp., Gnathodus simplicatus, Polygnathus mehli, Pseudopolygnathus minutus, Spathognathodus scitulus, Taphrognathus sp. and Spathognathodus sp. This assemblage, combined with the lack of Mestognathus beckmanni, was taken to be indicative of a late Courceyan age (Barclay 1989). However, this contrasts with the Chadian age

suggested by forams recovered from the Gilwern Oolite in the same study (Barclay 1989).

The base of the Gilwern Oolite includes the Craig y Gaer Coral Bed (sensu Barclay 1989). This is equivalent to Bed 7 (Coral Bed) of George's (1954) Marker Beds; which are in turn equivalent to the Clydach Beds of George et al. (1976). George (1954) suggested a Zaphrentis Zone age (= late Courceyan) for the Coral Bed, due to the presence of Hapsiphyllum cf. koninckí; however Mitchell (In: Barclay 1989) suggests these to be eroded examples of Palaeosimilia murchisoni, and this has only been recovered from post-Courceyan rocks.

An Arundian age for the Gilwern Oolite (and the Llanelly Formation) was suggested by Ramsbottom (1976), following a thin-section foram study. However Barclay (1989) reports that Ramsbottom's findings have not been endorsed by subsequent studies, and lithological examination of the original slide suggests sample mixing during preparation. Mitchell (1976) also proposed an Arundian age for the Gilwern Oolite, on the basis of its coral fauna.

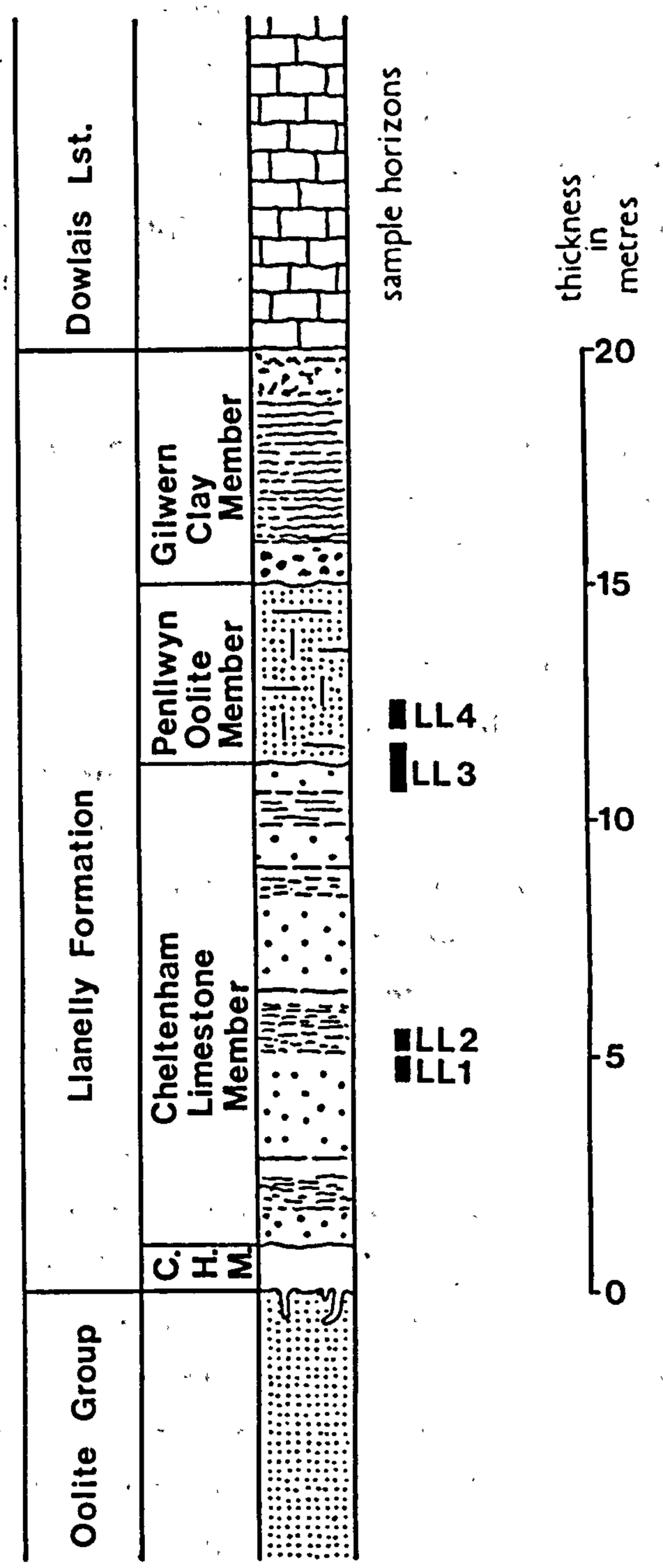
In summary, depending on which biostratigraphical group and interpretation are favoured, the Gilwern Oolite Formation may be considered as late Courceyan, Chadian or Arundian in age.

The Llanelly Formation itself (probably the Penllwyn Oolite Member) is reported by Barclay (1989) to have yielded a small, facies- controlled conodont assemblage which includes Spathognathodus scitulus s.f. (= ?Hindeodus scitulus Pa element). Other fossils reported from the Llanelly Formation include the alga Koninckopora inflata and archaediscid forams (George 1954), the Viséan spore Lycospora pusilla (Barclay and Jones 1978), and brachiopods referred to Composita sp. and Linoprotonia cf. corrugatohemispherica (Barclay 1989). George (1954) inferred a C_2S_1 (Arundian) age from his findings, and Barclay (1989) notes that the macrofossils do not give a precise age.

The only other age determinations for the Llanelly Formation have been made through lithological correlation studies; from which Ramsbottom (1973) and Wright et al. (1987) suggested an Arundian age, and George et al. (1976) a Chadian age.

The limited conodont fauna recovered from the Llanelly Formation in the present study has produced interesting, but equivocal biostratigraphical results. Wright (pers. comm. 1989) suggests that, from the field notebook description, it is probable that sample LL 3 (fig. 2.3.6) comes from the Uralloporella Bed at the base of the Penllwyn Oolite; and that sample LL 2 (barren) comes from an emergent (palaeosol) horizon within the Cheltenham Limestone.

figure 2.3.6 Approximate position of reconnaissance samples taken at Llanelly Quarry.



NOTES

The lithological column is based on field observations and figs 16, 17 and 18 of Wright et al. (1987). The ornamentation is schematic rather than strictly accurate.

Because of the reconnaissance nature of the sampling, the exact positions from which samples were taken can only be determined to the accuracy shown here.

Figure 2.1.1 and appendix D give locational details for Llanelly Quarry.

The two samples from the Penllwyn Oolite (LL 3 and LL 4) produced the following conodont elements:

?Hindeodus scitulus (Pb x1)

Vogelgnathus campbelli (Pa x1)

'Apatognathus' cuspidatus s.f. (x2).

Sample LL 4 also contained a broken and juvenile cavusgnathoid Pa element which is probably referable to Patrognathus.

Pb elements of ?Hindeodus scitulus have been recovered from the Z Zone (late Courceyan) of the Avon Gorge (Rhodes et al. 1969), and Pa elements have been recorded from Namurian rocks in northern England (Varker and Sevastopulo 1985). The recovery of a ?Hindeodus scitulus Pb element from the Penllwyn Oolite corroborates the findings reported by Barclay (1989); but as stated, the long range of this species means that it is of little biostratigraphical use. Vogelgnathus campbelli has a stratigraphical range from the mid-Chadian Thornton Limestone (Metcalfe 1981) to rocks equivalent in age to the Namurian, in the U.S.A. (Norby and Rexroad 1985); and 'Apatognathus' cuspidatus s.f. is known to range from Chadian to at least Brigantian times in the Craven Lowlands (Metcalfe 1981). This suggests a Chadian lower limit for the age of the fauna.

The genus Patrognathus is toward the top of its stratigraphical range in mid-Arundian times (Varker and Sevastopulo 1985), and if the rather juvenile specimen recovered in sample LL 4 is correctly assigned, this suggests a mid-Arundian upper age limit for the Penllwyn Oolite (but see comments on Patrognathus in stratigraphical aspects, above).

Sample LL 1 from the Cheltenham Limestone Member (fig. 2.3.6) has produced two Pa elements of Clydagnathus gilwernensis (Plate 1 fig 5). This species is uncommon and has only previously been reported from late Famennian and early Courceyan rocks. Rhodes et al. (1969) cite Cl. gilwernensis as the oldest species of Clydagnathus, and list it as typical of the lower part of their lowest Avonian Pat. variabilis - B. ac. plumulus Zone; and Druce (1969) recovered 38 specimens from the lowest Tournaisian Burt Range Formation of the Bonaparte Basin in Australia.

There appears to be an anomaly between the stratigraphical position of the Cheltenham Limestone, as outlined above, and the known range of Cl. gilwernensis. A number of possible explanations warrant discussion. If the reported range of Cl. gilwernensis is accurate and comprehensive, this occurrence would be most easily explained by the reworking of Courceyan fossils into the Cheltenham Limestone. However this is unlikely because lower Courceyan rocks are separated from the sample horizon by approximately 40 m of high energy shoreface deposits, interspersed with numerous emergent horizons which result from ten-or-so transgression/regression events (Wright 1986). Thus, to be included in the Cheltenham Limestone, a Courceyan fossil

would have to have survived more than ten reworking events over a ten to fifteen million year period. The specimen illustrated in Plate 1 is unusually pristine compared with the other specimens recovered in this study, and this is not readily compatible with the depositional scenario outlined above. Further, a reworked specimen would be most likely to occur as part of a basal lag, but sample LL 1 was taken some 5 m above the base of the Cheltenham Limestone Formation.

If Cl. gilwernensis was restricted to Courceyan times, a second possible explanation could be the presence of a large stratigraphical break between the Cheltenham Limestone and the Penllwyn Oolite. In this case the Penllwyn Oolite, with its mid-Chadian to early Arundian conodont fauna could be separated from the Cheltenham Limestone by a depositional break representing at least six million years (Harland et al. 1981). Although there are two prominent calcrete geosols at the top of the Cheltenham Limestone (the Darrenfellen and Cwm Dyar geosols of Wright et al. 1987), their thickness and mode of development would only suggest a break of some thousands of years by analogy with modern examples (Wright pers. comm. 1989). The strongest argument against this explanation is however the late Courceyan/early Chadian nature of the microfauna from the underlying Gilwern Oolite, implying the Cheltenham Limestone fauna to be latest Courceyan at the very oldest.

From the above it seems likely that the range of Cl. gilwernensis must be extended upwards at least as far as latest Courceyan times, and probably into mid-Chadian / early Arundian times. Such an extension to the range is not as incredible as it may at first seem because it is generally accepted that the stratigraphical range of shallow water, facies-controlled forms is difficult to establish (e.g. Austin and Davies 1984). By their very nature, marginal marine environments, in which genera such as Clydagnathus flourished, tend to be comparatively transient; and continuous sequences illustrating purely evolutionary developments are rarely if ever found.

The genus Patrognathus provides a precedent for such an extension of stratigraphical range. When first named, by Rhodes et al. (1969), Patrognathus was thought to be restricted to the K Zone (lower Courceyan), however subsequent studies have established that a form of Patrognathus which is extremely similar to that first described by Rhodes et al. (1969) is found in Arundian rocks (see discussion in section 2.2j). It is interesting to note that Rhodes et al. (1969) record Cl. gilwernensis occurring with Patrognathus in lower Courceyan rocks, and that the present study also records these two forms co-occurring - but in the (presumably) much younger rocks of the Llanelly Formation. This association is probably of more use as an indicator of marginal marine environments, throughout the lower Carboniferous, than of any particular stratigraphical horizon.

2.3f Conclusions.

1) The South Wales Arundian conodont fauna can be divided into four major generic associations on the basis of abundance and relative distribution:
   1. Gnathodus
   2. Idioprioniodus, Kladognathus, Lochriea and ?Hindeodus
   3. Vogelgnathus and Hindeodus
   4. Polygnathus, Patrognathus, Cavusgnathus and Mestognathus.

2) A distinction can be made between a distal shelf biofacies dominated by group 1 (above), and a proximal shelf biofacies in which group 4 (above) accounts for an appreciable component of the fauna.

3) Conodont elements are more abundant in the distal shelf biofacies than the proximal shelf biofacies.

4) The distribution patterns of co-occurring species are markedly different. This suggests facies control on distribution at the species level.

5) The factors affecting species distribution are more subtle than those reflected in the broadscale cycles of sedimentary régimes outlined by Dixon (1921).

6) Polygnathus bischoffi was confined to shallow water environments in Arundian times.

7) Mestognathus, Patrognathus and Cavusgnathus constitute an appreciable component of the mid-ramp fauna but are rarely found in the outer ramp.

8) The recovery of elements of Clydagnathus gilwernensis, ?Hindeodus scitulus, Vogelgnathus campbelli and 'Apatognathus' cuspidatus s.f. from peritidal rocks of the Llanelly Formation suggests that these forms were able to live in extremely near-shore, restricted environments.

9) Relative abundance patterns for each Dixon cycle show a crude correlation from site to site.

10) Studies of conodont biofacies should be made at a specific rather than generic level where possible.

11) Gnathodus is the most abundant Arundian conodont genus in outer and distal mid-ramp settings, and species of Gnathodus s.s. are viewed as bottom dwellers - essentially confined to the most seaward of the cross-shelf biofacies. G. aff. girtyi may have inhabited slightly shallower environments than G. texanus and G. cuneiformis. G. homopunctatus and G. mermaidus have a patchy vertical distribution and have only been recovered from outer ramp settings. G. symmutatus commonly occurs in shallower settings than other species of Gnathodus.

12) Mature elements of Idioprioniodus and Kladognathus are found throughout the mid and outer ramp, and this may be indicative of a pelagic life-habit.

13) It is likely that the different species of conodont animal had different life habits, with some forms being quite strongly influenced by the nature of the substrate (e.g. G. homopunctatus), and others being relatively free-swimming (e.g. I. aff. healdi).

14) At least for carbonate-ramp settings of Arundian age, the Dinantian biofacies model of Sandberg and Gutschick (1984) has more subdivisions than are actually seen.

15) Conodonts can be used to subdivide rocks of the Pen-y-Holt Formation (outer ramp) into three successive stratigraphical biozones.

16) There is a marked similarity between the conodont fauna of the Embsay Limestone of the Craven Lowlands (Metcalfe 1981), and that of the Pen-y-Holt Limestone.

17) The conodonts which have been recovered from the Llanelly Formation are stratigraphically long ranging forms, but suggest a Chadian to mid-Arundian age.

18) The stratigraphical range of Polygnathus bischoffi is extended upwards slightly to mid-Arundian times (middle of Dixon's mid-ramp Group 4), compared with the range reported by Varker and Sevastopulo (1985).

19) The stratigraphical range of Clydagnathus gilwernensis is substantially extended upwards, at least to mid-Chadian times.

20) The stratigraphical range of Gnathodus cuneiformis is provisionally extended from early Chadian to early Arundian times (cf. Lane et al. 1980).

21) The results of the present study, and that of Chauff (1983), suggest that future studies may result in an extension to the range of Idioprioniodus healdi, down into late Courceyan times.

22) The stratigraphical range of Cavusgnathus altus is extended slightly downwards into early Arundian times.

23) The occurrence of Gnathodus mermaidus in rocks of Arundian age is confirmed.

24) It is suggested that Gnathodus girtyi arose from a form here termed G. aff. girtyi in post-Arundian times.

25) The M, Sa and Sc elements of the Kladognathus apparatus appear to have remained relatively stable through time while the Sb element was more changeable.

26) The recovery of left and right elements of 'Apatognathus' cuspidatus s.f. in the same sample as a Pb element of ?Hindeodus scitulus, in the extremely restricted fauna of the Llanelly Formation, provides circumstantial evidence that these may be part of the same apparatus. This would mean that either there is more variation in the shape of the ?Hindeodus M element than is presently understood; or there is a wider range of apatognathid forms within the same apparatus. Alternatively, this observation coupled with the distributional data for apatognathid forms (appendix C), may indicate an older species of ?Hindeodus which includes in its apparatus forms here referred to 'A.' cuspidatus, and a younger species as described in section 2.2e. Further work is needed to resolve which of these suggestions (if any) are correct.

27) The overall picture of conodont phylogenetic patterns which arises from the present study indicates that faunal changes occurred gradually throughout Arundian time, and the over-rigorous application of an "event philosophy" of conodont biostratigraphy is not supported.

PART THREE

TECHNIQUES USED IN CONODONT STUDIES

3.1 SAMPLE PREPARATION TECHNIQUES USED IN THE STUDY OF CONODONTS.

A review follows of sample preparation techniques available to conodont workers. Topics covered include: sampling; breakdown of host rock (limestones, shales, black shales, marls, ironstones and cherts); sieving; concentration (magnetic, density and interfacial); picking; moulds/casts, and photography.

3.1a Sampling.

On rare occasions conodont elements, or their imprints, are visible in the field and it may be possible to study them with a hand lens. Visible conodont elements usually occur on bedding planes where they may appear either as distinct apparatuses (Schmidt, 1934) or as discrete elements (Matthews, 1969). Ivanov (1987) recommends using a X6-10 glass lens for scanning wetted bedding surfaces in argillaceous slates, cherts and jaspers (e.g. novaculites). Plastic lenses rapidly become scratched and opaque. When studying such "bedding-plane assemblages" it is often easiest to make a cast of the rock surface and take it back for analysis in the laboratory (Matthews, 1969). Any cast has to be taken from a mould, and there is a variety of materials available for making them (see section 3.1f).

The majority of conodont elements, however, are collected unseen in the field, and samples of the host-rock are returned to the laboratory for breakdown. Freeing the conodont elements from the host rock has the advantage over bedding-plane studies of allowing a more accurate three-dimensional study. Studies of conodont biostratigraphy and palaeoecology have advanced to a stage that requires exact and correlated sampling, and this should be related to an understanding of the structure and sedimentology of the area. Conodont elements have been recovered from a wide variety of marine rocks, ranging in age from Upper Cambrian to Upper Triassic. The best rock types to collect are usually clean, undolomitised bioclastic limestones and unindurated marine mudstones or shales. These often contain conodont elements, and are comparatively easy to process. Cherts and similar rocks can often be broken down in hydrofluoric acid, and in this case smaller samples are usually sufficient (e.g. 500 g). Potentially any marine rock of the correct age can be collected for conodont analysis but limitations imposed by rock break-down methods should be borne in mind.

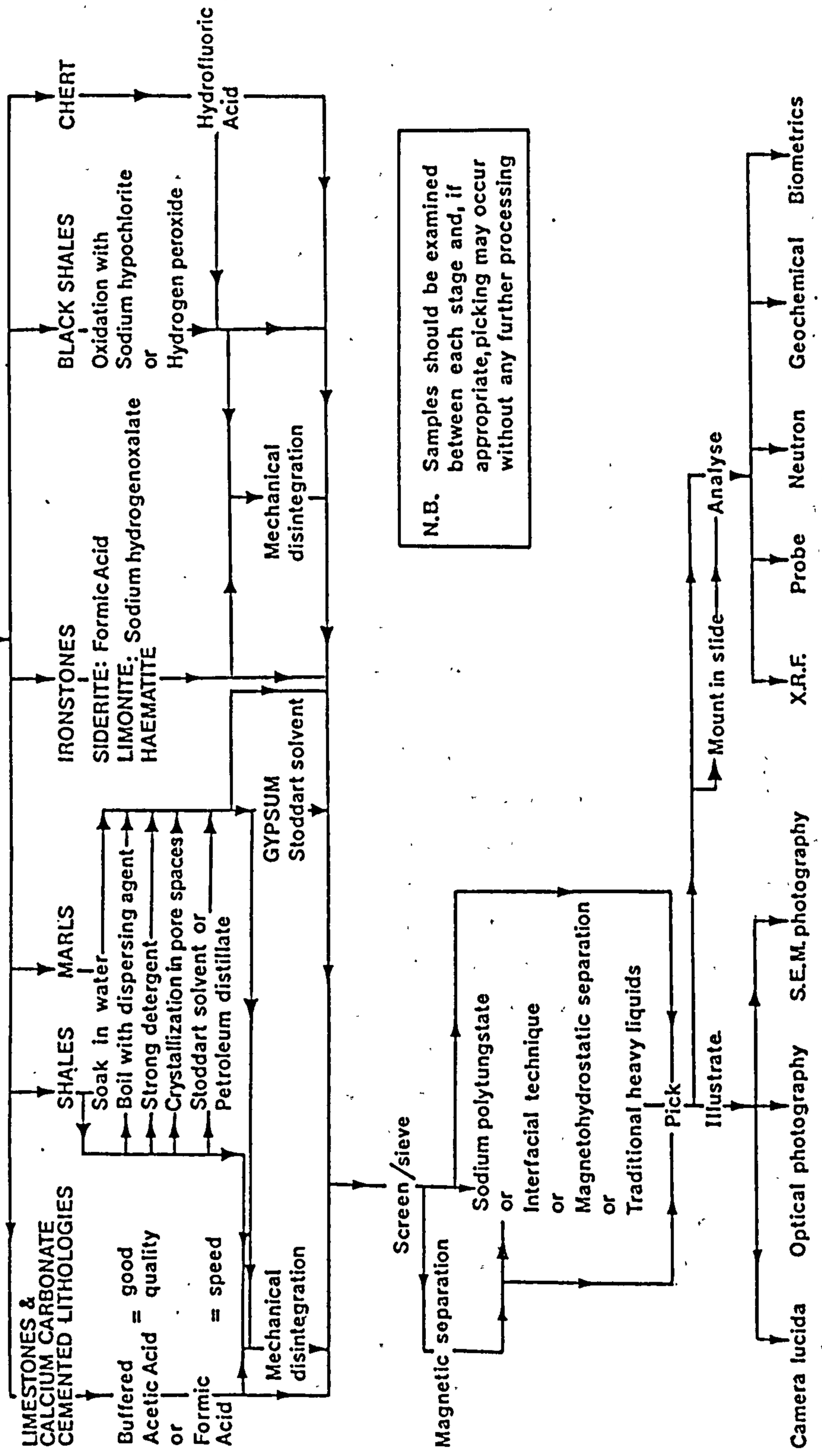
The detailed nature of the sampling procedure is determined by the lithology, the purpose of the study, and the time and facilities available. Collinson (1965) outlines a three-phase operation: initial reconnaissance

comprises continuous channel (i.e. bed-by-bed) sampling of the best exposed representative units, followed by resampling of intervals of high abundance to investigate diversity of the fauna, and finally bulk resampling may occur where faunas are sparse but significant. Particularly at the reconnaissance stage, time-efficiency must be weighed against representativeness when deciding on the best combination of spot and channel sampling.

It is important that sample sites are exactly located and recorded, using accurate measurements from a datum surface, or plotted directly on a log. In some cases it may be advisable to mark sample sites with suitable weatherproof paint, a spray can is the easiest way of effecting this in the field. Sample blocks or sample bags should be clearly numbered in permanent ink as each sample is taken. Jones (1969) suggests leaving the clearly labelled samples at their appropriate sites and photographing the whole locality. Some workers use a Polaroid camera to record each sample site and annotate the photograph in the field, although this can become rather expensive. For each sample, notes should be made on the lithology and macrofauna, etc. (e.g. whether the microfauna is likely to be autochthonous or allochthonous).

Collinson (1965) points out that, because of the durability of conodont elements, extra care must be taken to guard against contamination. Sample bags should never be re-used and should be well sealed and checked for rips or punctures. Tools should be cleaned before each sample is taken. In the majority of cases, sample size should be about 2 kg, and because of these large samples, a tempered steel chisel saves much time. It may even be worthwhile to take a crowbar into the field. Safety goggles are essential when collecting well-indurated rocks. After sampling, the site should be left clean and tidy without any litter or loose rock chippings.

figure 3.1.1 Flow diagram illustrating the range of techniques and processes which may be used to prepare conodont samples for study (from Stone 1987). S.E.M = Scanning Electron Microscopy
X.R.F = X-Ray Fluorescence.



3.1b Rock disintegration techniques.

In order to liberate the contained conodont elements, rock samples must be broken down. Depending on the lithology involved, a variety of techniques are available to the conodont worker (fig. 3.1.1).

i) Limestones and carbonate-cemented rocks.

Since Graves and Ellison (1941) illustrated the effectiveness of the acid-digest technique, limestones have come to be amongst the most commonly studied conodont-bearing lithologies (Lindström, 1964; Collinson, 1965). The sample to be investigated is dissolved in a dilute acid which breaks down the limestone but not the conodont elements. For example, the reactions involved when dissolving limestones in acetic acid and formic acid are shown below.

(acetic): $CaCO_3 + 2(CH_3COOH) \text{-----} > 2(CH_3CO_2).Ca + CO_2 + H_2O$
(formic): $CaCO_3 + HCOOH \text{-----} > Ca(CHO_2)_2 + CO_2 + H_2O$

Yields in conodont-bearing limestones are commonly about 10-15 elements per kg (Collinson, 1965) but may range up to 20,000 per kg (Jeppsson, pers. comm. 1985). Collinson (1965) suggests collecting samples of approximately 2 kg although, depending on the purpose of the study and the lithology involved, this can vary from 0.1 kg (Lindström, 1964) to over 75 kg (Jeppsson, 1983). It is often advisable to keep some of the sample back for reference (e.g. for making a thin section).

Many workers crush their samples into 3 cm chips, in order to speed up the acid-digestion process. However the mechanical stress imposed on the conodont elements by crushing may damage them; and empirically it does not seem to markedly reduce the overall time taken to complete the breakdown, particularly when samples are in the form of hammer chippings. Dégardin (1975) and Jeppsson and Fredholm (1987) feel there is no long-term gain from crushing, especially with sparse or metamorphosed faunas.

Conodont elements can be recovered using very "low-tech" equipment; Collinson (1963) dissolved limestone in standard polyethylene buckets, and traditionally this is how the bulk of conodont work (including my own) has been done. If possible, samples should be supported half way up the bucket in a plastic sieve (or something similar). This greatly improves the ease of sample handling, as well as protecting the conodont elements from mechanical damage when they drop to the bottom. Supporting samples near the top of the bucket also decreases the processing time through improving circulation and preventing insoluble mud from settling on the limestone and choking the reaction, (Müller, 1962). Further, the denser calcium acetate sinks to the bottom leaving any unspent acid at the top, and the decrease in hydrostatic pressure near the top of the vessel allows CO_2 to escape more easily (Jeppsson pers. comm. 1985).

The amount of rock per bucket may range from 0.5 kg to 2.5 kg depending on the situation, although 1-2 kg is about the optimum. It is good practice to use covers on the buckets as the effervescence due to expelled CO_2 can be quite violent, particularly in rocks rich in carbonate. The residue resulting from the digestion process is usually wet-sieved into different size fractions (see section 3.1c), and carefully washed out into labelled filter papers. Rock left undissolved is returned for further breakdown with fresh acid.

Recently I have devised a system in which up to 40 samples are dissolved simultaneously in one large acid tank. this reduces handling time, decreases the chance of damaging conodont elements during processing, improves safety and allows chemicals to be used without waste. I hope to be able to release details of this system in the near future. Dr. L. Jeppsson of Lund University in Sweden addresses the problem of processing large samples (>80 kg) with acetic acid, and substitutes large plastic tubs (such as are used for commercial meat handling etc.) for polyethylene buckets (Jeppsson 1987). The increased volume overcomes the need to exchange acid, and the buffered sample (see above) is left until all carbonate has been removed (about 5-10 days). For ease of handling the tubs are held in fitted frames on wheels, and all the acid and buffer solution is handled using an automated system.

A number of acids have been utilised for conodont studies (Jeppsson, 1987), most commonly: acetic, monochloracetic and formic, and all of these must be diluted as they will not react strongly unless ionised by water. In some cases the acids used to digest the limestones can also attack the conodont elements and both Ziegler et al. (1971) and Jeppsson et al. (1985) suggest that some of the unbalanced, sparse or barren faunas reported in the literature may be reflections of the destructive powers of some acid digests.

Acetic acid (ethanoic acid, CH_3COOH) was suggested by St. Clair (1935) as a means of obtaining insoluble residues from limestones and was used for conodont studies at least as early as 1941 (Graves and Ellison, 1941). Acetic acid should be diluted to a concentration of between 10-15 % because when using a stronger solution a proportion of the acid is wasted. According to Dégardin (1975) metamorphosed conodont elements may be damaged if left for over 6 hours in acetic acid, and Jeppsson et al. (1985) illustrated that, at least in some cases, 1/2 hour is enough to cause damage. They suggest that damage to the conodont elements is normally prevented by the production of calcium acetate and the change in pH, as $CaCO_3$ reacts with acetic acid. Consequently the total time spent in acid before the solution is buffered by calcium acetate seems to be more critical than the concentration of acid used, and until enough calcium acetate has been formed to buffer the solution, conodont elements (particularly the smaller elements) will be attacked. If so, elements in rocks with comparatively low $CaCO_3$ content (e.g. calcareous shales or carbonate-cemented sandstones) are particularly at risk. To overcome this problem,

Jeppsson et al. (1985) suggested buffering all samples by using an acid solution consisting of 7 % concentrated acetic acid with 63 % water and 30 % of the filtered solution left after the digestion of previous samples. More recently, Jeppsson (pers. comm. 1988) has found that a lower proportion of buffer solution is required. As long as the pH is maintained above a certain value, and there is a plentiful supply of free Ca ions, etching is obviated. Alternatively Welch et al. (1964) add a non-reactive liquid which is denser than the acid solution (e.g. ethylene glycol) to form a protective layer at the base of the digestion vessel. von Bitter and Millar-Campbell (1984) suggest that the free chloride present in some grades of acetic acid could ionise to form dilute HCl, and this could explain the destructive effects of acetic acid as HCl is known to dissolve conodont elements. However these authors do not present any quantitative data in support of their claim. A limitation to the use of acetic acid is its extreme slowness in dissolving dolomites.

Beckmann (1952) suggested the use of **monochloroacetic acid** (ClCHCOOH) as a faster and more efficient alternative when working with dolomites and muddy limestones. Ziegler et al. (1971) highlight the dangers of the acid dissolving conodont elements as well as limestone if samples are left in the acid for long periods of time. They report a 95 % increased yield for the same sample when sieved every 48 hours as opposed to being left for 2 weeks. Even then, some elements showed signs of corrosion. Since the work of Ziegler et al. (1971), use of monochloracetic acid has largely been abandoned (Jeppsson et al. 1985). More recently, many workers have substituted formic acid (methanoic acid, HCOOH) which can dissolve dolomite and generally works 1.5 to 2 times more quickly than acetic acid (Ivanov 1987). Formic acid probably dissolves argillaceous limestones more effectively than either of the above (Ziegler et al. 1971). Opinions vary as to the destructive properties of formic acid. Merrill (pers. comm. 1985) reports that acid concentrations as high as 45 % produce no apparent signs of etching if the sample is sieved every 24 hours, although this observation is entirely empirical. Ivanov (1987) compared the destructive properties of 5 % and 10 % formic and acetic acid solutions, and found that after 4 hours 20 % of the conodont elements had completely dissolved - the 5 % solutions caused most damage, and the formic acid was slightly more damaging than the acetic, but the differences were not significant. Buffering the formic acid with calcium formate as for calcium acetate (above) virtually stopped all corrosion, but after 24 hours the specimens became whitened. My own experiments (see below) support the findings of Ivanov, and calcium formate is found to be more effective than sodium formate in preventing acid damage. A sample of dolomite was treated with an unbuffered solution of 10 % (by volume) formic acid and, over 24 hours the pH ranged from 3.2 to 3.6 and all conodont elements were dissolved. A similar sample was buffered with calcium formate and over 24 hours the pH ranged from 3.45 to 3.7

and all conodont elements were preserved. The buffered solution had a dolomite dissolution capacity approximately 95 % as effective as the unbuffered solution. Rixon (1976) states that mixtures of acetic acid and formic acid are highly corrosive to conodont elements; therefore great care must be taken to wash samples thoroughly if they are being changed from one acid to another. The physiological hazards associated with the use of formic acid are greater than with acetic acid, as formic acid liquid causes bad skin burns, and the vapour can cause eye damage and a severe sore throat. Masks, gloves and protective clothing should be worn whenever formic acid is being used, and all dissolving should take place in a well ventilated room, with an extraction fan.

Although unbuffered **hydrochloric acid** (HCl) is corrosive to conodont elements, (von Bitter and Millar-Campbell, 1984; Jeppsson et al. 1985) both Jeppsson et al. (1985) and Dorning (1987) show that when buffered, HCl is non-destructive and can be used to extract conodont elements. Dorning (1987) outlines an integrated conodont and palynomorph extraction technique, and Jeppsson et al. (1985) report a controlled experiment involving dissolution of limestone using 37 % (concentrated) HCl.

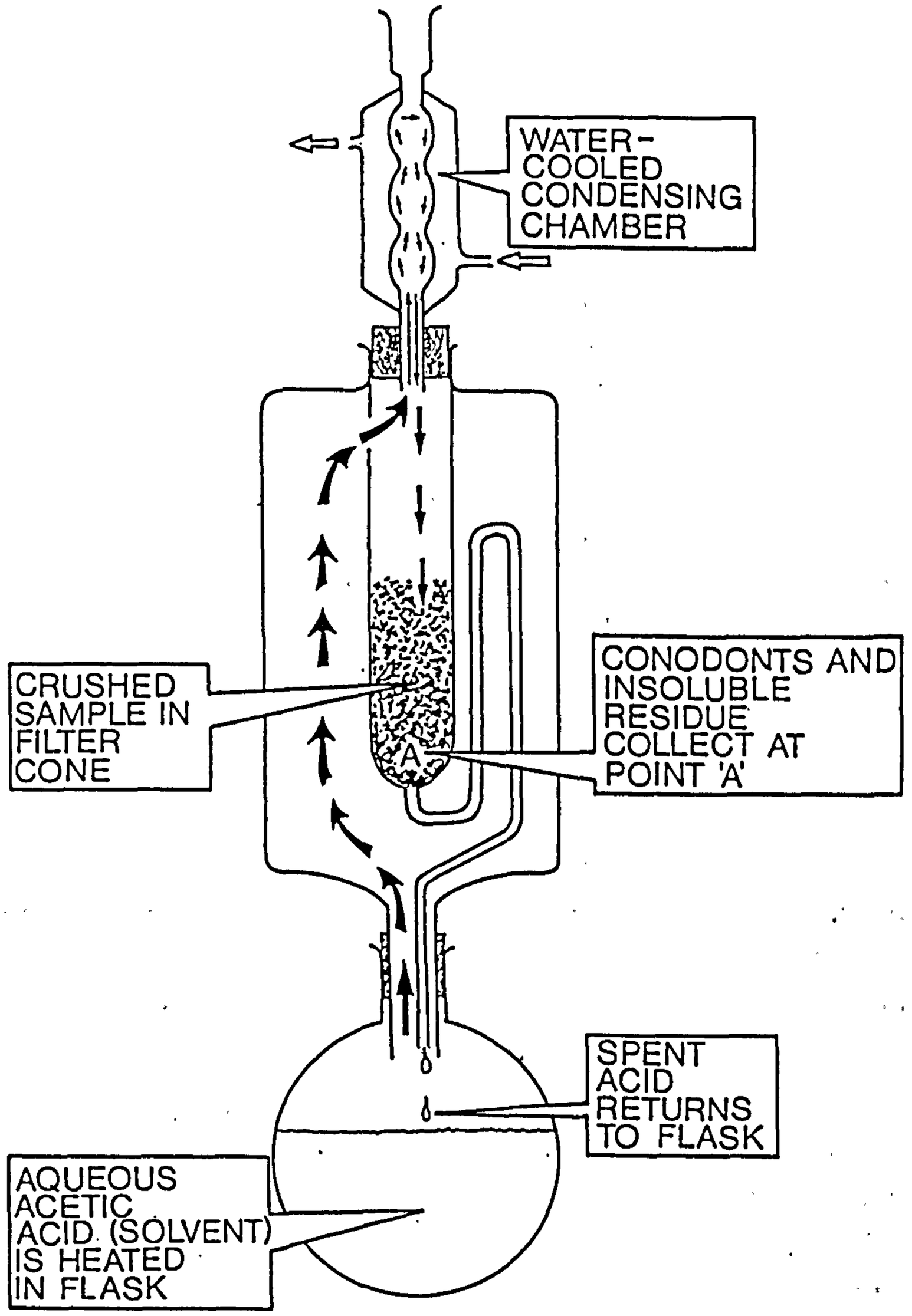
Finally, although developed for extraction from siliceous rocks (see section 3.1b,iv), the **hydrofluoric acid** (HF) method, in which the apatite component of the element becomes fluoridized, is potentially applicable to any rock type (Orchard, 1987). Unfortunately, the quality of the elements recovered is often rather poor.

The formic or acetic acid treatment is carried out in fume cupboards in many laboratories, but if ventilation is adequate the buckets can simply be stacked on racks. Barnes (1987) uses mobile racks and buckets of rectangular cross-section (for added space efficiency). Racks are built, with bucket dimensions in mind, of an angle-iron framework and solid plywood shelves (to prevent spillage problems), with a wheel at each corner. For filling and sieving the entire rack is wheeled to the sink and to the acid. Water is added with a long hose, and measured volumes of acid can be added using a small (e.g. 1/3hp, 115V) electric peristaltic pump with an enclosed motor, and acid resistant tubing.

Zhang (1987) dissolves limestone samples in a "tower" through which acid is continuously circulated by means of two storage vessels and an electric pump. He records an approximate 3-fold speeding up of the acidising process and recovery of 8 times more well preserved elements than with the standard process.

If the temperature of the acid digest is raised by approximately 20°C, above room temperature, dissolving time is halved (Jeppsson and Fredholm, 1987). However the risk of acid damage to the conodont elements is also increased and extra care must be taken to achieve the exact relative quantities of acid and calcium acetate suggested by Jeppsson et al. (1985).

figure 3.1.2 Stylized diagram of a Soxhlet extraction system. Showing how it may be used to dissolve a limestone sample.



With particularly difficult limestones or carbonate-cemented rocks, the speed and efficiency of the acetic acid digestion may be increased by the use of a Soxhlet extractor (Mann and Saunders, 1975), although risk of acid damage to conodont elements may be increased (Merrill, pers. comm. 1986). This is commercially available apparatus (see fig. 3.1.2) which circulates continuously purified hot solvent (aqueous acetic acid) through the sample (limestone) and continuously removes all dissolved material which then crystallises (as calcium acetate) in a separate flask. Using a standard 2 l capacity system, 500 g of $CaCO_3$ may be dissolved using 600 g of glacial acetic acid. The flask should never be heated by a direct flame or hot-plate; rather an electric heating mantle is recommended.

ii) Shales, black shales and marls.

The breakdown potential of these rocks varies greatly, depending on the degree of metamorphism and induration which they have undergone and on their detailed lithology. For this reason no standard method can be recommended for processing such rocks. Shales comparatively rich in organic matter may be X-rayed to establish the presence of conodont elements prior to breakdown (Peters et al. 1970; Norby and Avcin, 1987).

With the softer marls or calcareous shales, claystones and semiconsolidated materials, simply **soaking in water** for one to two hours may cause sufficient disintegration for the residue to be poured through a sieve stack (see section 3.1c). Use of a water jet with a 'rose' may be required during sieving. Some marls respond to treatment with **acetic acid** but it is important to buffer the solution as outlined above (section 3.1b,i).

Hard clays and clay-cemented rocks which do not disintegrate on soaking, may respond to one or two hours slow boiling with a **dispersing agent** mixed in water. The boiling process should be slow to avoid unnecessary agitation. Some workers recommend crushing the sample, prior to boiling, into 2-3 cm fragments to increase the surface area available for reaction; but the danger of stressing and breaking the elements must be balanced against the reduction in processing time. Following disintegration (e.g. after 2 hours) the sample is poured through a sieve stack (see section 3.1c) and washed with tap water followed by distilled water (Rixon, 1976). The most commonly used dispersing agent is sodium carbonate (Na_2CO_3) of which only small quantities are needed: a spoonful per reaction. Aluminium containers should not be used as sodium carbonate is highly corrosive to them. Common alternative dispersing agents are sodium hydroxide (caustic soda, NaOH) and sodium hexametaphosphate ("Calgon" or Graham's salt, $(NaPO_3)_6$). Sodium hydroxide may be used as a 20 % solution (Pokorny, 1963), and sodium hexametaphosphate should be added to water until the solution feels slippery when rubbed between the fingers. Note that the partly dissolved material is dangerously sharp, and so care must be taken during

stirring (Rixon, 1976). Any loss through evaporation can be replaced during the boiling process.

A number of techniques involve the use of a **surfactant** (a substance which reduces the surface tension of a liquid and thus allows it to penetrate a solid). Zingula (1968) describes use of Quaternary O for disaggregating hard shales and argillaceous sandstones or limestones. This is a tertiary amine compound which was marketed in the U.S.A. by Ciba Geigy. However it appears that Quaternary O is no longer in production and the currently available compound Miramine has been tested at the University of Tennessee, as an alternative, used in exactly the same way, and produces comparable results (Newsletter of the Canadian Association of Palynologists 1986/7, p9). Miramine is available in the U.S.A. from the Miranol Chemical company, 68 Culver Rd., Dayton, NJ 08810. A 20 % solution is made with warm water and added to boiling water containing the sample, and the mixture is kept boiling until the sample breaks down. Stirring may be necessary during the boiling to stop chippings from sticking to the bottom of the beaker and to combat froth build-up. To overcome the problems of smell, samples may be processed in a fume cupboard, although this has never proved a problem to me. Jones (1969) suggests using surfactants such as trisodium phosphate (Na_3PO_4)in a slightly different way. The dry crushed sample is heated in a bowl until quite hot and then one teaspoonful per pint of water detergent solution is suddenly added; this technique has the advantage of being quite rapid.

Crystallisation of a solution which has entered the pores and cracks in a rock can result in mechanical disintegration. Jones (1969) suggests boiling the crushed sample in a concentrated solution of sodium thiosulphate ($Na_2S_2O_3.5H_2O$, "photographic hypo") until the rock fragments are saturated. The saturated chippings are then poured into a shallow dish and left to dry. As the solution evaporates, crystals of sodium thiosulphate form in the rock, which disintegrates. Pokorny (1963) suggests sodium sulphate (glauberite, $Na_2SO_4.10H_2O$) as an alternative and notes the potential for automation when hundreds of samples are to be processed in a day (see Wicher, 1942). An even cheaper alternative is to use ice, by letting water fill the pore spaces and cracks in the rock and then freezing it. Pokorny (1963) suggests covering the sample in water and applying a vacuum until no more bubbles escape, in order to expel all air from the pore spaces. The sample is then returned to atmospheric pressure and frozen. Alternatively, if no vacuum is available, the sample can be boiled and then frozen at -30°C.

Jones (1969) has also successfully disintegrated shales through rapid **heating and cooling** using a blow-torch, and through boiling under pressure in an autoclave. Cooking shales in a microwave oven should potentially lead to mechanical breakdown through expansion of air in the pore spaces. Problems arise though because the rock heats up very quickly (e.g. 170°C in 2 minutes);

this will alter the CAI of the conodont elements and may make them fragile. Plastic containers melt at these temperatures so pyrex (or an equivalent) must be used. Also in my experiments the breakdown has been very limited indeed. Perhaps some experimentation with regard to soaking, freezing, etc., prior to 'cooking' is indicated. Jeppsson (pers. comm. 1985) suggests a 'popcorn' method involving sealing of the pores with oil after soaking in water.

Black shales often respond to **oxidation** of the organic matter they contain. Pokorny (1963) suggests crushing the sample and soaking it in a 10-15 % solution of hydrogen peroxide (H_2O_2) in water. Boiling may occur in a matter of seconds or may take 10-15 minutes and disintegration is often total. A drop of diluted ammonium hydroxide (NH_4OH), added to the beaker can increase the reaction dramatically; however, heat is produced and the reaction may be violent. Higgins (in Lindström 1964) and Higgins and Spinner (1969) suggest a 15 % solution of sodium hypochlorite ($NaClO_3$) in water as an alternative oxidising medium. Sodium hypochlorite is contained in household bleach (4 % - 6 %). Duffield and Warshauer (1979) suggest a technique involving oxidation followed by deflocculation of the remaining clastic particles with Quaternary O. A 1 kg sample is crushed, placed in a plastic bucket and soaked in 3-4 l of household bleach for 2 weeks. 100 g of sodium hydroxide beads (NaOH) are added to facilitate the reaction. After breakdown the sample is sieved and the non-disintegrated material is returned for further breakdown. After the final sieving the material not disintegrated is boiled in Quaternary O (see above) and sieved while still warm. Then and Dougherty (1983) describe a speedier adaptation of the above in which 150 g of the crushed sample is first dry sieved through a 10 mesh (2000μm) sieve, then placed in a glass beaker and barely covered with 30 % hydrogen peroxide. Effervescence may occur in a matter of seconds and water can be added to dampen violent reactions. After one hour, or when bubbling has stopped, the sample is soaked in 300 ml of a 50 % solution of water and household bleach, on an oscillating hot plate, for 1-2 hours. To increase the reaction a 0.3 M base solution (10 g NaOH pellets to 750 ml of water) is substituted for the water. The sample is then wet sieved and soaked in a beaker of 20 ml stock Quaternary O (5 % solution) and 300 ml water for a few hours. Wet sieving is then followed by oscillation for 1-2 hours. Resistant samples are returned for further breakdown. Note: hydrogen peroxide and sodium hydroxide can cause severe skin burns and rubber gloves, a lab coat and a face mask should be worn. Processing should be carried out in a fume cupboard as noxious fumes are produced when treating sulphides with bleach (Merrill 1980).

Lighter-coloured shales not responding to any of the above techniques may react to treatment with an **organic solvent**, e.g. dry-cleaning fluid (Stoddard solvent), petrol (gasoline in the U.S.A.), paraffin (kerosene in the U.S.A.), petroleum ether or white spirit (Layne 1950, Swift 1987a, Varker 1987a).

Collinson (1963) describes a technique using Stoddard solvent (or any low-volatility low-flammability dry-cleaning fluid). The sample is thoroughly dried, e.g. in an oven at 150-200°C (Mapes and Mapes 1982), and is then allowed to soak in the fluid for approximately two hours. The fluid is drained off and filtered for re-use. Hot water with detergent is added to the sample, which, after soaking, should disintegrate to a sludge which can be sieved. Any shale not broken down can be dried and treated again. If, after sieving, the residue consists of a large percentage of gypsum, Mapes and Mapes (1982) suggest a technique for its removal. The residue is totally redried, e.g. 24 hours at 150-200°C, and then resoaked in Stoddard solvent for about one hour. The solvent is then decanted, and the residue soaked in water for no longer than 30 minutes, followed immediately by washing through appropriate sieves. Note that these researchers point out that the actual chemical function of the Stoddard solvent is unknown, although Solakius (1983) suggests that in the case of petrol (gasoline) the hot water causes the organic solvent in the pore spaces to expand, causing mechanical breakdown. Haynes (1981) notes that the technique was originally discovered by a French oil company drilling in the Sahara, where it was noticed that dark shales outcropping near the drilling platform disintegrated after being soaked in waste petroleum.

Jones, (1969) suggests that black fissile shales may be examined for conodont elements by breaking the sample into 8-10 cm blocks and then splitting each block into thin laminae using single-edged razor blades. These surfaces are then examined using a binocular microscope.

If all else fails, including use of HF on shales with any silica content (section 3.1b,iv), some recognisable conodont fragments may be recovered by simply crushing the shale finely then using a separation method (section 3.1d).

iii) Ironstones or rocks cemented by iron minerals.

In siderite-rich samples, formic acid can be used, as outlined in section 3.1b,i. For goethite (limonite)-rich samples, Freeman (1982) and Merrill (1987a) suggest use of sodium hydrogen oxalate solution, which is made up by mixing 100 parts of anhydrous oxalic acid with 93 parts of sodium bicarbonate in distilled (i.e. calcium-free) water. Samples are processed in quantities of approximately 10 g per each 150 ml of solution, by boiling for 1 hour. Thioglycollic acid in 5 % aqueous solution (Howie 1974) may be used to digest goethite and haematite but it can dissolve conodont elements and so should be buffered with 9 g of calcium phosphate (e.g. bone meal) per litre for pristine specimens. The major drawback to the use of thioglycollic acid is that of cost, and for goethite Freeman (1982) suggests that sodium hydrogen oxalate (see above) is superior. Pyrite can be oxidized to goethite (Merrill 1980) by being immersed in a 7.5 % aqueous solution of sodium hypochlorite and NaOH for 1 to 3 hours (Merrill pers. comm. 1985). Alternatively, pyrite may be heated until

it can be removed magnetically, or conodont elements may be 'floated off' from pyrite using methylene iodide in a density separation (Hamar 1966) as outlined in section 3.1d,ii. (Note that sodium hypochlorite is toxic and corrosive and releases chlorine when mixed with acids.)

iv) Cherts and siliceous rocks: HF treatment.

Conodont elements have been recovered from chert, using hydrofluoric acid (HF), at least since 1968 (Hayashi 1968), although fluoridisation is more destructive to fossils composed of calcium phosphate than it is to those composed of calcium carbonate. When processing siliceous rocks, a smaller sample (200-250 g) than for limestones or shales is usually taken. All carbonate should first be removed by the standard acid treatment outlined in section 3.1b,i. This avoids the formation of insoluble fluorides during the HF treatment. Passagno and Newport (1972) outline the general procedure in which samples are crushed, using a rock crusher or steel mortar and pestle, into 1-5 cm fragments. These fragments are placed in a plastic beaker of dilute HF in a fume cupboard; a sample of approximately 250 g can be processed in a 1 l beaker (Orchard 1987). The beaker should never be more than half full to allow for substantial frothing during digestion. Excessive frothing can be combated by spraying acetone into the beaker, thus reducing the surface tension and allowing the bubbles to escape more easily (Benham pers. comm. 1987). Relative concentrations of acid used vary from 5 % or 6 % (Sevastopulo and Keegan 1980, Orchard 1987) to 10 % (Barrick 1987), but it may be necessary to experiment in order to achieve the best results. For some rocks, stronger solutions and shorter digestion times (e.g. 50 % HF for from 5 minutes to 1 hour) may be more effective, although effervescence is more vigorous and may damage the conodont elements (Sevastopulo and Keegan 1980). Care must be taken when calculating the percentage of acid as it is usually supplied at a specified concentration, e.g. 60 %. After 24 hours or less (Barrick 1987 suggests 6-8 hours) the HF is decanted off and the sample is washed in dilute HCl (e.g. 20 % solution), to drive off any remaining HF and to alter any fluorides into soluble chlorides. The HCl is decanted off and replaced with water several times until the liquid remaining is neutralised. The sample can then be sieved, and any undigested material returned for further breakdown. Orchard (1987) reports that no buffers are necessary during processing but that the samples should be sieved every 24 hours. After each batch has been processed, the acid may be recovered and re-used up to 4 or 5 times (Barrick 1987). It is safer and more straightforward if the acid is discarded. HF should be neutralised before disposal and the system used should be carefully considered with regard to local safety requirements. 2-3 hours in HF is enough to etch and whiten conodont elements (Isozaki and Matsuda 1980), and although volume reduction of the sample is often rather low at each sieving (4 % to 8 %), increasing the

immersion time in HF does not increase conodont yields (Orchard, 1987).

Barrick (1987) reports that abundances recovered are highest on days 2, 3 and 4 of the process and then fall off rapidly. Total abundances are often as high as thousands of elements per kg. When treated with HF, the apatite component of the conodont element is fluoridised, resulting in a volume increase and consequent cracking and distortion of the element. Although few good-quality elements are recovered, the fragments are often large enough to be identified. Fluoridisation of conodont elements also reduces their density to an approximate sp.gr. of 2.6 (Orchard, 1987), hence a density separation (section 3.1d,ii) cannot be used. However residues are usually small enough for no separation to be required.

By far the most time-efficient way of using HF is by combining it with hydrogen peroxide (H_2O_2) as described by Magné and Dufaure (1964). 100 g of the crushed sample is placed in a 1 l plastic beaker, and 0.2 l of 43 % H_2O_2 and 0.3 l of 'pure' HF (i.e. the strongest concentration available) is poured on. After 20-30 minutes the reaction goes strongly exothermic for a few minutes and then dies down. The liquid is decanted off and water is gently added until the liquid is neutralised. The sample is washed with water and gently sieved.

Merrill (pers. comm. 1985) suggests sitting the beakers in a polyethylene washing-up bowl, in the fume cupboard, in case of any overflow. Just prior to use, fresh 50 % H_2O_2 is diluted to the correct volume. 52 % HF was found to be the maximum concentration available. Results are varied, although in general the technique works well, and in many cases produces beautifully preserved conodont elements. It appears that most of the dissolution actually takes place within the few tens of seconds when the reaction is at its most violent. Drawbacks to the technique are that, with some rocks, dissolution is only partial or slow and that, when the technique is carried out in small quantities, the cost is prohibitive, particularly with respect to 'fresh' supplies of H_2O_2. Nevertheless the technique is remarkably rapid, such that a sample may be received from the field, processed and a conodont age determination given, in as little as 1 hour.

It is emphasised that HF is extremely dangerous and should only be used with a properly designed fume cupboard and safety shower, protective clothing, rubber gloves and a face mask.

3.1c Sieving.

After the conodont-bearing rock has been broken down (as described in section 3.1b), the insoluble residue is often separated into a number of conodont-bearing size fractions. This is most commonly done by pouring the entire sample through a sieve stack (see Rixon 1976). Lids and bottom containers, supplied with the commercially available sieve stacks, are not used. Sieves are either graded in terms of "mesh size" (apertures per cm) or in terms of the aperture dimension in μm. A suitable range of mesh sizes is 200 (75μm), 120 (125μm), 60 (250μm) and 25 (710μm). Much of the fraction retained in the 25 mesh (71μm) consists of undigested rock, which may be returned for further breakdown. The above size range is only a general guide and, when studying some of the larger elements (e.g. some of the Devonian platform conodont elements), a coarser sieve should be substituted for the 25 mesh (710 μm). Water should be gently sprayed through the loaded sieve stack, in a sink with a settling tank, until no further fine or clay material is being washed out. Care must be taken not to damage or block the plumbing system. Use of a plastic 'rose' to break up the spray helps to overcome the problems of mechanical breakage of the conodont elements. If a sample is particularly clay-rich, the entire stack may be fully immersed and sieved, or the sample may be washed through a fine mesh of commercially produced cotton or nylon fabric (i.e. a mesh between 40μm and 75μm) prior to sieving, to eliminate the clay fraction.

After sieving, the residue from each sieve is washed into a labelled filter paper, allowed to drain and dried in a cool drying oven. Splitting of the conodont-bearing size range into two or more fractions may make it easier to achieve efficient separations (see section 3.1d). Between each sample the sieves should be thoroughly cleaned to prevent any possibility of contamination.

3.1d Separation and concentration (see also Fig. 3.1.1).

It is common for the dried residue from shale and limestone samples to consist of over 99 % unwanted "gangue", the nature of which will vary depending on the original rock. To facilitate accurate and untaxing picking of the conodont elements, they may be concentrated in some way; a number of methods are used. Chert residues are usually small enough for no concentration to be necessary.

i) Electromagnetic separation (Dow, 1960, 1965).

As the magnetic susceptibility of conodont elements (diamagnetic), quartz (diamagnetic) and dolomite (paramagnetic) is different, a two phase separation is possible. The first phase separates out the ferromagnetic component (e.g. goethite, haematite) and the second phase separates the remaining less magnetic components. Using either a Franz- or Cook-type electromagnetic separator which consists of a powerful adjustable electromagnet and a vibrating chute divided into two channels, an inward side slope of between 5° (Merrill, pers. comm. 1985) and 10° (Dow, 1960) is set, and the forward slope is set between 20° (Dow, 1960) and 30° (Merrill, pers. comm. 1985). The forward slope controls the speed of the particles, and experimentation may be necessary as a steeper slope is required when dealing with finer particles (Jeppsson, pers. comm. 1985). the washed and dried residue is fed into the hopper and allowed to run down the chute as a continuous single-file stream of particles. The vibrator should be on and initial amperage set between 0.6 (Merrill, pers. comm. 1985) and 1.0 (Dow, 1960). The 'non-magnetic' portion (inner channel) should contain all the conodont elements and the quartz/dolomite component, whereas the outer-channel portion should comprise the ferromagnetic component. If this is not so, the amperage should be adjusted empirically until the required separation is achieved (settings may vary from one machine to another). Note that clogging and false results may occur if the initial amperage, the speed of the particles down the chute or the feed rate of the sample is too high. At every stage of the separation, two or more runs may be necessary.

Settings for the second phase of the operation depend on the nature of the 'non-magnetic' portion. If a large proportion consists of conodont elements, further separation may not be necessary. If dolomite makes up a large proportion, further digestion with formic acid or a density separation using unaltered TBE (see below, section 3.1d,ii) may be indicated. However, if the dolomite contains any Fe a second run can be made with revised settings of the order of side slope -2° and forward slope 10° (Dow, 1960). Amperage should be set at a maximum and the vibrator should be on. At these settings, the dolomite (which is paramagnetic if it contains small amounts of Fe) goes into the magnetic channel whereas conodont elements (and quartz) go into the 'non-magnetic' channel. Separation of iron-free quartz from conodont elements using the isodynamic separator is considered by many workers to be too delicate and intricate to be worthwhile. The same settings are used as for dolomite, with an amperage of approximately 0.9. As conodont elements are slighly less diamagnetic than quartz, they go into the 'magnetic' channel.

Depending on the particular conditions involved with each different type of sample, slight variations on the above procedure may prove profitable. Varker (1987b) suggests a number of modifications for use with shale samples of low conodont concentration. A recently available addition to the standard magnetic

separators (from GBL Electronics Inc., St. Bruno, Quebec) is an attachable "vibrating track-feeder" which allows increased control over the flow rate. Alternatively it may be possible to get hold of a magnetic separator capable of processing more bulky samples, as the limited flow rate is a major drawback to the use of Franz and Cook separators. Examples of faster laboratory electromagnetic separators are:

(i) Carpco magnetic separator, Carpco Research and Engineering Incorporated, Jacksonville, Florida, U.S.A.

(ii) Davies magnetic separator ("non-entertaining"), model No. 45V, D.M. Works, Ware, Hertfordshire, England.

ii) Traditional heavy liquid separation.

Ellison (1944) states the relative density of conodont elements as ranging between sp.gr. 2.84-3.10. Thus they are more dense than common gangue minerals, e.g. quartz (sp.gr. 2.65) and calcite (sp.gr. 2.715). Consequently one of the most commonly used separation techniques is density separation in a heavy liquid. The two liquids most commonly used have been bromoform (tribromomethane, $CHBr_3$; sp.gr. 2.89) and tetrabromoethane / TBE (acetylene tetrabromide, $(CHBr_2)_2$; sp.gr. 2.96). Rarely it may be necessary to separate conodont elements from a residue which is more dense than they are, in which case methylene iodide (diiodomethane, CH_2I_2 ; sp.gr. 3.325) may be used.

Recently there has been an increased awareness of the dangers to health involved with the use of such heavy liquids (Brem et al. 1974, Sax 1979, Hauff and Airey 1980). Tetrabromoethane and similar halogenated alkanes are carcinogenic. Increasingly in the literature reports are being made of workers whose untimely deaths are thought to have been linked with intensive use of such heavy liquids (e.g. Coombs 1974). There are also short term toxicity effects: both bromoform and tetrabromoethane are easily absorbed metabolic poisons, when metabolised in the body they produce carbon monoxide in the blood, thus reducing its oxygen carrying capacityand causing light headedness, dizziness and coma. Both these liquids are also very easily absorbed and cumulative systemic poisons, they collect in fatty tissue, the brain, lungs, liver and kidneys. Repeated exposure results in excessive damage to these organs, and can also cause haemorrhaging. Little work has been done on the toxicity of methylene iodide, but at this stage there seems no justification for viewing it any differently from the above.

If these liquids are used for density separations, the entire process should be carried out in an efficient fume cupboard using protective gloves and cuffs. Nitrile and high grade PVC are slightly more resistant than natural rubber or normal PVC to halogenated hydro-carbons, but they will attack all types of natural and synthetic gloves. Should swelling occur switch to another pair of gloves and allow the swollen gloves to dry and return to normal.

When using TBE the specific gravity should firstly be adjusted to 2.8 by diluting with ethyl alcohol or acetone, so that a ramiform conodont element will sink and calcite will float; bromoform can be used straight from the bottle. The sample is added to the liquid in a separating funnel with an outlet large enough to prevent clogging and is stirred vigorously. The quantity of the sample should be small enough to allow free movement of all particles. The sample should be stirred at half-hour intervals, or a continuous stirring mechanism may be used (Charlton, 1969; Davis and Webster, 1985). When no further settling-out is visible, the 'heavy' fraction containing the conodont elements may be run off into a labelled filter paper in a funnel over a large recovery bottle. Because of the expense, as much heavy liquid as possible is recovered. Standard grade 4 filter paper is commonly used, although Barnes and O'Brien (1987) suggest using coffee filters. After being allowed to drain, the filter paper and separated sample are thoroughly washed, either by using a squirter bottle of acetone or similar solvent (e.g. petrol/gasoline or alcohol) or by full immersion in a series of beakers of solvent (Sevastopulo, pers.comm. 1985). A bromoform/TBE and acetone mixture is extremely flammable and on igniting produces toxic fumes. When using a squirter bottle, it is important to start washing at the edge of the filter paper.

The remaining 'light' fraction and heavy liquid is run off as above. Any clogging in the funnel may be overcome by fitting over the top of the funnel an inflated rubber glove which can be squeezed to force air through (Ryley, 1987) or by inverting the funnel and washing the residue out of the wider end using a wash bottle of solvent. The separating flask should be thoroughly washed out with solvent between each sample to avoid contamination. The washed filter papers may be left in a fume cupboard to dry. If any trace of the smell of the heavy liquid remains, the washing process must be repeated or the sample may be cleaned in a Soxhlet extractor (Fig. 3.1.2) using acetone as the solvent, (see also Freeman, 1975). Merrill and Ziegler (pers. comm. 1985) use a basic magnetic separation (section 3.1d,i) as a matter of course before using heavy liquids - to increase efficiency of separation. Ziegler also suggests boiling samples in NaOH for 10 to 15 minutes before using heavy liquids as this cleans the samples and increases the percentage conodont element recovery (as a result of decreased rafting in the light fraction).

A number of methods are used to reclaim the heavy liquid from the acetone/heavy liquid washings. As outlined by Krumbein and Pettijohn (1938), Turner (1966), Benjamin (1971) and Hauff and Airey (1980), the solution may be mixed with water in excess, and then the water and its contained solvent can be continuously removed (i.e. poured off) and replaced with fresh water until the proper density is reached (sp.gr. 2.8). This method involves loss of heavy liquid from 2 % to 44 %. More simply, the solvent can be allowed to evaporate from an evaporating dish placed in a fume cupboard, until the correct density is

reached. Hauff and Airey (1980, p.16) outline a 'flash evaporation' method of recovering both the heavy liquid and the solvent. Mileson and Jeppsson (1983) suggest a more sophisticated development of this technique in which the solution is not heated. The liquid is placed in a flask connected to another flask twice its volume, which in turn is connected to a vacuum pump. The pressure is lowered until the mixture starts to boil, whereupon the system is sealed, the vacuum pump is disconnected and the larger flask is placed in a freezer at approximately -25°C. The solvent evaporates from the small flask (at room temperature) and condenses in the large flask. This method allows more complete recovery than 'excess water' methods and does less damage to the heavy liquid.

Halogenated hydrocarbons (e.g. bromoform and tetrabromoethane) break down and darken in colour over time, particularly if exposed to heat, water or ultraviolet radiation (Hauff and Airey 1980). With repeated use the liquid may darken so much as to make it difficult to observe the effect of separation. von Bitter et al. (1978) compare several methods for decolourising tetrabromoethane, with respect to effectiveness, cost and speed. They recommend that 250 ml of the discoloured liquid should be passed through a 5 cm x 60 cm glass column filled with 250 g of 30-60 Fuller's earth (attapulgus clay). In view of the recommendation made by Hanna (1927) that Fuller's earth be used for decolourising bromoform, von Bitter et al. assume their results to be equally applicable to bromoform.

iii) Sodium polytungstate.

This is a recently introduced commercial compound marketed by the Sometu Company of Berlin. It is supplied as a powder which can be dissolved in de-ionised or distilled water to produce a liquid with a potential range in density from sp. gr. 1.0 to 3.1. (manufacturer's figures). Procedures differ slightly from those used with traditional heavy liquids as the liquid is both non-toxic and water soluble. A number of problems are encountered when using sodium polytungstate at densities as high as sp. gr. 2.8, associated with its viscosity and with the evaporation of water from the solution during separation. The high viscosity greatly increases the time taken for a separation, and in some cases may even mean that ramiform elements remain suspended in the "light" fraction (Merrill, 1987c). Water loss increases the density and viscosity of the solution, and causes the crystallisation of sodium polytungstate which both cements particles together and blocks up the funnel.

Merrill (1987c) overcomes the problem of viscosity by separating samples in a centrifuge (10 min at 2,000 rev's per min). The "light" fraction can be poured off separately, into a filter paper, by dipping the centrifuge tubes in liquid nitrogen to freeze the lower half containing the "heavy" fraction. Once the remainder has melted again it is poured out into another filter paper. The

short time taken for the separation virtually overcomes the problem of evaporation.

Alternatively Krukowski (1988), links up the separation funnel to a vacuum pump to overcome the viscosity, and to overcome evaporation uses lids or plastic film across the top of the separating funnels and does not use a fume cupboard. Savage (1988) uses the liquid at a density of sp. gr. 2.78, rather than the standard sp. gr. of 2.82; this helps to overcome viscosity problems and although the size of the "heavy" residue is increased, it is still small enough for easy picking.

Dry sodium polytungstate sticks to glass, hence plastic ware and a teflon stirring rod are to be preferred. Krukowski uses a funnel with a hose and clamp rather than a stopcock, as this can crush the conodonts. It is important that there is no change in temperature during separation otherwise the density will change. Opinions on settling times and the degree of stirring needed, vary from author to author (Gregory and Johnson 1987, Krukowski 1988, Savage 1988). In general 6 hours and 3 stirs seem to produce acceptible results. Formation of $CaWO_4$ can cause problems, and all possible sources of Ca ions must be excluded (e.g. tap water). Therefore distilled or de-ionised water should be used (i.e. without Ca salts or Ca ions), and dolomite residues should not be separated. Samples should be cleaned of all lichen etc. before separation, to avoid clogging of the funnel. The salt can be reclaimed by washing in copious amounts of distilled water, and then evaporating the water off in a fume cupboard or low temperature drying oven (e.g. 75°C). A quicker way of reclaiming the salt may be to place the entire filter paper and its contents in a Soxhlet extractor (Merrill 1987c). After about 175 runs, the salt begins to break down to sodium tungstate (Na_2WO_4) and can no longer be used. Large amounts of tungsten in the residue results in the sodium polytungstate going blue through reduction of tungsten. A drop or two of 3 % H_2O_2 will restore the colour.

iv) Interfacial separation.

The standard technique (Freeman, 1982; Merrill, 1985 and 1987b) relies on the relative hydrophobic qualities of calcium phosphate such that, unlike most gangue minerals, when immersed in a mixture of water and kerosene (the American term for paraffin) or any insoluble organic liquid, the calcium phosphate is preferentially wetted by the kerosene which forms a film enveloping the particle (e.g. conodont element). The particles and their 'envelopes' can then be removed by being made to adhere to a substrate which the kerosene softens (e.g. paraffin wax) so that the particle becomes attached, allowing substrate and particle to be removed together. Freeman (1982) describes two variations of the above method using the same principles. One method substitutes an unfoamed polystyrene food container (yoghurt carton) as

the substrate, and tetrachloroethylene as the insoluble organic liquid. The other method traps calcium phosphate in the interface between water and kerosene/paraffin.

The procedure for the standard technique was demonstrated at the ECOS IV meeting (1985) by Merrill and Freeman. A 1 % detergent solution is made up (Fairy liquid in the U.K. or Dawn in the U.S.A. is suitable, but the choice of detergent is not critical). The detergent ensures that the kerosene/paraffin disperses to form a suspension. The washed sample is poured into a screw-topped beaker and thoroughly wetted with kerosene; detergent solution is added to a depth of 2-3 cm and the beaker is briefly shaken. Paraffin wax flakes (1-2 cm long and 1-2 mm thick) are then added and the beaker is agitated by hand for 5 min. For ease of pouring-off, the beaker is completely filled with detergent solution and tapped lightly to dislodge any gangue particles 'rafted' on the wax. The wax flakes are poured into a filter paper of the type designed for cleaning oil in deep-fat fryers and placed (in a funnel over a beaker) in an oven just hot enough to melt the wax, until all the wax has filtered through (this is then remelted and new wax flakes are made). The procedure is repeated another four times with the remainder of the sample. Any residual traces of paraffin wax remaining in the sample concentrate can be removed either by using a Soxhlet extractor (Merrill, pers. comm. 1985) with 60-80 petroleum ether as the solvent (see Fig. 3.1.2) or by repeated washing with a dispersion of kerosene in hot aqueous detergent solution, followed by washing in the hot aqueous detergent solution, before air drying (Freeman, pers. comm. 1985). Note that kerosene/paraffin is highly inflammable and should be used with care.

The advantage of the above method is that it provides an alternative to the poisonous and carcinogenic heavy liquids. It is also cheap and requires no expensive equipment. There is much scope for experimentation and adaptation. However, although recovery can be nearly total (Merrill, pers. comm. 1985), I have found that yields are often rather low.

v) Magnetohydrostatic separation (MHS).

Stone and Saunders (1987) outline an application of work by Andres (1976) and Parsonage (1977 and 1978) in which a high-density liquid is created by placing a paramagnetic solution in an inhomogeneous magnetic field. This method shows great potential for providing a safe, cheap, efficient and elegant density separation. A major drawback to using the Franz or Cook separator as the magnetic source is the low rate of sample throughput resulting from the very narrow gap between the pole pieces in these separators. Recently the Intermagnetics General Corporation of New York has marketed a series of "Magstream" separators in which MHS is combined with a centrifuge to provide a fast and efficient separation. Unfortunately these machines are extremely expensive.

vi) High frequency dielectrical separation.

Following the criteria outlined by Wang Yu-Xian (1981) it should be possible to separate apatite (dielectric constant, 7.41-9.5) from quartz (dielectric constant, 4.27-4.34), although the dielectric constants of dolomite and calcite appear to be too close to that of apatite. An application of this method appears to offer much scope for experimentation, particularly when trying to separate materials of similar density and magnetic properties.

Note that, for testing the efficiency of any extraction and concentration system, attention is drawn to the work of von Bitter and Millar-Campbell (1984) who introduce a known number of distinctive apatite grains (sp.gr. 3.1-3.2) to the sample prior to processing and then check the percentage recovery after processing.

3.1e Picking and mounting.

Even after judicious use of the processing and concentration techniques outlined above, the sample residue is likely to consist of a large proportion of gangue. A number of methods are used to pick out the conodont elements. Most commonly, the residue is spread out in a home-made or commercial shallow picking tray, the bottom of which is marked in numbered squares. At no point should the sample layer be more than one particle thick. Using a binocular microscope, each square is examined in turn and all conodont fragments are carefully lifted out using a slightly wetted fine paint-brush, a bristle which is either dampened or slightly rubbed with wax, a mounted needle - the tip of which is finely covered with Plasticine (or similar proprietary modelling clay) or by use of an electrostatic method (Barnes et al. 1987). Alternatively, Stinemeyer (1965) describes construction of a vacuum-needle picking device. The elements are transferred to a cavity slide (see below) and may at this stage be loosely grouped into pectiniforms, ramiforms or 'others' to await more detailed examination and classification. There is always a danger of dropping or damaging specimens en route between picking tray and storage slide, as this is usually done without the microscope; hence a little dexterity and concentration are required. In order for the whole process to occur under the microscope a 'holed' tray may be used in which the holes are positioned directly above a secured storage slide, and each element is 'posted' through. The latter technique is refined by the use of electrostatic picking.

If a sample is particularly poor in conodont elements and pristine condition is not a necessity, a method outlined by Schopf and Simpson (1970) may be used to speed up the picking. A piece of filter paper is soaked in an ammonium molybdate solution (200 ml ammonium molybdate solution plus 20 ml of 10% HCl plus a few small crystals of stannous chloride) for 15 min. When it turns

blue, the filter paper is removed and, whilst still damp, the sample residue is sprinkled over it and allowed to dry under a heat lamp for about 5 min. A white spot should occur surrounding every particle of phosphate in the sample. Formation of the spot depends on the formation of ammonium molybdophosphate, i.e. phosphate is removed from the conodont elements in the reaction; consequently, there is some etching and minor damage to conodont elements involved in the process.

Once the sample residue has been picked clean of all its conodont elements, it can be bagged, labelled and put aside. The conodont elements can be more thoroughly examined using the binocular microscope and identified. Initial sketches can be made using a camera lucida attachment on the binocular microscope. Proprietary cavity slides are commonly provided with 48, 60 or 100 divisions and may contain an auxiliary cavity for preliminary picking. Before use slides should be coated with a semipermanent glue which allows some repositioning when hydrated, such as gum arabicum which consists of 30 g of Acacia gum in 60 g of water plus 2 ml of glycerine and 52 ml of carbolic acid (Jeppsson, 1974, p.5) or gum tragacanth. Single-or multiple-hole slides can be obtained for mounting type specimens or important examples. The built-in sliding cover-slip of clear plastic which is often provided with proprietary slides may be replaced by a glass cover-slip if specimens cling to the plastic because of static electricity (Jones, 1969, p.16). Cullison (1934) describes construction of a slide in which a mirror makes up half the base, thus allowing simultaneous examination of both top and bottom sides of the conodont under the binocular microscope.

Some careful cleaning of the conodont elements is usually possible using a very fine paintbrush and much water, but the elements are often very brittle, particularly those of high colour alteration index (CAI) and extreme care must be taken. Ultrasonic cleaning tends to fragment the conodont elements (van den Boogard, pers. comm. 1985). Finally all the elements and their slides can be catalogued. Invaluable aids to identification are the Catalogue of Conodonts edited by Ziegler (1973, 1975, 1977, 1981) and the revised Treatise of Invertebrate Paleontology, part W (Clark et al. 1981).

3.1f Casts and moulds.

When conodont elements are seen on the surface of a rock their study may be enhanced if a cast is made of the elements. Any cast has to be taken from a mould, which can be made from a variety of materials. Compounds which can be mixed and used at room temperature are easier to work with than the polyvinal chloride pastes and hot-melt compounds, for which temperatures of 150°C and 120°C are needed during use. Rixon (1976) suggests that the silicone rubber cold cure silastomers are the easiest to use of the room temperature

mould materials, although expense and mechanical weakness can cause problems. Rubber latex seems to be most commonly used amongst conodont workers (e.g. Ellison 1987, Hunicken and Ortega 1987), and has been used as a mould material since the 1930's (Fischer 1939). It has the great advantage of being highly elastic, although many workers find there is considerable shrinkage when it sets. Other materials used for making moulds are the sodium alginate dental compounds to which water is added to form a gel, the polysulphide rubbers and the dental rubber impression compounds in which two components are mixed to form the mould material. These last three materials are particularly useful for 'the travelling palaeontologist' (Rixon 1976).

When using silicone rubber or rubber latex the surface of the specimen should be clean and sound and may be consolidated with Butvar B98 or similar, and any cracks filled with water soluble putty. Removal of the dried mould is made easier by pre-coating the specimen with either a liquid detergent such as 'Teepol' in the case of silicone rubber, or, if necessary, with silicone fluid in the case of rubber latex.

The method of use is broadly similar with both compounds. With silicone rubber a dam of Plasticine or modelling clay is built around the specimen. The room temperature vulcanizing silicone rubber is mixed with the catalyst in a disposable container, following the specific instructions. If a slightly lower proportion of catalyst is used, the setting time is increased and the degree of shrinkage is decreased. In order to expel all bubbles Cheney, of the National Museum of Natural History, Washington D.C. (Briggs pers. comm. 1985) suggests putting the mixture into a vacuum (30 inches of mercury) immediately prior to pouring. This causes the rubber to rise and degass. The mixture should be poured directly onto the specimen at a controlled and steady rate, and then left to dry. Care should be taken not to trap any air bubbles.

When using latex, plasticine should only be used if covered in shellac, butvar or similar substances as its oil content attacks the rubber. If the rubber is painted on rather than poured, and a thin mould is made, in order to keep its shape when casting, a 'mother' or mould box can be made by building up the dam walls and pouring plaster of Paris over the mould before removing it from the specimen.

Traditionally casts have been made of plaster of Paris, in which case care has to be taken in mixing to avoid trapping any air bubbles. To facilitate removal, the mould may be lightly coated in silicone oil or grease before the plaster is carefully poured in. After drying, the resulting cast may be painted with dry colours, or after being sealed (e.g. with Butvar B98 or a similar plastic) with acrylic paint or microscopy stains (Rixon 1976). An advantage of the silicone rubber mould is that casts may also be made from medium to low viscosity plastic epoxy or polyester resin, and from fibreglass. These resins may be pre-coloured if required. The resulting cast may be photographed using the

scanning electron microscope.

If conodont elements are partially buried within a non-calcareous host rock, the visible portion can be sketched or photographed and then the conodont dissolved with a pippetted 10-20 % HCl solution (Ivanov 1987). The resulting natural mould is often finely preserved and can be cleaned up with a medium-hard wire brush. A cast of the etched surface can be made from PVA glue, plasticine wetted in soapy water, or any of the materials mentioned above.

3.1g Photography.

Early workers and many current researchers produce illustrations of conodont elements using light photography. However, transmission electron microscopy and more particularly scanning electron microscopy (SEM) have now come into routine use and have provided magnifications large enough to spark off a whole new area of conodont research: i.e. detailed studies of conodont ultrastructure, as reviewed by Burnett (1987a).

i) Light photography.

Photographs may be taken using a low-power photomicroscope, either as stereo-pairs for three-dimensional viewing (Evitt, 1949) or as single plates. Jones (pers. comm. 1985) suggests taking stereo-pair photographs of a natural or artificial conodont mould and then displaying them reversing the stereo-pair; this will produce pseudoscopy and show the mould as a positive feature.

Using a very small amount of gum arabicum (Jeppsson, 1974) or a similar glue, specimens may be mounted either directly on a dark background slide or on a small (1-3 cm) piece of glass and fixed to a universal stage (Jeppsson, pers. comm. 1985). The obvious advantage of the latter is the ease of adjustment or orientation of the specimens without risk of damage. Barnett (1970) describes how to construct a cheap Plexiglas 'orienting stage' which is less cumbersome than the universal stage and simple enough to be constructed in the workshop of most institutions.

Specimens being photographed to illustrate CAI (Epstein et al. . 1977) or distribution of white matter, etc., should be uncoated. Black, transparent or particularly shiny specimens are usually lightly coated, either with magnesium oxide dust (or 'smoke') or with ammonium chloride. For the former the specimen, mounted on its slide, is held above burning magnesium ribbon. In order to direct the coating an upturned (heat-proof!) funnel may be supported between the ribbon and the specimen (Merrill, pers. comm. 1985). The magnesium oxide 'dust' washes off with water. Dusting with ammonium chloride is perhaps more common but, since it is hygroscopic, the process should be carried out immediately prior to photographing in conditions of low humidity. Either it can be applied as a fine spray in liquid form, or a quantity of

ammonium chloride crystals may be placed in a 'puffer' (Cooper, 1935) and heated until the smoke from the 'puffer' is blue, when the slide is held about 20 cm away and lightly coated. It is very difficult to get a fine even coating on complex surfaces, and any excess, which may result in frost-like spikes, should be cleaned off with alcohol, which does not affect the water-soluble glue (Sparling, pers. comm. 1985). Ammonium chloride should be carefully removed after photographing as it will eventually produce HCl which can damage the conodont (Jeppsson et al. 1985).

For high-quality photographs, the specimen should be illuminated from two sides at 45° to the stage and the intensity of the lights balanced until a satisfactory image is obtained (Marsh, pers. comm. 1985). To avoid reflections from an uncoated specimen, either it may be immersed in a very small cup of alcohol mounted on the stage (Jeppsson, 1974), or diffuse lighting could be used. To produce the latter, either a 'ring lamp' or very bright normal lighting with a cylinder of white paper between the lights and the specimen can be used.

When using a high magnification, a major limitation with the photomicroscope is the restricted depth of field obtainable. By closing down the aperture depth of field is increased but resolution is lost. Normally it is impossible to increase depth of field above about 1/10 mm at 100x magnification (Hay and Sandberg, 1967). Although light photography must be used for CAI illustrations, the combination of small overall size and high relief, particularly in the more ornate genera, causes many workers to feel that optical methods are not satisfactory for routine photography. Magnifications are generally inadequate for detailed studies of ultrastructure.

ii) scanning electron microscopy.

Since the late 1960s (Hay and Sandberg, 1967; Honjo and Berggren, 1967), SEM photography has developed as the most accurate, efficient and frequently used means of illustrating microfossils for publication. The great advantage over light photography is the much greater depth of field available with high resolution over a range of magnifications from 15x to 500,000x (Hay and Sandberg, 1967).

Specimens to be photographed should be mounted on an SEM stub (usually an aluminium disc). A number of methods are employed for holding the specimens in place. To provide a smooth background the surface of the stub may be covered with a thin layer of melted wax W. Either a portion of the wax is made tacky with a hot needle and the specimen is positioned, or the wax is left to harden and a small amount of water-soluble glue is used (e.g. gum tragacanth or gum arabicum) or a 'glue-stick', such as a UHU stick may be used (Uyeno, pers. comm. 1985). Alternatively the stub can be covered with a thin film of melted Lakeside 70 cement, which is soluble in alcohol, and is treated in the same way as wax W to affix the specimen (Hansen, 1968). With a smooth stub,

specimens can be affixed using a thin coating of acrylic polymer varnish (e.g. shellac) in which the specimen is positioned while the surface is still just tacky (Britten, pers. comm. 1985). Merrill (pers. comm. 1985) suggests the use of double-sided sticky tape although this must be of a type which does not shrink during irradiation. Honjo and Berggren (1967) use Neoplen glue for mounting, and the Cambridge Scanning Company use Durofix glue (Hansen, 1968), but these glues are not easy to remove from the specimens.

Using the standard mode of operation, with an accelerating voltage of 20 kV, the surface of the specimen must be electrically conductive to avoid build up of charge. Hence the specimen may be coated with an ultrathin layer of noble metal (e.g. gold, platinum/palladium, or a mixture of these), using either vacuum evaporation or sputtering techniques. Other substances used for coating are: carbon (see below), silicon monoxide, aluminium and certain organic polymers (Merrill, pers. comm. 1985). Many non-conductive surfaces can be examined without coating if the accelerating voltage is greatly reduced, usually to between 1 kV and 3 kV (Hay and Sandberg, 1967), although some resolution is lost. Following the specific operating instructions, the stub is locked in the stage and is ready for viewing. The stage is capable of rotation and tilt around two axes as well as linear motion along x, y and z axes to enable orientation of the specimen. Stereoscopic pairs of photographs for true three-dimensional representation can be taken easily by tilting the specimen about one of the rotational axes (6° is standard for printed viewing).

A major disadvantage of the standard method outlined above, particularly with type specimens, is that, once covered in noble metal, the conodont element can no longer be examined 'as new' and discrimination between white matter and hyaline matter is impossible. To overcome this problem, Repetski and Brown (1982) outline a technique in which the specimen is coated with carbon using a vacuum chamber, and in which the gun potential of the scanning electron microscope is reduced from 20 kV to 10 kV. Although extremely high (greater than 4000x) magnifications are not possible, the details of the specimen are not obscured. Alternatively, Hansen (1968) describes a method of removing gold from plated specimens, in which the specimen is removed from the stub and placed in a small flask of an aqueous solution of 0.1-1.0 % NaCN with one or two drops of 1 molar NaOH solution. Air is bubbled through the flask for about 15 min, in which time the gold should have been fully removed. Note that this entire process should be carried out in a fume hood as the CN compounds are highly poisonous. Burnett (1987b) explains how gold/palladium can be removed by soaking in a 10 % solution of FeCl for 6 hours. Carbon coatings can best be removed by low temperature plasma ashing for short periods.

Smith (1987) points out a number of advantages of using "backscatter electron" mode, rather than the standard secondary electron mode, when

illustrating carbon coated shale bedding plane assemblages. The relative atomic number of the specimen controls its appearance in backscatter mode. The higher the number, the brighter the image. Conodont elements, with an atomic weight of approximately 12.5, have a pale to mid-grey tone. Advantages over using a secondary electron image are: better depiction of relief, increased depth of field and no charging problems.

The final prints may be trimmed, and the edges darkened with a pen and then set out on a suitable background (e.g. black card, or exposed photographic paper) with any numbers and labels added as required. Using standard light photography, 'plates' for publication can be made.

APPENDIX A: CONODONT RECOVERY FOR EACH LOCALITY.

1. CASTLEMARTIN FIRING RANGE

Pa elements	: 447	Total weight of
Pb elements	: 36	rock processed: 87.878 Kg
M elements	: 46	
S elements	: 416	Average yield : 11.14/Kg
Apatognathids:	32	
Total No.	979	

2. STACKPOLE QUAY

Pa elements	: 39	Total weight of
Pb elements	: 3	rock processed: 10.910 Kg
M elements	: 2	
S elements	: 31	Average yield : 7.52/Kg
Apatognathids:	7	
Total No.	82	

3. LYDSTEP HAVEN

Pa elements	: 8	Total weight of
Pb elements	: /	rock processed: 26.938 Kg
M elements	: 1	
S elements	: 2	Average yield : 0.52/Kg
Apatognathids:	3	
Total No.	14	

4. GILTAR POINT

Pa elements	: 17	Total weight of
Pb elements	: /	rock processed: 30.420 Kg
M elements	: 3	
S elements	: 16	Average yield : 1.91/Kg
Apatognathids:	22	
Total No.	58	

5. TENBY SOUTH BEACH

Pa elements	: 27	Total weight of
Pb elements	: /	rock processed: 12.285 Kg
M elements	: 4	
S elements	: 22	Average yield : 4.80/Kg
Apatognathids:	6	
Total No.	59	

6. BURRY HOLMS

no conodonts recovered

Total weight of rock processed: 1.700 Kg

7. THURBA HEAD

Pa elements	:	1
Pb elements	:	/
M elements	:	1
S elements	:	4
Apatognathids:		1
Total No.		7

Total weight of rock processed: 22.015 Kg

Average yield : 0.32/Kg

8. PORT EYNON (Holkerian)

Pa elements	:	17
Pb elements	:	/
M elements	:	4
S elements	:	7
Apatognathids:		/
Total No.		38

Total weight of rock processed: 7.005 Kg

Average yield : 5.43/Kg

9. CASWELL BAY

Pa elements	:	3
Pb elements	:	/
M elements	:	/
S elements	:	4
Apatognathids:		1
Total No.		8

Total weight of rock processed: 36.125 Kg

Average yield : 0.22/Kg

10. LLANELLY QUARRY

Pa elements	:	6
Pb elements	:	/
M elements	:	1
S elements	:	/
Apatognathids:		3
Total No.		10

Total weight of rock processed: 6.020 Kg

Average yield : 1.66/Kg

TOTAL NUMBER OF CONODONT ELEMENTS RECOVERED: 1,255

TOTAL WEIGHT OF ROCK PROCESSED: 241.151 Kg

AVERAGE YIELD: 5.20/Kg

APPENDIX B: CONODONT SAMPLE NUMBERING SYSTEM.

1. Castlemartin.

THESIS NO.	PROC NO.	SAMPLING NO.	CONODONTS ABSENT
CM1	JSP64	JSP26	
CM2	JSP65	JSP27	
CM3	JSP66	JSP28	
CM4	JSP72	JSP29	
CM5	JSP73	JSP30	
CM6	JSP74	JSP31	
CM7	JSP75	JSP32 a	
CM8	JSP76	JSP32 b	+
CM9	JSP88	JSP33	
CM10	JSP77	JSP34	+
CM11	JSP1	JSP1	
CM12	JSP48	JSP1 Ex bot	
CM13	JSP47	JSP1 Ex mid	
CM14	JSP46	JSP1 Ex top	
CM15	JSP2	JSP2	
CM16	JSP51	JSP2 Ex bot	
CM17	JSP50	JSP2 Ex mid	
CM18	JSP49	JSP2 Ex top	
CM19	JSP3	JSP3	
CM20	JSP53	JSP3 Ex bot	
CM21	JSP52	JSP3 Ex top	
CM22	JSP87	JSP9	
CM23	JSP86	JSP8	
CM24	JSP85	JSP7	
CM25	JSP84	JSP6	+
CM26	JSP5	JSP5	
CM27	JSP4	JSP4	
CM28	JSP54	JSP13	
CM29	JSP55	JSP14	
CM30	JSP56	JSP15	
CM31	JSP57	JSP16	
CM32	JSP83	JSP17	
CM33	JSP81	JSP18	
CM34	JSP82	JSP19	
CM35	JSP80	JSP20	
CM36	JSP79	JSP21	
CM37	JSP78	JSP22	
CM38	JSP69	JSP23	
CM39	JSP70	JSP24	
CM40	JSP71	JSP25	
CM41	JSP68	JSP2 *	
CM42	JSP67	JSP1 *	
CM43	JSP127	JSPD "spare"	

2. Stackpole Quay.

THESIS NO.	PROC NO.	SAMPLING NO.	CONODONTS ABSENT
SQ1	JSQ58	JSQ4	
SQ2	JSQ94	JSQ3	
SQ3	JSQ93	JSQ2	
SQ4	JSQ128	JSQA "spare"	
SQ5	JSQ92	JSQ1	+

3. Lydstep Haven.

THESIS NO.	PROC NO.	SAMPLING NO.	CONODONTS ABSENT
LS1	JSLS100	JSLS1	
LS2	JSLS104	JSLS2	
LS3	JSLS98	JSLS3	
LS4	JSLS95	JSLS5	+
LS5	JSLS101	JSLS4	
LS6	JSLS59	JSLS6	
LS7	JSLS96	JSLS7	
LS8	JSLS99	JSLS8	+
LS9	JSLS102	JSLS9	+
LS10	JSLS103	JSLS10	
LS11	JSLS105	JSLS11	+
LS12	JSLS97	JSLS12	

4. Giltar Point.

THESIS NO.	PROC NO.	SAMPLING NO.	CONODONTS ABSENT
GL1	JSGL113	JSGL1	
GL2	JSGL114	JSGL2	
GL3	JSGL115	JSGL3	+
GL4	JSGL106	JSGL4	+
GL5	JSGL107	JSGL6	
GL6	JSGL62	JSGL7	+
GL7	JSGL108	JSGL8	
GL8	JSGL63	JSGL9	
GL9	JSGL61	JSGL10	
GL10	JSGL116	JSGL11	
GL11	JSGL117	JSGL12	+
GL12	JSGL112	JSGL13	+
GL13	JSGL118	JSGL14	
GL14	JSGL109	JSGL15	
GL15	JSGL110	JSGL16	
GL16	JSGL111	JSGL17	

5. Tenby South Beach.

THESIS NO.	PROC NO.	SAMPLING NO.	CONODONTS ABSENT
T1	JST124	JST1	
T2	JST123	JST2	+
T3	JST60	JST3	+
T4	JST122	JST4	
T5	JST121	JST5	
T6	JST119	JST6	

6. Burry Holms.

THESIS NO.	PROC NO.	SAMPLING NO.	CONODONTS ABSENT
BH1	JSX120	"X"	+

7. Thurba Head.

THESIS NO.	PROC NO.	SAMPLING NO.	CONODONTS ABSENT
TH1	JSG11&11a	JSG1	
TH2	JSG12	JSG2	+
TH3	JSG13	JSG3	
TH4	JSG14	JSG4	
TH5	JSG15&16	JSG5&6	
TH6	JSG17&17a	JSG7	
TH7	JSG18-21	"A"	

8. Port Eynon. (HOLKERIAN)

THESIS NO.	PROC NO.	SAMPLING NO.	CONODONTS ABSENT
PE1	JSG22-25	"B"	

9. Caswell Bay.

THESIS NO.	PROC NO.	SAMPLING NO.	CONODONTS ABSENT
CB1	JSG30-35	"D"	
CB2	JSG26-29	"C"	
CB3	JSG36	"RON3"	+
CB4	JSG37-42	"E"	+
CB5	JSG43-45	"F"	

10. Llanelly Quarry.

THESIS NO.	PROC NO.	SAMPLING NO.	CONODONTS ABSENT
LL1	JSL90	JSL A	
LL2	JSL126	JSL B	+
LL3	JSL91	JSL C	
LL4	JSL125	JSL D	

In the above tables, sampling no. refers to numbers used in the field notebook; proc no. refers to numbers used in the processing log, and thesis no. refers to the sample numbers used in this thesis. The latter are placed in stratigraphical order.

Throughout this thesis the following abbreviations are used for sample localities, and are included as part of the sample numbers.

CM = Castlemartin Tank Range
SQ = Stackpole Quay
LS = Lydstep Haven
GP = Giltar Point
T = Tenby South Beach
BH = Burry Holms
TH = Thurba Head and bay to east
PE = Port Eynon
CB = Caswell Bay
LL = Llanelly Quarry

(For precise sample locations see fig 2.1.1 and Appendix D).

APPENDIX C: IDENTIFIABLE CONODONT ELEMENTS RECOVERED FROM EACH SITE.

The total numbers of each identifiable conodont element which have been recovered in the present study are tabulated in the following tables. The results are presented in a standard form for each sample locality (see fig. 2.1.1).

The sample numbers refer to figures 2.1.4, 2.1.5, 2.1.6 and 2.3.6; and the following generic abbreviations are used:

C. = Cavusgnathus

Cl. = Clydagnathus

G. = Gnathodus

H. = Hindeodus

?H. = ?Hindeodus

I. = Idioprioniodus

K. = Kladognathus

L. = Lochriea

M. = Mestognathus

Pat. = Patrognathus

Pol. = Polygnathus

V. = Vogelgnathus

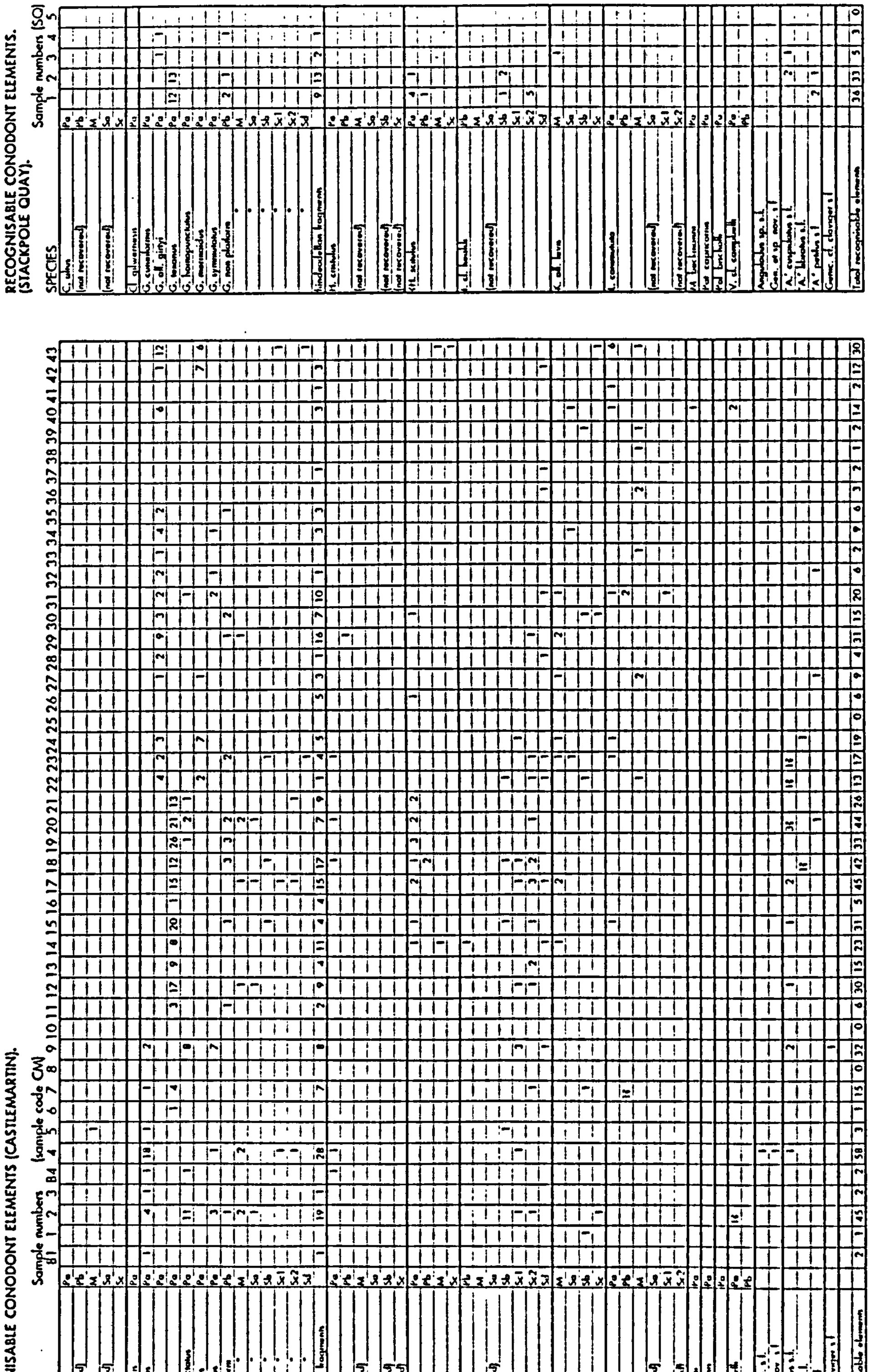
'A.' ='Apatognathus' s.f.

G. = Geniculatus s.f.

- "hindeodellan fragments" refers to denticulated-bar fragments with the characteristic interspersal of larger and smaller denticles, as seen in elements of Hindeodella s.f. The figure given is the best estimate of the number of individual elements present in the sample.

- In table C.4: CB = Caswell Bay
  TH = Thurba Head
  PE = Port Eynon

table C.1 Recognisable conodont elements from the outer ramp sites



RECOGNISABLE CONODONT ELEMENTS (LYDSTEP HAVEN).
(sample code LS)
Sample numbers

SPECIES		1	2	3	4	5	6	7	8	9	10	11	12
C. alius	Pa												
(not recovered)	Pb												
	M							1					
(not recovered)	Sa												
	Sc												
Cl. gilwernesis	Pa												
G. cuneiformis	Pa		3										
G. alt. girtyi	Pa												1
G. texanus	Pa			1									
G. homopunctatus	Pa												
G. mermaidus	Pa												
G. symmutatus	Pa							1					
G. non-platform	Pb												
"	M												
"	Sa												
"	Sb												
"	Sc1												
"	Sc2												
"	Sd												
hindeodellan fragments													
H. cristulus	Pa												
	Pb												
(not recovered)	M												
	Sa												
(not recovered)	Sb												
(not recovered)	Sc												
?H. scitulus	Pa												
	Pb												
	M												
	Sc												
I. cl. healdi	Pb												
	M												
(not recovered)	Sa												
	Sb												
	Sc1												
	Sc2												
	Sd												
K. alt. levis	M												
	Sa												
	Sb												
	Sc												
L. commutata	Pa												
	Pb												
	M												
(not recovered)	Sa												
	Sc1												
(not recovered)	Sc2												
M. beckmanni	Pa					1							
Pat. capricornis	Pa	1											
Pol. bischofi	Pa												
V. cl. campbelli	Pa												
	Pb												
Angulodus sp. s.l.													
Gen. et sp. nov. s.l.													
'A.' cuspidatus s.l.								1					
'A.' libratus s.l.													
'A.' petilus s.l.													
Genic. cl. claviger s.l.													
Total recognisable elements		1	3	1	0	1	1	2	0	0	0	0	1

RECOGNISABLE CONODONT ELEMENTS (GILTAR POINT).
(sample code GL)
Sample numbers

SPECIES		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
C. alius	Pa					1		1							1		
(not recovered)	Pb																
	M																
(not recovered)	Sa																
	Sc									1							
Cl. gilwernesis	Pa																
G. cuneiformis	Pa																
G. alt. girtyi	Pa																
G. texanus	Pa																
G. homopunctatus	Pa																
G. mermaidus	Pa																
G. symmutatus	Pa														2		
G. non-platform	Pb																
"	M															1	
"	Sa																
"	Sb																
"	Sc1																
"	Sc2																
"	Sd																
hindeodellan fragments															2		
H. cristulus	Pa																1
	Pb																
(not recovered)	M																
	Sa																
(not recovered)	Sb																
(not recovered)	Sc																
?H. scitulus	Pa														1	1	
	Pb													1			
	M															2	
	Sc																
I. cl. healdi	Pb																
	M									1							
(not recovered)	Sa																
	Sb									1							
	Sc1																
	Sc2													1			
	Sd																
K. alt. levis	M		1														
	Sa														1		
	Sb																
	Sc																
L. commutata	Pa																
	Pb																
	M																
(not recovered)	Sa																
	Sc1																
(not recovered)	Sc2																
M. beckmanni	Pa																
Pat. capricornis	Pa					1		2									
Pol. bischofi	Pa					1								1			
V. cl. campbelli	Pa														3		
	Pb														1		
Angulodus sp. s.l.																	
Gen. et sp. nov. s.l.																	
'A.' cuspidatus s.l.								1							4		
'A.' libratus s.l.																	
'A.' petilus s.l.										1				2	2		
Genic. cl. claviger s.l.																	
Total recognisable elements		0	1	0	0	3	0	4	0	2	2	0	0	3	11	14	1

RECOGNISABLE CONODONT ELEMENTS (TENBY).
(sample code T)
Sample numbers

SPECIES		1	2	3	4	5	6
C. alius	Pa						
(not recovered)	Pb						
	M						
(not recovered)	Sa						
	Sc						
Cl. gilwernesis	Pa						
G. cuneiformis	Pa						
G. alt. girtyi	Pa						
G. texanus	Pa						
G. homopunctatus	Pa						
G. mermaidus	Pa						
G. symmutatus	Pa					6	
G. non-platform	Pb						
"	M						
"	Sa						
"	Sb						
"	Sc1						
"	Sc2						
"	Sd						
hindeodellan fragments					1	8	
H. cristulus	Pa					1	
	Pb						
(not recovered)	M						
	Sa						
(not recovered)	Sb						
(not recovered)	Sc						
?H. scitulus	Pa						
	Pb						
	M					1	
	Sc						
I. cl. healdi	Pb						
	M						
(not recovered)	Sa						
	Sb					1	
	Sc1						
	Sc2					1	
	Sd					1	
K. alt. levis	M					2	
	Sa					1	
	Sb						
	Sc						
L. commutata	Pa					8	
	Pb						
	M						
(not recovered)	Sa						
	Sc1						
(not recovered)	Sc2						
M. beckmanni	Pa					6	
Pat. capricornis	Pa						
Pol. bischofi	Pa	1					
V. cl. campbelli	Pa						
	Pb						
Angulodus sp. s.l.							
Gen. et sp. nov. s.l.							
'A.' cuspidatus s.l.							
'A.' libratus s.l.							
'A.' petilus s.l.						1	
Genic. cl. claviger s.l.							
Total recognisable elements		1	0	0	1	37	0

table C.2 Recognisable conodont elements from the mid-ramp sites

table C.3

RECOGNISABLE CONODONT ELEMENTS (LLANELLY QUARRY).

SPECIES		(sample code LL) Sample numbers 1	2	3	4
C. altus	Pa				
(not recovered)	Pb				
	M				
(not recovered)	Sa				
	Sc				
Cl. ailwernesis	Pa	2			
G. cuneiformis	Pa				
G. aff. girtyi	Pa				
G. texanus	Pa				
G. homopunctatus	Pa				
G. mermaidus	Pa				
G. symmutatus	Pa				
G. non-platform	Pb				
"	M				1
"	Sa				
"	Sb				
"	Sc1				
"	Sc2				
"	Sd				
hindeodellan fragments					
H. cristulus	Pa				
	Pb				
(not recovered)	M				
	Sa				
(not recovered)	Sb				
(not recovered)	Sc				
?H. scitulus	Pa				
	Pb			1	
	M				
	Sc				
I. cf. healdi	Pb				
	M				
(not recovered)	Sa				
	Sb				
	Sc1				
	Sc2				
	Sd				
K. aff. levis	M				
	Sa				
	Sb				
	Sc				
L. commutata	Pa				
	Pb				
	M				
(not recovered)	Sa				
	Sc1				
(not recovered)	Sc2				
M. beckmanni	Pa				
Pot. capricornis	Pa				1?
Pol. bischoffi	Pa				
V. cf. campbelli	Pa				1
	Pb				
Angulodus sp. s.l.					
Gen. et sp. nov. s.l.					
'A.' cuspidatus s.l.				2	
'A.' libratus s.l.					
'A.' petilus s.l.					
Genic. cf. claviger s.l.					
Total recognisable elements		2	0	3	3

RECOGNISABLE CONODONT ELEMENTS (GOWER PENINSULA).
(for sample codes see introduction).

SPECIES		Sample codes CB	TH	PE
C. altus	Pa			
(not recovered)	Pb			
	M			
(not recovered)	Sa			
	Sc			
Cl. ailwernesis	Pa			
G. cuneiformis	Pa			
G. aff. girtyi	Pa			13
G. texanus	Pa		1	
G. homopunctatus	Pa			
G. mermaidus	Pa			
G. symmutatus	Pa			
G. non-platform	Pb			
"	M			
"	Sa			
"	Sb			
"	Sc1			
"	Sc2			
"	Sd			
hindeodellan fragments			1	
H. cristulus	Pa			
	Pb			
(not recovered)	M			
	Sa			1
(not recovered)	Sb			
(not recovered)	Sc			
?H. scitulus	Pa	1		1
	Pb			
	M			
	Sc			
I. cf. healdi	Pb			
	M			
(not recovered)	Sa			
	Sb			
	Sc1			
	Sc2	1		
	Sd	1		
K. aff. levis	M		1	1
	Sa			1
	Sb			
	Sc			
L. commutata	Pa			2
	Pb			1
	M			2
(not recovered)	Sa			
	Sc1			
(not recovered)	Sc2			
M. beckmanni	Pa			
Pot. capricornis	Pa			
Pol. bischoffi	Pa			
V. cf. campbelli	Pa			
	Pb			
Angulodus sp. s.l.				
Gen. et sp. nov. s.l.				
'A.' cuspidatus s.l.				
'A.' libratus s.l.				
'A.' petilus s.l.		1		
Genic. cf. claviger s.l.				
Total recognisable elements		4	3	22

table C.4

The average conodont-yield per kg for each of Dixon's sedimentological groups - at different sites

i) OUTER RAMP FAUNAS

Dixon group (section 2.1d)	Approx. thickness (m)		No of samples		Av. Yield/kg	
	CM	SQ	CM	SQ	CM	SQ
Group 9	40	37	13	1	4.3	0.0
Group 8	16	32	8	1	5.8	1.5
Group 7	57	90	4	3	14.2	11.0
Group 6	17		1		0.0	
Group 5	33		5		11.0	
Group 4	46		5		5.3	

ii) MID-RAMP FAUNAS

Dixon group (section 2.1d)	Approx thickness (m)			No of samples			Av. Yield/kg		
	LS	GL	T	LS	GL	T	LS	GL	T
Group 5	3	5	7	2	1		0.2	0.5	
Group 4	49	66	26	3	6	1	0.0	2.5	0.0
Group 3	2	3	11	1	2	2	0.9	0.5	4.5
Group 2	30	10	29	3	2	1	0.3	1.0	0.0
Group 1	3	7	7	3	5	2	0.8	0.5	0.3

NB In the above, the following abbreviations are used for sample localities:
CM = Castlemartin
SQ = Stackpole Quay
LS = Lydstep Haven
GL = Giltar Point
T = Tenby South Beach

APPENDIX D: DETAILS OF SAMPLE LOCALITIES. (see figure 2.1.1)

1. Castlemartin
   -clifftop in Castlemartin Ranges (M.O.D.), Dyfed.
   -base of section (gulley to east of Hobbyhorse Bay): SR 8885 9565
   -top of section (Green Bridge of Wales): SR 9250 9440

2. Stackpole Quay
   -clifftop to south of the quay at Stackpole Quay, Dyfed.
   -base of section: SR 9940 9550
   -top of section: SR 9950 9540

3. Lydstep Haven (Lydstep Point)
   -clifftop on eastern edge of Lydstep Point, Dyfed.
   -base of section: SS 0880 97950
   -top of section: SS 0925 9750

4. Giltar Point
   -cliffs on north side of Giltar Point, Dyfed.
   -base of section: SS 1240 9840
   -top of section: SS 1250 9830

5. Tenby
   -cliffs at Tenby South Beach, Dyfed.
   -base of section: SN 1370 0040
   -top of section: SN 1340 0030

6. Burry Holms
   -cliffs on north side of headland, Gower Peninsula.
   -SS 4050 9280

7. Thurba Head
   -clifftop on east side of Thurba Head, Gower Peninsula.
   -SS 4215 8695

8. Port Eynon
   -coastal section to west of Port Eynon Point, Gower Peninsula.
   -SS 4670 8440

9. Caswell Bay
   -cliffs to east and west of Caswell Bay, Gower Peninsula.
   -SS 5930 8760

10. Llanelly Quarry
   -quarry face at Llanelly Quarry,
   - SO 2230 1240

REFERENCES

Ahr, W.M., 1973. The carbonate ramp; an alternative to the shelf model. Transactions of the Gulf Coast Association of Geological Societies, 23rd Annual Convention, 221-225.

Aldridge, R.J., 1982. A fused cluster of coniform conodont elements from the late Ordovician of Washington Land, Western North Greenland. Palaeontology, 25, 425-430.

Aldridge, R.J., 1987. Conodont palaeobiology: a historical review. In: Aldridge, R.J. (Ed.), Palaeobiology of conodonts. Ellis Horwood, Chichester, 11-34.

Aldridge, R.J., 1988. Extinction and Survival in the Conodonta. In: Larwood, G.P., (Ed.), Extinction and Survival in the Fossil Record. Systematics Association Special Volume 34, Clarendon Press, Oxford, 231-256.

Aldridge, R.J., Austin, R.L. and Husri, S., 1968. Viséan conodonts from North Wales and Ireland. Nature, 219, 225-258.

Aldridge, R.J. and Briggs, D.E.G., 1986. Conodonts. In: Hoffman, A. and Nitecki, M.H. (Eds.), Problematic fossil taxa. Oxford monographs on geology and geophysics, 5. Oxford University Press, New York, 227-239.

Aldridge, R.J., Briggs, D.E.G., Clarkson,E.N.K. and Smith, M.P., 1986. The affinities of conodonts - new evidence from the Carboniferous of Edinburgh, Scotland. Lethaia, 19, 279-291.

Aldridge, R.J., Rickards, R.B. and Theron, J.N., 1988. Giant conodont assemblages from the Lower Palaeozoic of South Africa; a tale of beautiful promise. In: Palaeontological Association Annual Conference Abstracts, Aston, 2.

Aldridge, R.J., Smith M.P., Norby R.D. and Briggs D.E.G., 1987. The architecture and function of of Carboniferous polygnathacean conodont apparatuses. In: Aldridge, R.J. (Ed.), Palaeobiology of conodonts. Ellis Horwood, Chichester, 62-75.

Andres, U., 1976. Magnetohydrodynamic and Magnetohydrostatic Methods of Mineral Separation. John Wiley, New York, 1-224.

Armstrong, H.A. and Purnell, M.A., 1987. Dinantian conodont biostratigraphy of the Northumberland Trough. Journal of Micropalaeontology, 6, 97-112.

Armstrong, W.G. and Halstead Tarlo, L.B., 1966. Amino acid components in fossil calicified tissues. Nature, 210, (5035), 481-482.

Austin, R.L., 1973. Modification of the British Avonian conodont zonation and a reappraisal of European Dinantian conodont zonation and correlation. Annales, Société Géologique de Belgique, 96, 523-532.

Austin, R.L., 1974. The Biostratigraphic Distribution of Conodonts in Great Britain and The Republic of Ireland. International Symposium on Belgian Micropalaeontological Limits Namur. Geological Survey of Belgium, Brussels, Publication No 3, 2-17.

Austin, R.L., 1976. Evidence from Great Britain and Ireland concerning West European Dinantian conodont palaeoecology. In: Barnes, C.R. (Ed.), Conodont palaeoecology, Geological Society of Canada Special Paper, 15, 201-224.

Austin, R.L., 1987. Conodonts of the Arundian (Dinantian) stratotype boundary beds from Dyfed, South Wales. In: Hart, M.B. (Ed.), Micropalaeontology of Carbonate Environments. Ellis Horwood Limited, Chichester, 238-255.

Austin, R.L. and Aldridge, R.J., 1973. Conodonts from horizons with Goniatites crenistria Phillips, in North Wales and the Isle of Man. Geological Magazine, 11, 37-42.

Austin, R.L., Conil, R. and Husri, S., 1970. Correlation of the age of the Dinantian rocks north and south of the Shannon, Ireland. Les Congrès et Colloques de l'Universite de Liège, 55, 179-192.

Austin, R.L. and Davies, R.B., 1984. Problems of recognition and implications of Dinantian conodont biofacies in the British Isles. In: Clark, D.L. (Ed.), Conodont Biofacies and Provincialism, Geological Society of America Special Paper, 196, 195-228.

Austin, R.L. and Hill, P.J., 1973. A Lower Avonian (K Zone) Conodont Fauna from near Tintern, Monmouthshire, Wales. Geologica et Palaeontologica, 7, 123-134.

Austin, R.L. and Husri, S., 1974. Dinantian conodont faunas of County Clare Limerick and Leitrim an appendix by S. Husri. International Symposium on Belgian Micropalaeontological Limits Namur. Geological Survey of Belgium, Brussels, Publication No 3, 18-69.

Austin, R.A. and Mitchell, M., 1975. Middle Dinantian platform conodonts from County Fermanagh and County Tyrone, Northern Ireland. Bulletin of the Geological Survey of Great Britain, 55, 43-54.

Austin, R.L., Orchard, M.J. and Stewart, I.J., 1985. Conodonts of the Devonian System from Great Britain. In: Higgins, A.C. and Austin R.L., (Eds.), A stratigraphical index of conodonts, Ellis Horwood, Chichester, 93-166.

Austin, R.L. and Rhodes, F.H.T., 1969. A conodont assemblage from the Carboniferous of the Avon Gorge, Bristol. Palaeontology, 12, 400-405.

Avcin, M.J., 1974. Des Moinesian conodont assemblages from the Illinois Basin. Ph. D. Thesis, Graduate College of the University of Illinois at Urbana-Champaign, 1-152.

Baesemann, J.F., 1973. Missourian (Upper Pennsylvanian) conodonts of northeastern Kansas. Journal of Paleontology, 47, 689-710.

Barclay, W.J., 1989. Geology of the South Wales Coalfield Part II the country around Abergavenny. Memoir of the British Geological Survey. Her Majesty's Stationery Office, London, 1-147.

Barclay, W.J. and Jones, D.G., 1978. Recent boreholes in the attenuated Carboniferous strata of the Blaenavon - Pontypool area, Gwent. Bulletin of the Geological Survey of Great Britain, 67.

Barnes, C.R., 1967. A questionable conodont assemblage from Middle Ordovician limestone, Ottowa, Canada. Journal of Paleontology, 41, 1557-1560.

Barnes, C.R., 1976. Preface. In: Barnes, C.R. (Ed.), Conodont Palaeoecology. Geological Association of Canada Special Paper, 15, vii-ix.

Barnes, C.R., 1987. Improved laboratory techniques for processing conodont samples. In: Austin, R.L. (Ed.), Conodonts: Investigative techniques and Applications. Ellis Horwood Limited, Chichester, 35-37.

Barnes, C.R. and Fåhræus, L.E., 1975. Provinces communities and the proposed nektobenthic habit of Ordovician conodontophorids. Lethaia, 8, 133-149.

Barnes, C.R., Fredholm, D. and Jeppsson, L., 1987. Improved techniques for picking of microfossils. In: Austin, R.L. (Ed.), Conodonts: Investigative techniques and Applications. Ellis Horwood Limited, Chichester, 74-76

Barnes, C.R., Kennedy, D.J., McCracken, A.D., Nowlan, G.S. and Tarrant, G.A., 1979. The structure and evolution of Ordovician conodont apparatuses. Lethaia, 12, 125-151.

Barnes, C.R. and Nowlan, G.S., 1975. Conodonts; a thing of the past-and of the future. Geoscience Canada, Toronto, 2, 85-89.

Barnes, C.R. and O'Brien, F.H.C., 1987. Coffee and conodonts: cheap filtration. In: Austin, R.L. (Ed.), Conodonts: Investigative techniques and Applications. Ellis Horwood Limited, Chichester, 67.

Barnes, C.R. and Poplawski, M.L.S., 1973. Lower and Middle Ordovician conodonts from the Mystic Formation, Quebec, Canada. Journal of Paleontology, 47, 760-790.

Barnes, C.R., Rexroad, C.B. and Miller, J.F., 1973a. Lower Palaeozoic conodont provincialism. In: Rhodes, F.H.T. (Ed.), Conodont palaeozoology, Geological Society of America Special Paper, 141, 157-190.

Barnes, C.R., Sass,D.B. and Monroe,E.A, 1973b. Ultrastructure of some Ordovician conodonts. In: Rhodes, F.H.T. (Ed.), Conodont Paleozoology, Geological Society of America Special Paper, 141, 1-30.

Barnes, R.D., 1980. Invertebrate zoology (fourth edition). Holt-Saunders International Editions, Saunders College, Philadelphia, 1-1089.

Barnett, S.G., 1970. A new stage for orienting microfossils. Journal of Paleontology, 44, 1133.

Barrick, J.E., 1987. Conodont biostratigraphy of the Caballos Novaculite (Early Devonian - Early Mississippian), northwestern Marathon Uplift, west Texas. In: Austin, R.L. (Ed.), Conodonts: Investigative techniques and Applications. Ellis Horwood Limited, Chichester, 120-135.

Barskov, I.S., Alekseyev, A.S. and Goreva, N.V., 1977. The taxonomic and nomenclatural status of conodonts of the genus Gnathodus Pander, 1856. Paleontologicheskij Zhurnal, 4, 131-134.

Bassler, R.S., 1925. Classification and stratigraphic use of conodonts. Geological Society of America Bulletin, 36, 218-220.

Beckmann, H., 1949. Conodonten aus dem Iberger Kalk (Ober Devon) des Bergischen Landes und ihr Feinbau. Senckenbergiana, 30, 153-168.

Beckmann, H., 1952. Zur Anwendung von Essigsaure in der Mikropaläontologie. Paläontologische Zeitschrift, 26, 138.

Behnken, F.H., 1975. Leonardian and Guadalupian (Permian) conodont biostratigraphy in Western and Southwestern United States. Journal of Paleontology, 49, 284-315.

Beinert, R.J., Klapper, G., Sandberg, C.A. and Ziegler, W., 1971. Revision of Scaphignathus and description of Clydagnathus? ormistoni n. sp. (Conodonta, Upper Devonian). Geologica et Palaeontologica, 5, 81-91.

Belka, Z., 1983. Evolution of the Lower Carboniferous conodont genus Mestognathus. Acta Geologica Polonica, 33, 73-84.

Belka, Z., 1985. Lower Carboniferous conodont biostratigraphy in the northeastern part of the Moravia-Silesia Basin. Acta Geologica Polonica, 35, 33-59.

Belka, Z. and Groessens, E., 1986. Conodont succession across the Tournaisian-Viséan boundary beds at Salet, Belgium. Société Géologique de Belgique, Bulletin, 95, 257-280.

Bengtson, P., 1988. Open nomenclature. Palaeontology, 31, 223-227.

Bengtson, S., 1976. The structure of some Middle Cambrian conodonts and the early evolution of conodont structure and function. Lethaia, 9, 185-206.

Bengtson, S., 1980. Conodonts: the need for a functional model. Lethaia, 13, 320.

Bengtson, S., 1983. A functional model for the conodont apparatus. Lethaia, 16, 38.

Bengtson, S., 1983a. The early history of Conodonta. Fossils and Strata, 15, 5-19.

Benjamin, R.E.K., 1971. Recovery of heavy liquids from dilute solutions. American Mineralogist, 56, 613-619.

Bergström, S.M. and Sweet, W.C., 1966. Conodonts from the Lexington limestone (Middle Ordovician) of Kentucky and its lateral equivalents in Ohio and Indiana. Bulletins of American Paleontology. Paleontological Research Institution Ithaca, New York, 50, 271-441.

Bergström, S.M. and Orchard, M.J., 1985. Conodonts of the Cambrian and Ordovician Systems from the British Isles. In: Higgins, A.C. and Austin, R.L. (Eds.), A stratigraphical index of conodonts, Ellis Horwood, Chichester, 32-67.

Bischoff, G., 1956. Oberdevonische Conodonten aus der Rheinischen Schiefergebirge. Notizblatt Hessische Landesamt für Bodenforschung, Wiesbaden, 84, 115-137.

Bischoff, G., 1957. Die Conodonten-Stratigraphie des rhenoherzinischen Unterkarbons mit Berucksichtigung der Wocklumeria-Stufe und der Devon Karbon-Grenze. Abhandlung des Hessischen Landesamtes für Bodenforschung, Wiesbaden, 19, 1-64.

Bischoff, G. and Ziegler, W., 1956. Das Alter der Urfer Schichten im Marburger Hinterland nach Conodonten. Notizblatt Hessische Landesamt für Bodenforschung, Wiesbaden, 84, 138-169.

Branson, E.B. and Mehl, M.G., 1933-4. University of Missouri Studies, 8, No's 1 to 4, 5-300.

Branson, E.B. and Mehl, M.G., 1938a. Conodonts from the Lower Mississippian of Missouri. University of Missouri Studies, 13, 128-148.

Branson, E.B. and Mehl, M.G., 1938b. The conodont genus Icriodus and its stratigraphic distribution. Journal of Paleontology, 12, 156-166.

Branson, E.B. and Mehl, M.G., 1940. Denison University Bulletin 40, (14), 167-209.

Branson, E.B. and Mehl, M.G., 1941. New and little known Carboniferous conodont genera. Journal of Paleontology, 15, 97-106.

Branson, E.B. and Mehl, M.G., 1944. Conodonts. In: Shimer, H.W. and Shrock, R.R., (Eds.), Index fossils of North America. Wiley, New York, 235-246.

Branson, E.R., 1934. Conodonts from the Hannibal Formation of Missouri. University of Missouri Studies, 8, 301-343.

Brem, H., Stein, A.B. and Rosenkrantz, H.S., 1974. The mutagenicity and DNA-modifying effect of haloalkanes. Cancer Research, 34, 2576-2579.

Briggs, D.E.G., 1984. The search for paleontology's most elusive entity; the conodont animal. Field Museum of Natural History Bulletin, 55, 11-18.

Briggs, D.E.G., Clarkson, E.N.K. and Aldridge, R.J., 1983. The conodont animal. Lethaia, 16, 1-14.

Burnett, R.D., 1987a. A short review of the application of scanning electron microscopy in conodont studies. In: Austin, R.L. (Ed.), Conodonts: Investigative techniques and Applications. Ellis Horwood Limited, Chichester, 146-148.

Burnett, R.D., 1987b. A new technique for the examination of conodont ultrastructure by SEM. In: Austin, R.L. (Ed.), Conodonts: Investigative techniques and Applications. Ellis Horwood Limited, Chichester, 148-149

Butler, M., 1973. Lower Carboniferous conodont faunas from the Eastern Mendips, England. Palaeontology, 16, 477-517.

Charlton, D.S., 1969. An improved technique for heavy liquid separation of conodonts. Journal of Paleontology, 43, 590-592.

Chatterton, B.D.E., 1974. Middle Devonian conodonts from the Harrogate Formation, southeastern British Columbia. Canadian Journal of Earth Science, 11, 1461-1484.

Chauff, K.M., 1981. Multielement conodont species from the Osagean (Lower Carboniferous) in Midcontinent North America and Texas. Palaeontographica, 175, 140-169.

Chauff, K.M., 1983. Multielement conodont species and an ecological interpretation of the Lower Osagean (Lower Carboniferous) conodont zonation from Midcontinent North America. Micropaleontology, 29, 404-429.

Clark, D.L., 1972. Early Permian crisis and its bearing on Permo-Triassic conodont taxonomy. Geologica et Palaeontologica, 1, 147-158.

Clark, D.L., Sweet, W.C., Bergström, S.M., Klapper, G., Austin, R.L., Rhodes F.H.T., Müller, K.J., Ziegler, W., Lindström, M., Miller, J.F. and Harris, A.G., 1981. Treatise on Invertebrate Paleontology Part W Miscellanea, Supplement 2, Conodonta. The Geological Society of America and The University of Kansas, Boulder Colorado, 1-202.

Clarke, W.J., 1960. Scottish Carboniferous conodonts. Transactions of the Edinburgh Geological Society, 18, 1-31.

Clayton, G., Higgs, K., Gueinn, K.J. and Van Gelder, A., 1974. Palynological correlations in the Cork Beds (upper Devonian -?upper Carboniferous) of southern Ireland. Proceedings of the Royal Irish Academy, 74, 145-155.

Clayton, G. and Sevastopulo, G.D., 1981. Discussion on the recognition and division of the Tournaisian Series in Britain. Journal of the Geological Society of London, 138, 104-105.

Collinson, C.W., 1963. Collection and preparation of conodonts through mass production techniques. Illinois State Geological Survey Circular, 343, 1-16.

Collinson, C.W., 1965. Conodonts. In: Kummel, B. and Raup, D., (Eds.), Handbook of Paleontological Techniques, Freeman, San Francisco, California, 94-102.

Collinson, C.W., Avcin, M.J., Norby, R.D. and Merrill, G.K., 1972. Pennsylvanian conodont assemblages from La Salle County, northern Illinois. Illinois State Geological Survey Guidebook Series, 10, 1-37.

Collinson, C.W., Rexroad, C.B. and Thompson, T.L., 1971. Conodont Zonation of the North American Mississippian. In; Sweet, W.C. and Bergström, S.M., (Eds.), Symposium on Conodont Biostratigraphy. Geological Society of America Memoir, 127, 353-394.

Collinson, C.W., Scott, A.J. and Rexroad, C.B., 1962. Six charts, showing biostratigraphic zones, and correlations based on conodonts from Devonian and Mississippian rocks of the Upper Mississippi Valley. Illinois State Geological Survey, Circular 328, 1-32.

Conil, R., 1959. Recherches stratigraphiques sur les terraines Dinantiens dans le bord nord du Bassin de Namur. Acadamie Royale de Belgique Classe des Sciences Mémoirs, 4(2), XIV, 1-176.

Conil, R., Groessens, E. and Lys, M., 1976. Etude micropaléontologique de la tranchée d'Yves-Gomezée (Tn3-V1-V2, Belgique). Société Géologique de Belgique, Bulletin, 82, 201-239.

Conil, R., Groessens, E. and Pirlet, H., 1977. Nouvelle charte stratigraphique du Dinantien type de la Belgique. Annales de la Société Géologique du Nord, 96, 363-371.

Conil, R., Lys, M. and Mauvier, A., 1964. Critères micropaléontologiques essentiels des formations types du Carbonifère (Dinantien) du bassin Franco-Belge. Compte Rendu cinqième Congrès International de stratigraphie et de géologie du Carbonifère, Paris 1963, 325-332.

Conway Morris, S., 1976. A new Cambrian lophophorate from the Burgess Shale of British Columbia. Palaeontology, 19, 199-222.

Conway Morris, S., 1980. Conodont function: falacies of the tooth model. Lethaia, 13, 107-108.

Conway Morris, S. and Harper, E., 1987. Inferred changes in genome size of conodonts over 270 million years. In: Palaeontological Association Annual Conference Abstracts, Bristol, 4.

Coombs, D.S., 1974. Colin Osborne Hutton (obituary). Proceedings of the Royal Society of New Zealand, 102, 110-117.

Cooper, C.L., 1935. Ammonium chloride sublimate apparatus. Journal of Paleontology, 9, 357-359.

Cooper, C.L., 1939. Conodonts from a Bushberg - Hannibal Horizon in Oaklahoma. Journal of Paleontology, 13, 379-422.

Cooper, C.L. and Sloss, L.L., 1943. Conodont fauna and distribution of a Lower Mississippian black shale in Montana and Alberta. Journal of Paleontology, 17, 168-172.

Cullison, J.S., 1934. A suitable tray for comparative examination of minute opaque objects under the binocular microscope. Journal of Paleontology, 8, 247.

Davis, L. and Webster, G.D., 1985. A modified funnel for heavy mineral separations. Journal of Paleontology, 59, 1505-1506.

Dean, M.T., 1987. Carboniferous conodonts from the Lower and Upper Limestone Groups of the Scottish Midland Valley. M. Phil. Thesis, University of Nottingham. 1-204.

Dégardin, J.M., 1975. Method of extraction of Silurian conodonts from slightly metamorphosed limestones from the Eseva valley. Geologica et Palaeontologica, 9, 61-63.

Denham, R.L., 1944. Conodonts. Journal of Paleontology, 18, 216-218.

Dickson, J.A.D., Ford, T.D. and Swift, A., 1987. The stratigraphy of the Carboniferous rocks around Castleton, Isle of Man. Proceedings of the Yorkshire Geological Society, 46, 203-228.

Dixey, F. and Sibley, T.F., 1918. The Carboniferous Limestone Series on the south-eastern margin of the South Wales coalfield. Quarterly Journal of the Geological Society of London, 73, 111-164.

Dixon, E.E.L., 1921. The country around Pembroke and Tenby. Memoir of The Geological Survey of Great Britain. His Majesty's Stationery Office, London, 1-220.

Dixon, E.E.L. and Vaughan, M., 1912. The Carboniferous succession in Gower (Glamorganshire). Quarterly Journal of the Geological Society of London, 67, 477-571.

Dorning, K.J., 1987. Integrated conodont and palynomorph preparation of small samples for biostratigraphical and palaeotemperature analysis. In: Austin, R.L. (Ed.), Conodonts: Investigative techniques and Applications. Ellis Horwood Limited, Chichester, 51-52.

Dow, V.E., 1960. Magnetic separation of conodonts. Journal of Paleontology, 34, 738-743.

Dow, V.E., 1965. Magnetic separation of conodonts. In: Kummel, B. and Raup, D., (Eds.), Handbook of Paleontological Techniques, Freeman, San Francisco, California, 263-267.

Dreeson, R., Sandberg, C.A. and Ziegler, W., 1986. Review of late Devonian and early Carboniferous conodont biostratigraphy and biofacies models as applied to the Ardenne shelf. Annales, Société Géologique de Belgique, 109, 27-42.

Druce, E.C., 1969. Upper Palaeozoic conodonts from the Bonaparte Gulf Basin, north-western Australia. Australia Bureau of Mineral Resources, Geology and Geophysics, Bulletin 98.

Druce, E,C., 1970. Lower Carboniferous conodonts from the Northern Yarrol Basin, Queensland. Australia Bureau of Mineral Resources, Geology and Geophysics, Bulletin 108, 91-113.

Druce, E.C., 1973. Upper Paleozoic and Triassic conodont distribution and the recognition of biofacies. In: Rhodes, F.H.T. (Ed.), Conodont Paleozoology, Geological Society of America Special Paper, 141, 921-237.

Druce, E.C., Rhodes, F.H.T. and Austin, R.L., 1972. Statistical analysis of British Carboniferous conodont faunas. journal of the Geological Society of London, 128, 53-70.

Du Bois, E.P., 1943. Evidence on the nature of conodonts. Journal of Paleontology, 17, 155-159.

Duffield, S. and Warshauer, S.M., 1979. Two step process for extraction of microfossils from indurated organic shales. Journal of Paleontology, 53, 746-747.

Dunn, D.L., 1965. Late Mississippian conodonts from the Bird Spring Formation in Nevada. Journal of Paleontology, 39, 1149-1150.

Dzik, J., 1986. Chordate affinities of the conodonts. In: Hoffman, A. and Nitecki, M.H. (Eds.), Problematic fossil taxa. Oxford monographs on geology and geophysics, 5. Oxford University Press, New York, 240-254.

Ebner, F., 1977. Die Gleidung der Karbons von Graz mit Conodonter, Austria. Geologischen Bundesanstalt Jahrbuch, 120, 449-493.

Eichenberg, W., 1930. Conodonten aus des Culm des Harzes. Paläontologische Zeitschrift, 12, 177-182.

Eldredge, N. and Gould, S.J., 1972. Punctuated equilibria: an alternative to phyletic gradualism. In: Schopf, T.J.M., (Ed.), Models in Paleobiology. Freeman, San Francisco, 82-115.

Elias, M.K., 1956. Upper Missisippian and Lower Pennsylvanian formations of southern Oaklahoma. American Association of Petroleum Geologists, Petroleum Geology of Southern Oaklahoma, 1, 56-134.

Ellison, S., 1941. Revision of Pennsylvanian conodonts. Journal of Paleontology, 15, 107-143.

Ellison, S., 1944. The composition of conodonts. Journal of Paleontology, 18, 133-140.

Ellison, S., 1987. Examples of Devonian and Mississippian conodont lag concentrates from Texas. In Austin, R.L. (Ed.), Conodonts: Investigative techniques and Applications. Ellis Horwood Limited, Chichester, 77-93.

Ellison, S. and Graves, R.W., 1941. Lower Pennsylvanian (Dimple Limestone) conodonts of the Marathon Region Texas. Missouri University, School of Mines and Metallurgy, Bulletin Technical Series, 14(3), 1-13.

Epstein, A.G., Epstein, J.B. and Harris, L.D., 1977. Conodont color alteration - an index to organic metamorphism. United States Geological Survey Professional Paper, 995, 1-27.

Evitt, W.R., 1949. Stereophotography as a tool of the paleontologist. Journal of Paleontology, 23, 566-570.

Fahlbusch, K., 1964. Die Stellung der Conodontida im Biologischen System. Palaeontographica, 123, 137-201.

Fåhræus, L.E., 1983. Phylum Conodonta Pander 1856 and nomenclatural priority. Systematic Zoology, 32, 455-459.

Fåhræus, L.E., 1984. A critical look at the treatise family-group classification of conodonta: an exercise in eclecticism. Lethaia, 17, 293-305.

Fåhræus, L.E., 1985. Histomorphology of soft tissue conodont matrix. In: Aldridge, R.J., Austin, R.L. and Smith, M.P., (Eds.), Fourth European Conodont Symposium (ECOS IV) Abstracts, 10-11.

Fåhræus, L.E. and Fåhræus van Ree, G.E., 1986. Soft tissue matrix of decalcified pectiniform elements of Hindeodella confluens. In: Aldridge, R.J. (Ed.), Palaeobiology of conodonts. Ellis Horwood, Chichester, 103-110.

Fay, R.O., 1952. Catalogue of conodonts. University of Kansas Paleontological contributions (Vertebrata), 3, 1-206.

Fewtrell, M.D. and Smith D.G., 1978. Stratigraphic significance of calcareous microfossils from the Lower Carboniferous rocks of the Skipton area, Yorkshire. Geological Magazine, 115, 225-271.

Fewtrell, M.D. and Smith, D.G., 1981. Discussion on the recognition and division of the Tournaisian Series in Britain. Journal of the Geological Society of London, 138, 103-105.

Fischer, A., 1939. Rubber casts and molds of fossils. Journal of Paleontology, 13, 621.

Flügel, H.W. and Ziegler, W., 1957. Die Gliederung des Oberdevons und Unterkarbons am Steinberg westlich Graz mit Conodonten. Mitteilungen Naturwissenschaftlicher Verein für Steiermark, 87, 25-60.

Freeman, E.F., 1975. The isolation and ecological implications of the microvertebrate fauna of a Lower Cretaceous lignite bed. Proceedings of the Geological Association, 86, 307-312.

Freeman, E.F., 1982. Fossil bone recovery from sediment residues by the interfacial method. Palaeontology, 25, 471-484.

Freeman, E.F. and Merrill, G.K., 1985. Safe cheap and efficient concentration techniques for conodonts. In: Aldridge, R.J., Austin, R.L. and Smith, M.P. (Eds.), Fourth European Conodont Symposium (ECOS IV) Abstracts, 11.

Garwood, E.J., 1913. The lower Carboniferous succession in the north west of England. Quarterly Journal of the Geological Society of London, 68, 449-596.

George, T.N., 1954. Pre-Seminulan Main Limestone of the Avonian Series in Breconshire. Quarterly Journal of the Geological Society of London, 110, 283-322.

George, T.N., 1972. The classification of Avonian limestones. Quarterly Journal of the Geological Society of London, 128, 221- 256.

George, T.N., Johnson, G.A.L., Mitchell, M., Prentice, J.E., Ramsbottom, W.H.C., Sevastopulo, G.D. and Wilson, R.B., 1976. A correlation of Dinantian rocks in the British Isles. Special report of The Geological Society of London, 7, 1-87.

George, T.N. and Wagner, R.H., 1972. International Union of Geological Sciences Subcommission on Carboniferous Stratigraphy. Proceedings and report of the general assembly at Krefeld, August 21-22. Compte Rendu Septième Congrès International de stratigraphie et de géologie du Carbonifère, Krefeld, 1971, 1, 139-147.

Globensky, Y.R., 1967. Middle and Upper Mississippian conodonts from the Windsor Group of the Atlantic Provinces of Canada. Journal of Paleontology, 41, 432-448.

Gould, S.J., 1983. Nature's great era of experiments. Natural History, 7/83, 12-21.

Graves, R.W. and Ellison, S., 1941. Ordovician conodonts of the Marathon Basin, Texas. Missouri University, School of Mines and Metallurgy, Bulletin Technical Series, 14(2), 1-26.

Grayson, R.C., Merrill, G.K. and Lambert, L.L., 1988. Phylogenetic significance of apparatus reconstructions of some mid-Carboniferous gnathodontid conodonts. Courier Forschungsinstitut Senckenberg, 102, 239.

Green, G.W. and Welch, F.B.A., 1965. Geology of the country around Wells and Cheddar. Memoir of the Geological Survey of The United Kingdom.

Gregory, M.R. and Johnston, K.A., 1987. A nontoxic substitute for hazardous heavy liquids - aqueous sodium polytungstate ($3Na_2WO_4.9WO_3.H_2O$) solution. New Zealand Journal of Geology and Geophysics, 30, 317-320.

Groessens, E., 1974. Distribution de Conodontes dans la Dinantien de la Belgique. In: Bouckaert, J. and Streel, M., (Eds.), International symposium on Belgian micropalaeontological limits from Emsian to Visean, Namur. 17, 1-193.

Gunnell, F.H., 1931. Conodonts from the Scott Limestone of Missouri. Journal of Paleontology, 5, 244-252.

Gunnell, F.H., 1933. Conodonts and fish remains from the Cherokee, Kansas City and Waubensee Groups of Missouri and Kansas. Journal of Paleontology, 7, 261-297.

Gutschick, R.C. and Sandberg, C.A., 1983. Mississippian continental margins of the conterminous United States. In: The shelfbreak; critical interface on continental margins. Society of Economic Paleontologists and Mineralogists Special Publication, 33, 79-96.

Gutschick, R.C., Sandberg, C.A. and Sando, W.J., 1980. Mississippian shelf margin and carbonate platform from Montanna to Nevada. In: Fouch, T.D. and Magathan, E.R. (Eds.), Paleozoic paleogeography of the west-central United States, Rocky Mountain paleogeography symposium 1, Denver SEPM, Rocky Mountain section, 111-128.

Hamar, G., 1966. The Middle Ordovician of the Oslo Region, Norway, 22. Preliminary report on conodonts from the Oslo-Asker and Ringerike districts. Norsk Geologisk Tidsskrift, 46, 27-83.

Hanna, M.A., 1927. Clarification of oil-discolored bromoform. Journal of Paleontology, 1, 145.

Hansen, H.J., 1968. A technique for removing gold from plated calcareous microfossils. Micropaleontology, 14, 499-500.

Hass, W.H., 1941. Morphology of conodonts. Journal of Paleontology, 15, 71-81.

Hass, W.H., 1953. Conodonts of the Barnett Formation of Texas. United States Geological Survey Professional Paper, 243, 69-94.

Harland, W.B., Cox, A.V., Llewellyn, P.G., Pickton, C.A.G., Smith, A.G. and Walters, R., 1981. A geologic timescale. Cambridge University Press, Cambridge, 1-131.

Harley, J., 1861. On the Ludlow bone bed and its crustacean remains. Quarterly Journal of the Geological Society of London, 18, 542-552.

Harris, R.W. and Hollingsworth, R.V., 1933. New Pennsylvanian conodonts from Oaklahoma. American Journal of Science, 25, 193-204.

Hauff, P.L. and Airey, J., 1980. The handling, hazards and maintenance of heavy liquids in the geologic laboratory. US Geological Survey Circular, 827, 1-24.

Hay, W.W. and Sandberg, P.A., 1967. The scanning electron microscope, a major breakthrough for micropaleontology. Micropaleontology, 13, 407-418.

Hayashi, S., 1968. The Permian Conodonts in Chert of the Adoyama Formation, Ashiyo Mountains, Central Japan. Earth Science, 22, 63-77.

Haynes, J., 1981. Foraminifera. Macmillan, London, 1-433.

Hibbard, R.R., 1927. Conodonts from the Portage Group of Western New York. American Journal of Science, 13, 189-208.

Higgins, A.C., 1961. Some Namurian conodonts from North Staffordshire. Geological Magazine, 98, 210-224.

Higgins, A.C., 1962. Conodonts from the Griotte Limestone of North West Spain. Notas y Communicaciones Instituto Geologico y Minero de España, 65, 5-22.

Higgins, A.C., 1975. Conodont zonation of the Late Viséan and early Westphalian strata of the south and central Pennines of northern England. Bulletin of the Geological Survey of Great Britain, 55, 1-90.

Higgins, A.C., 1981a. Coprolite conodont assemblages from the Lower Westphalian of North Staffordshire. Palaeontology, 24, 437-441.

Higgins, A.C., 1981b. The distribution of conodonts in relation to the palaeogeography of Late Viséan-Namurian time. In: Neale, J.W. and Brasier, M.D., (Eds.), Microfossils from Recent and fossil shelf seas, 35-51.

Higgins, A.C., 1985. The Carboniferous System: Part 2 - Conodonts of the Silesian Subsystem from Great Britain and Ireland. In: Higgins, A.C. and Austin R.L., (Eds.), A stratigraphical index of conodonts, Ellis Horwood, Chichester, 210-227.

Higgins, A.C. and Austin, R.L., (Eds.) 1985. A stratigraphical index of conodonts. Ellis Horwood Limited, Chichester. 1-263.

Higgins, A.C. and Bouckaert, J., 1968. Conodont stratigraphy and palaeontology of the namurian of Belgium. Mémoires pour servir à l'explication des Cartes géologiques et minières de la Belgique, 10, 1-64.

Higgins, A.C. and Spinner, E.G., 1969. Techniques for the extraction of selected microfossils. Geology, 12-28.

Higgins, A.C. and Varker,.J., 1982. Lower Carboniferous conodont faunas from Ravenstonedale, Cumbria. Palaeontology, 25, 145-166.

Hinde, G.J., 1879. On conodonts from the Chazy and Cincinnati group of the Cambro-Silurian, and from the Hamilton and Genesee-shale divisions of the Devonian in Canada and the United States. Quarterly Journal of the Geological Society of London. 35, 351-369.

Hinde, G.J., 1900. Notes and descriptions of new species of Scotch Carboniferous conodonts. Transactions of the Natural History Society of Glasgow, 5, 338-346.

Hitchings, V.H. and Ramsay, A.T.S., 1978. Conodont assemblages: a new functional model. Palaeogeography, Palaeoclimatology, Palaeoecology, 24, 137-149.

Holmes, G.B., 1928. A bibliography of the conodonts with descriptions of Early Mississippian species. Proceedings of the United States National Museum, 72, (5), 1-38.

Honjo, S. and Berggren, W.A., 1967. Scanning electron microscope studies of planktonic foraminifera. Micropaleontology, 13, 393-406.

Horowitz, A.S. and Rexroad, C.B., 1982. An evaluation of statistical reconstructions of multielement conodont taxa from Middle Chesterian rocks (Carboniferous) in southern Indiana. Journal of Paleontology, 56, 959-969.

Howie, F.M.P., 1974. Introduction of thioglycollic acid in preparation of vertebrate fossils. Curator, 17, 159-166.

Huddle, J.W., 1934. Conodonts from the New Albany shale of Indiana. Bulletins of American Paleontology, Paleontological Research Institution, Ithaca, New York, 32, 141-175.

Huddle, J.W., 1972. Historical introduction to the problems of conodont taxonomy. Geologica et Palaeontologica, 1, 3-16.

Hunicken, M.A. and Ortega, G.C. 1987. Lower Llanvirn - Lower Caradoc (Ordovician) conodonts and graptolites from the Argentine Central Precordillera. In Austin, R.L. (Ed.), Conodonts: Investigative techniques and Applications. Ellis Horwood Limited, Chichester, 136-145

Igo, H., 1973. Lower Carboniferous conodonts from the Akiyoshi Limestone Group, southwest Japan. Transactions and Proceedings of the Palaeontological Society of Japan, 92, 185-199.

Igo, H. and Koike, T., 1964. Carboniferous conodonts from the Omi Limestone, Niigata Prefecture, Central Japan. Transactions and Proceedings of the Palaeontological Society of Japan, 33, 179-193.

Igo, H. and Koike, T., 1965. Carboniferous conodonts from Yobara Akiyoshi Limestone, Japan. Transactions and Proceedings of the Palaeontological Society of Japan, 59, 83-91.

Isozaki, Y. and Matsuda, T., 1980. Age of the Tamba Group along the Hozugawa "anticline", Western Hills of Kyoto, southwest Japan. Journal of Geosciences Osaka City University, 23, 115-134.

Ivanov, K.S., 1987. Methods of conodont search and separation (in Russian). Methodological recommendations, Urals Scientific Centre of the USSR Academy of Sciences, Sverdlovsk, 1-117.

James, U.P., 1884. On conodonts and fossil annelid jaws. Cincinnati Society of Natural History Journal, 7, 143-149.

Janvier, P., 1983. L'"animal-conodonte" enfin demasqué? La Recherche, 14, (145), 832-833.

Jenkins, T.B.H., 1974. Lower Carboniferous conodont biostratigraphy of New South Wales. Palaeontology, 17, 909-924.

Jeppsson, L., 1971. Element arrangement in conodont apparatuses of Hindeodella type and in similar forms. Lethaia, 4, 101-123.

Jeppsson, L., 1974. Aspects of Late Silurian conodonts. Fossils and Strata, 6, 1-54.

Jeppsson, L., 1979. Conodont element function. Lethaia, 12, 153-171.

Jeppsson, L., 1982. Are conodonts animals or ...? In: Jeppsson, L. and Löfgren, A. (Eds.), Third European Conodont Symposium (ECOS III) Abstracts. Publications from the Institutes of Mineralogy Palaeontology and Quaternary Geology, University of Lund, Sweden, 238, 24-25.

Jeppsson, L., 1983. Silurian conodont faunas from Gotland. Fossils and Strata, 15, 121-144.

Jeppsson, L., 1987. Some thoughts about future improvements in conodont extraction methods. In: Austin, R.L. (Ed.), Conodonts: Investigative techniques and Applications. Ellis Horwood Limited, Chichester, 45-51.

Jeppsson, L. and Fredholm, D., 1987. Temperature dependance of limestone dissolution in conodont extraction. In: Austin, R.L. (Ed.), Conodonts: Investigative techniques and Applications. Ellis Horwood Limited, Chichester, 39-42.

Jeppsson, L., Fredholm, D. and Mattiasson, B., 1985. Acetic acid and phosphatic fossils - a warning. Journal of Paleontology, 59, 952-956.

Johnston, I.S. and Higgins, A.C., 1981. Conodont faunas from the Lower Carboniferous rocks at Hookhead County Wexford. J. Earth Sci. R. Dublin Soc. 4, 83-96.

Jones, D.J., 1969. Introduction to Microfossils. Hafner, New York, 1-406.

Kent, P.E., 1975. The tectonic development of Great Britain and the surrounding seas. In: Woodland, A.W. (Ed.), Petroleum and the continental shelf of north-west Europe, 3-28.

Klapper, G., 1971. Patrognathus and Siphonodella (Conodonta) from the Kinderhookian (Lower Mississippian) of western Kansas and southwestern Nebraska. Kansas State Geological Survey Bulletin, 202, (3), 1-14.

Klapper, G. and Barrick, J.E., 1978. Conodont ecology: pelagic versus benthic. Lethaia, V11, 15-23.

Klapper, G. and Philip, G.M., 1971. Devonian conodont apparatuses and their vicarious skeletal elements. Lethaia, 4, 429-452.

Klapper, G. and Philip, G.M., 1972. Familial classification of reconstructed Devonian conodont apparatuses. Geologica et Palaeontologica, 1, 97-114.

Koike, T., 1967. A Carboniferous succession of conodont faunas from the Atetsu Limestone in southwest Japan. Tokyo Kyoiku Daigaku Scientific Reports, 93, 279-318.

Kozur, H. and Mostler, H. 1971. Holothurien-Sklerita und Conodonten aus der Mittel- und Obertrias von Köveskal (Balatonhochland, Ungarn). Geologische und Paläontologische Mitteilungen der Universität Innsbruck, 1 (10), 1-36.

Krukowski, S.T., 1988. Sodium metatungstate: a new heavy-mineral separation medium for the extraction of conodonts from insoluble residues. Journal of Paleontology, 62, 314-316.

Krumbein, W.C. and Pettijohn, F.J., 1938. Manual of Sedimentary Petrography. Appleton-Century-Crofts, New York, 1-549.

Landing, E., 1977. Prooneotodus tenuis (Müller 1959) apparatuses from the Taconic allochthon eastern New York; construction, taphonomy and the protoconodont 'supertooth' model. Journal of Paleontology, 51, 1072-1084.

Lane, H.R., 1968. Symmetry in conodont element pairs. Journal of Paleontology, 42, 1258-1263.

Lane, H.R., 1974. Mississippian of Southeastern New Mexico and West Texas, a wedge on wedge relation. American Association of Petroleum Geologists Bulletin, 58, 269-282.

Lane, H.R., Sandberg, C.A. and Ziegler, W., 1980. Taxonomy and phylogeny of some Lower Carboniferous conodonts and preliminary standard post Siphonodella zonation. Geologica et Palaeontologica, 14, 117-164.

Lane, H.R. and Ziegler, W., 1979. Gnathodus Pander, 1856 (Conodonta): proposed designation of type species under the plenary powers Z.N.(S.) 2279. Bulletin of Zoological Nomenclature, 36, 57-62.

Lange, F.G., 1968. Conodonten-Gruppenfunde aus Kalken des tieferen Oberdevon. Geologica et Palaeontologica, 2, 37-57.

Layne, N.M., 1950. A procedure for shale disintegration. Micropaleontologist, 4, 21.

Leeder, M.R., 1976. Sedimentary facies and the origins of basin subsidence along the northern margin of the supposed Hercynian Ocean. Tectonophysics, 36, 167-179.

Lindström, M., 1955. Conodonts from the lowermost Ordovician strata of south-central Sweden. Geologiska Foereningens i Stockholm Foerhandlingar, 76, 517-603.

Lindström, M., 1964. Conodonts. Elsevier Publishing Company, Amsterdam, 1-196.

Lindström, M., 1970. A suprageneric taxonomy of the conodonts. Lethaia, 3, 427-445.

Lindström, M., 1973. On the affinities of conodonts. In: Rhodes, F.H.T., (Ed.) Conodont paleozoology. Geological Society of America Special Paper, 141, 85-102.

Lindström, M., 1974. The conodont apparatus as a food-gathering mechanism. Palaeontology, 17, 729-744.

Lindström, M. and Ziegler, W., 1971. Feinstrukturelle Untersuchungen an Conodonten 1, Die Uberfamilie Panderodontacea. Geologica et Palaeontologica, 5, 9-33.

Loomis, F.B., 1936. Are conodonts gastropods? Journal of Paleontology, 10, 663-664.

Magné, J. and Dufaure, G., 1964. Une methode nouvelle pour l'extraction rapide des microfossiles. Revue de Micropaleontologie, 7, 77-79.

Mann, F.G. and Saunders, B.C., 1975. Practical Organic Chemistry (4th edition). Longmans, London, 1-585.

Mapes, R.H. and Mapes, G., 1982. Removal of gypsum from microfossiliferous shales. Micropaleontology, 28, 218-219.

Mapes, R.H. and Rexroad, C.B., 1986. Conodonts from the Imo Formation (Upper Chesterian), North-central Arkansas. Geologica et Palaeontologica, 20, 113-123.

Marks, P. and Wensink, H., 1970. Conodonts and the age of the "Griotte" limestone Formation in the Upper Aragon Valley (Huesca Spain) Parts I and II. Proceedings Koninklijke Nederlandse Akadamie van Wetenschappen, 73, 238-275.

Mashkova, T.V., 1972. Ozarkodina steinhornensis (Ziegler) apparatus, its conodonts and biozone. Geologica et Palaeontologica, 1, 81-90.

Matthews, S.C., 1969. Two conodont faunas from the Lower Carboniferous of Chudleigh, S. Devon. Palaeontology, 12, 276-280, 1 plate.

Matthews, S.C., 1973. Notes on open nomenclature and on synonymy lists. Palaeontology, 16, 713-719.

Matthews, S.C. and Naylor, D., 1973. Lower Carboniferous conodont faunas from South West Ireland. Palaeontology, 16, 335-380.

Matthews, S.C. and Thomas, J.M., 1974. Lower Carboniferous conodont faunas from northeast Devonshire. Palaeontology, 17, 371-385.

Mehl, M.G. and Thomas, L.A., 1947. Conodonts from the Fern Glen of Missouri. Denison University Bulletin, 47, (5), 3-19.

Meischner, D., 1970. Conodonten - Chronologie des Deutschen Karbons. Compte Rendu sixieme Congrès International de stratigraphie et de géologie du Carbonifère, Sheffield 1967, 3, 1169-1180.

Merrill, G.K., 1962. Facies relationships in Pennsylvanian conodont faunas. Texas Journal of Science, 14, 418.

Merrill, G.K., 1965. Conodonts from the Burnham Limestone of central Texas. Texas Journal of Science, 17, 345-403.

Merrill, G.K., 1972. Taxonomy, phylogeny and biostratigraphy of Neognathodus in Appalachian Pennsylvanian rocks. Journal of Paleontology, 46, 817-829.

Merrill, G.K., 1973. Pennsylvanian non-platform conodont genera, I: Spathognathodus. Journal of Paleontology, 47, 289-315.

Merrill, G.K., 1980. Removal of pyrite from microfossil samples by means of sodium hypochlorite. Journal of Paleontology, 54, 633- 634.

Merrill, G.K., 1985. Interfacial alternatives to the use of dangerous heavy liquids in micropaleontology. Journal of Paleontology, 59, 479-481.

Merrill, G.K., 1987a. Use of sodium hydrogen oxalate to remove 'limonite' from 'limonite'- cemented sandstones. In: Austin, R.L. (Ed.), Conodonts: Investigative techniques and Applications. Ellis Horwood Limited, Chichester, 44-45.

Merrill, G.K., 1987b. Improvements in interfacial methods for conodont separations. In: Austin, R.L. (Ed.), Conodonts: Investigative techniques and Applications. Ellis Horwood Limited, Chichester, 55-63.

Merrill, G.K., 1987c. Cryogenic density separation of conodonts. In: Austin, R.L. (Ed.), Conodonts: Investigative techniques and Applications. Ellis Horwood Limited, Chichester, 63-66.

Merrill, G.K. and Merrill, S.M., 1974. Pennsylvanian non-platform conodonts, IIa: the dimorphic apparatus of Idioprioniodus. Geologica et Palaeontologica, 8, 119-130.

Merrill, G.K. and von Bitter, P.H., 1976. Revision of conodont biofacies nomenclature and interpretation of environmental controls in Pennsylvanian rocks of eastern and central North America. Life Sciences Contributions, Royal Ontario Museum, 108, 1-46.

Merrill, G.K. and von Bitter, P.H., 1984. Facies and frequencies among Pennsylvanian conodonts: Apparatuses and abundances. In: Clark, D.L. (Ed.), Conodont Biofacies and Provincialism, Geological Society of America Special Paper, 196, 251-261.

Metcalfe, I., 1981. Conodont zonation and correlation of Dinantian and early Namurian strata of the Craven Lowlands of northern England. Institute of Geological Sciences Report 80/10, 1-70.

Mikulic, D.G., Briggs, D.E.G. and Kluessendorf, J., 1985. A Silurian soft-bodied biota. Science, V228, 715-717.

Mileson, P. and Jeppsson, L., 1983. Heavy liquid and solvent recovery -an economical method. Journal of Sedimentary Petrology, 53, 673-674.

Mitchell, M., 1976. In: Annual Report for 1975, Institute of Geological Sciences, London, p116.

Mitchell, M., Reynolds, M.J., Laloux, M. and Owens, B., 1982. Biostratigraphy of the Knap Farm borehole at Cannington Park, Somerset. Institute of Geological sciences Report 82/5, 9-17.

Moore, C., 1863. On the palaeontology of mineral veins, and on the secondary age of some mineral veins in the Carboniferous limestone. Report of the British Association for the Advancement of Science, 82-83.

Moore, R.C., (Ed.) 1962. Treatise on Invertebrate Paleontology part W, Miscellanea. Geological Society of America and University of Kansas Press, Lawrence, Kansas,

Moore, R.C. and Sylvester-Bradley, P.C., 1957. Proposed insertion in the "Regles" of provisions recognising "parataxa" as a special category for the classification and nomenclature of discrete fragments or of life-stages of animals which are inadequate for identification of whole-animal taxa, with proposals of procedure for the nomenclature of "parataxa". Bulletin of Zoological Nomenclature, 15, 5-13.

Müller, K.J., 1962. Ein einfacher Behelf für die Lösungstechnik. Paläontologische Zeitschrift, 36, 265-267.

Müller, K.J. and Müller, E.M., 1957. Early Upper Devonian (Independance) conodonts from Iowa, Part 1. Journal of Paleontology, 31, 1069-1108.

Murchison, R.I., 1854. Siluria. The history of the oldest known rocks containing organic remains with a brief description of the distribution of gold over the earth. Murray, London, 1-523.

Murchison, R.I., 1867. Siluria. Fourth Edition (see above).

Murray, F.N. and Chronic, J., 1965. Pennsylvanian conodonts and other fossils from insoluble residues of the Minturn Formation (Desmoinesian), Colorado. Journal of Paleontology, 39, 594-610.

Neves, R., Gueinn, K.J., Clayton, G., Ioannides, N. and Neville, R.S.W., 1972. A scheme of miospore zones for the British Dinantian. Compte Rendu Septième Congrès International de stratigraphie et de géologie du Carbonifère, Krefeld, 1971, 1, 347-353.

Nicoll, R.S., 1976. The effect of Late Carboniferous-Early Permian glaciation on the distribution of conodonts in Australia. In: C.R. Barnes (Ed.), Conodont Paleoecology, Geological Association of Canada Special Paper, 15, 273-278.

Nicoll, R.S., 1977. Conodont apparatuses in an Upper Devonian palaeoniscid fish from the Canning basin, Western Australia. Bureau of Mineral Resources Journal of Australian Geology and Geophysics, 2, 217-228.

Nicoll, R.S., 1980. The multielement genus Apatognathus from the Late Devonian of the Canning Basin, Western Australia. Alcheringa, 4, 133-152.

Nicoll, R.S., 1982. Multielement composition of the conodont Icriodus expansus Branson and Mehl from the Upper Devonian of the Canning Basin, Western Australia. Bureau of Mineral Resources Journal of Australian Geology and Geophysics, 7, 197-213.

Nicoll, R.S., 1985. Multielement composition of the conodont species Polygnathus xylus xylus Stauffer 1940 and Ozarkodina brevis (Bischoff and Ziegler 1957) from the Upper Devonian of the Canning Basin, Western Australia. Bureau of Mineral Resources Journal of Australian Geology and Geophysics, 9, 133-147.

Nicoll, R.S., 1987. Form and function of the Pa element in the conodont animal. In: Aldridge, R.J. (Ed.), Palaeobiology of conodonts. Ellis Horwood, Chichester, 77-90.

Nicoll, R.S. and Rexroad, C.B., 1975. Stratigraphy and conodont paleontology of the Sanders Group (Mississippian) in State of Indiana and adjacent Kentucky. State of Indiana Geological Survey Bulletin, 51, 1-36.

Nicoll, R.S. and Rexroad, C.B., 1987. Re-examination of Silurian conodont clusters from Northern Indiana. In: Aldridge, R.J. (Ed.), Palaeobiology of conodonts. Ellis Horwood, Chichester, 49-61.

Nigmadzhanov, I.M., 1987. Nizhnekamennougolnie Konodonti Sredinnogo Tyan-Shanya. Moskovskei ordena Lenina, ordena oktyabriskoi revolyutsii i ordena Trudovogo Krasnogo Znameni Gosunarstvennyi Universitet im M.V. Lomonosova, Geologicheskei fakultet. dissertatsii na soiskanie uchenoi stepeni kandidata geologo-mineralogicheskikh nauk. Moskva. Paleontologiya i Stratigrafiya Spetsialnost, 04.00.09, 1-17. (In Russian).

Norby, R.D., 1974. Conodont apparatuses of the Heath Shale (Chesterian) of central Montana. Geological Society of America Abstracts with Programs, 6, 535.

Norby, R.D., 1976. Conodont apparatuses from Chesterian (Mississippian) strata of Montana and Illinois. Ph. D. Thesis, Graduate College of the University of Illinois at Urbana-Champaign, 1-295.

Norby, R.D. and Avcin, M.J., 1987. Contact microradiography of conodont assemblages. In: Austin, R.L. (Ed.), Conodonts: Investigative techniques and applications. Ellis Horwood Limited, Chichester, 153-167.

Norby, R.D. and Rexroad, C.B., 1985. Vogelgnathus, a new Mississippian conodont genus. State of Indiana Geological Survey Occasional Paper, 50, 1-12.

Nowlan, G.S., 1979. Fused clusters of the conodont genus Belodina Ethington from the Thumb Mountain Formation (Ordovician), Ellesmere Island, District of Franklin. Current Research Part A, Geological Survey of Canada Paper, 79-1A, 213-218.

Orchard, M.J., 1987. Conodonts from western Canadian chert: their nature, distribution and stratigraphic application. In: Austin, R.L. (Ed.), Conodonts: Investigative techniques and Applications. Ellis Horwood Limited, Chichester, 94-109.

Pander, C.H., 1851. In Barrande Sur une decouverte de fossiles faite dans la partie inferieure du terrain Silurien de Russie, par le docteur Pander. Bulletin de la Société Géologique France, 8, 251-259.

Pander, C.H., 1856. Monographie der fossilen Fische des Silurischen Systems der russisch-baltischen Gouvernements. Akademie der Wissenschaften St. Petersburg, 1-97.

Paproth, E., Conil, R., Bless, M.J.M., Boonen, P., Bouckaert, J., Carpentier, N., Coen, M., Delcambre, B., Deprijck, Ch., Deuzon, S., Dreesen, R., Groessens, E., Hance, L., Hennebert, M., Hibo, D., Hahn, G., Hahn, R., Hislaire, O., Kasig, W., Laloux, M., Lauwers, A., Lees, A., Lys, M., Op de Beek, K., Overlau, P., Pirlet, H., Poty, E., Ramsbottom, W., Streel, M., Swennen, R., Thorez, J., Vanguestaine, M., van Steenwinkel, M. and Vieslet, J.L., 1983. Bio- and lithostratigraphic subdivisions of the Dinantian in Belgium, A Review. Annales, Société Géologique de Belgique, 106, 185-239.

Parsonage, P., 1977. Small-scale separations of minerals by use of paramagnetic liquids. Transactions, Institution of Mining and Metallurgy, Section B, 86, B43-B46.

Parsonage, P., 1978. Design and testing of paramagnetic liquid separation systems. Report, Warren Spring Laboratory, Department of Industry, Gunnels Wood Road, Stevenage, Hertfordshire, 1-38.

Passagno, E.A. and Newport, R.L., 1972. A technique for extracting radiolaria from radiolarian cherts. Micropaleontology, 18, 231-234.

Perret, M.F., 1974. Biostratigraphy par conodontes du Carbonifère Inferieur des Pyrenees Bearnaises. Compte Rendu de l'Academie de Science de Paris, 279, 791-794.

Peters, W.G., Wallace, R.J., Odom, I.E. and Frost, S., 1970. Application of radiography to the study of microfossils in black shales and other sediments. Geological Society of America Abstracts with Programs, 2(6), 400-401.

Pietzner, H., Wahl, J., Werner, H. and Ziegler, W., 1968. Zur chemischen Zusammensetzung und Mikromorphologie der Conodonten. Palaeontographica, 128, 115-152.

Pilsbry, H.A., 1937. Are conodonts molluscan teeth? Nautilus, 50, 101.

Pokorny, V., 1963. In: E. Ingerson (Ed.), Principles of Zoological Micropalaeontology, International Series of Monographs on Earth Sciences, Pergamon Press, Oxford, 1-652.

Pollock, C.A., 1969. Fused Silurian conodont clusters from Indiana. Journal of Paleontology, 43, 929-935.

Powell, C.M., 1989. Structural controls on Palaeozoic basin evolution and inversion in southwest Wales. Journal of the Geological Society, London, 146, 439-446.

Priddle, J., 1974. The function of conodonts. Geology Magazine, 111, 255-257.

Puchkov, V.N., Klapper, G. and Mashkova, T.V., 1982. Natural assemblages of Palmatolepis from the Upper Devonian of the northern Urals. Acta Palaeontologica Polonica, 26, 281-298.

Ramovs, A., 1978. Mitteltriassiche Conodontenclusters in Slowenien, NW Jugoslawien. Paläontologische Zeitschrift, 52, 129-137.

Ramsay, A.T.S., 1985. Guide for the Palaeontological Association Carboniferous Group Annual Field Conference, Gower.

Ramsbottom, W.H.C., 1970. Carboniferous faunas and paleogeography in the south-west England region. Proceedings of the Ussher Society, V2, 144-157.

Ramsbottom, W.H.C., 1973. Transgressions and regressions in the Dinantian a new synthesis of British Dinantian stratigraphy. Proceedings of the Yorkshire Geological Society, 39, 567-607.

Ramsbottom, W.H.C., 1976. In: Annual Report for 1975, Institute of Geological Sciences, London, p116.

Ramsbottom, W.H.C., (Ed.), 1981. Field Guide to the Boundary Stratotypes of the Carboniferous Stages in Britain. Subcommission on Carboniferous Stratigraphy, (without pagination).

Ramsbottom, W.H.C. and Mitchell, M., 1980. The recognition and division of the Tournaisian Series in Britain. Journal of the Geological Society of London, 137, 61-63.

Rejebian, V.A., Harris, A.G. and Huebner, J.S., 1987. Conodont color and textural alteration: an index to regional metamorphism, contact metamorphism and hydrothermal alteration. Geological Society of America Bulletin, 99, 471-479.

Repetski, J.E., 1980. Early Ordovician fused conodont clusters from the western United States. In: Schönlaub, H.P., (Ed.), Second European Conodont Symposium (ECOS II), Guidebook, Abstracts. Abhandlungen der Geologischen Bundesanstalt, 35, 207-209.

Repetski, J.E. and Brown, W.R., 1982. On illustrating conodont type-specimens using the scanning electron microscope - new techniques and a recommendation. Journal of Paleontology, 56, 908-911.

Rexroad, C.B., 1957. Conodonts from the Chester Series in the type area of southwestern Illinois. Illinois State Geological Survey Report of Investigations, 199, 1-43.

Rexroad, C.B., 1958. Conodonts from the Glen Dean Formation (Chester) of the Illinois Basin. Illinois State Geological Survey Report of Investigations, 209, 1-27.

Rexroad, C.B., 1969. Conodonts from the Jacobs Chapel Bed (Mississippian) of the New Albany Shale in Southern Indiana. State of Indiana Geological Survey Bulletin, 41, 1-55.

Rexroad, C.B., 1981. Conodonts from the Vienna Limestone Member of the Branchville Formation (Chesterian) in southern Indiana. State of Indiana Geological Survey Occasional Paper, 34, 1-16.

Rexroad, C.B. and Burton, R.C., 1961. Conodonts from the Kinkaid Formation (Chester) in Illinois. Journal of Paleontology, 35, 1143-1158.

Rexroad, C.B. and Collinson, C.W., 1961. Preliminary Range Chart of Conodonts from the Chester Series (Mississippian) in the Illinois Basin. Illinois State Geological Survey Circular 319, 1-11.

Rexroad, C.B. and Collinson, C.W., 1963. Conodonts from the St. Louis Formation (Valmeyeran Series) of Illinois, Indiana and Missouri. Illinois State Geological Survey Circular, 355, 1-28.

Rexroad, C.B. and Collinson, C.W., 1965. Conodonts from the Keokuk, Warsaw, and Salem Formations (Mississippian) of Illinois. Illinois State Geological Survey Circular, 388, 1-26.

Rexroad, C.B. and Furnish, W.M., 1964. Conodonts from the Pella Formation (Mississippian) southcentral Iowa. Journal of Paleontology, 38, 667-676.

Rexroad, C.B. and Lane, H.R., 1966. Clarification of Cavusgnathus alta, type species of the conodont genus Cavusgnathus. Journal of Paleontology, 40, 1391-1392.

Rexroad, C.B. and Liebe, 1962. Conodonts from the Paoli and equivalent formations in the Illinois Basin. Micropaleontology, 8, 509-514.

Rexroad, C.B. and Merrill, G.K., 1985. Conodont biostratigraphy and paleoecology of Middle Carboniferous rocks in southern Illinois. Courier Forschungsinstitut Senckenberg, 74, 35-64.

Rexroad, C.B. and Nicoll, R.S. 1964. A Silurian conodont with tetanus? Journal of Paleontology, 38, 771-773.

Rexroad, C.B. and Nicoll, R.S., 1965. Conodonts from the Menard Formation (Chester Series) of the Illinois Basin. State of Indiana Geological Survey Bulletin, 35, 1-28.

Rexroad, C.B. and Scott, A.J., 1964. Conodont Zones in the Rockford Limestone and the Lower Part of the New Providence Shale (Mississippian) in Indiana. State of Indiana Geological Survey Bulletin, 30, 1-54.

Rexroad, C.B. and Thompson, T.L., 1979. A spathognathodont lineage of Mississippian conodonts. Lethaia, 12, 235-243.

Reynolds, S.H., 1921. The lithological succession of the Carboniferous Limestone (Avonian) of the Avon Section at Clifton. Quarterly Journal of the Geological Society of London, 77, 213-245.

Reynolds, S.H. and Vaughan, A., 1911. Faunal and lithological sequence in the Carboniferous Limestone Series (Avonian) of Burrington Combe (Somerset). Quarterly Journal of The Geological Society of London, 67, 342-392.

Rhodes, F.H.T., 1952. A classification of Pennsylvanian conodont assemblages. Journal of Paleontology, 26, 886-901.

Rhodes, F.H.T., 1953. Some British Lower Palaeozoic conodont faunas. Philosophical Transactions of the Royal Society of London Series B, 237, 261-334.

Rhodes, F.H.T., 1954. The zoological affinities of the conodonts. Biological Review (Cambridge Philosophical Society), 29, 419-452.

Rhodes, F.H.T. and Austin, R.L., 1971. Carboniferous conodont faunas of Europe. In; Sweet, W.C. and Bergström, S.M., (Eds.), Symposium on Conodont Biostratigraphy. Geological Society of America Memoir, 127, 317-352.

Rhodes, F.H.T. and Austin, R.L., 1985. Conodont assemblages from the Carboniferous of Britain. In: Dutro, J.T.Jr. and Pfefferkorn, H.W. (Eds.), Compte Rendu (Vol. 5) Neuvième Congrès International de stratigraphie et de géologie du Carbonifère, Washington and Champagne Urbana 1979. Southern Illinois University Press, 287-300.

Rhodes, F.H.T., Austin, R.L. and Druce, E.C., 1969. British Avonian (Carboniferous) conodont faunas and their value in local and intercontinental correlation. Bulletin of the British Museum of Natural History Geological supplement, 5, 1-313.

Richter, R., 1948. Einführung in die Zoologische Nomenklatlatur (second edition). Kramer, Frankfurt, 1-252.

Ride, W.D., Sabrosky, C.W., Bernard, G. and Melville, R.V., (Eds.), 1985. International Code of Zoological Nomenclature, Third Edition - adopted by the XX General Assembly ofthe International Union of Biological Sciences. University of California Press Berkely and Los Angeles, 1-338.

Rixon, A.E., 1976. Fossil Animal Remains, their Preparation and Conservation. Athlone Press of the University of London, London, 1-304.

Robertson, T., 1927. Geology of the South Wales Coalfield Part II the country around Abergavenny. Memoir of the Geological Survey of the United Kingdom. His Majesty's Stationery Office, London.

Romer, A.S. and Parsons, T.S., 1977. The vertebrate body (fifth edition). Holt Saunders International Editions, W.B. Saunders Company, Philadelphia, 1-624.

Roundy, P.V., 1926. The micro-fauna in Mississippian Formations of San Saba County, Texas. United States Geological Survey Professional Paper, 146, 1-63.

Ryley, C.C., 1987. Clearing clogged separating funnels. In: Austin, R.L. (Ed.), Conodonts: Investigative techniques and Applications. Ellis Horwood Limited, Chichester, 66-67.

Sandberg, C.A., 1976. Conodont biofacies of Late Devonian Polygnathus styriacus Zone in western United States. In: Barnes, C.R. (Ed.), Conodont palaeoecology, Geological Society of Canada Special Paper, 15, 171-186.

Sandberg, C.A., 1979. Devonian and lower Mississippian conodont zonation of the Great Basin and Rocky Mountains. In: Sandberg, C.A. and Clark, D.L. (Eds.), Conodont biostratigraphy of the Great Basin and Rocky Mountains. Brigham Young University Geology Studies, 26, 87-106.

Sandberg, C.A. and Dreesen, R., 1983. Alternate Late Devonian zonation for shallow water conodont biofacies. Geological Society of America Abstracts with Programs, 15, 220.

Sandberg, C.A. and Dreesen, R., 1984. Late Devonian icriodontid biofacies models and alternate shallow water conodont zonation. In: Clark, D.L. (Ed.), Conodont Biofacies and Provincialism, Geological Society of America Special Paper, 196, 143-178.

Sandberg, C.A. and Gutschick, R.C., 1979. Guide to conodont biostratigraphy of Upper Devonian and Mississippian rocks along the Wasatch Front and Cordilleran Hingeline, Utah. In: Sandberg, C.A. and Clark, D.L. (Eds.), Conodont biostratigraphy of the Great Basin and Rocky Mountains. Brigham Young University Geology Studies, 26, 107-134.

Sandberg, C.A. and Gutschick, R.C., 1980. Sedimentation and biostratigraphy of Osagean and Meramecian starved basin and foreslope, Western United States. In: Fouch, T.D. and Magathan, E.R. (Eds.), Paleozoic paleogeography of the west-central United States. Rocky Mountain Paleogeography Symposium 1, Denver, SEPM Rocky Mountain Section, 129-147.

Sandberg, C.A. and Gutschick, R.C., 1984. Distribution microfauna and source rock potential of Mississippian Delle phosphatic member of Woodman Formation and equivalents, Utah and adjacent states. In: Woodward, J., Meissner, F.F. and Clayton, J.L. (Eds.), Hydrocarbon source rocks of the Greater Rocky Mountain Region, Denver Colorado, Rocky Mountain Association of Geologists, 135-178.

Sandberg, C.A., Poole, F.G. and Gutschick, R.C., 1980. Devonian and Mississippian conodont zonation of Pilot and Chainman shales, Confusion Range Utah. In: Fouch, T.D. and Magathan, E.R. (Eds.), Paleozoic paleogeography of the west-central United States, Rocky Mountain paleogeography symposium 1, Denver, SEPM Rocky Mountain Section, 71-79.

Sandberg, C.A. and Ziegler, W., 1979. Taxonomy and biofacies of important conodonts of Late Devonian styriacus Zone, United States and Germany. Geologica et Palaeontologica, 13, 173-212.

Sandberg, C.A., Ziegler, W., Dreesen, R. and Butler, J.L., 1988. Late Frasnian Mass Extinction: Conodont Event Stratigraphy, Global Changes, and possible Causes. Courier Forschungsinstitut Senckenberg, 102, 263-307.

Sandberg, C.A., Ziegler, W., Leuteritz, K. and Brill, S.M., 1978. Phylogeny, speciation and zonation of Siphonodella (Conodonta, Upper Devonian and Lower Carboniferous). Newsletters on Stratigraphy, 7, 102-120.

Sando, W.J., Sandberg, C.A. and Gutschick, R.C., 1981. Stratigraphic and economic significance Of Mississippian sequence at North Georgetown Canyon Idaho, American Association of Petroleum Geologists Bulletin, 65, 1433-1443.

Sannemann, D., 1954. Neue stratigraphische Ergebnisse im Paläozoikum des Frankenwaldes auf Grund von Conodontenfunden. Neues Jahrbuch für Geologie und Paläontologie, 480-482.

Sannemann, D., 1955. Oberdevonische Conodonten. Senckenbergiana Lethaia, 36, 123-156.

Savage, N.M., 1988. The use of sodium polytungstate for conodont separations. Journal of Micropalaeontology (BMS), 7, 39-40.

Sax, N.I., 1979. Dangerous Properties of Industrial Materials (5th edition). Van Nostrand Reinhold, New York, 1-118.

Schmidt, H., 1934. Conodonten-Funde in Ursprunglichen Zusammenhang. Paläontologische Zeitschrift, 16, 76-85.

Schmidt, H., 1950. Nachträger zur Deutung der Conodonten. Decheniana, 104, 11-19.

Schmidt, H. and Müller, K.J., 1964. Weitere Funde von Conodonten-Gruppen aus dem oberen Karbon des Sauerlandes. Paläontologische Zeitschrift, 38, 105-135.

Schopf, T.J.M. and Simpson, D.R., 1970. A method for finding conodonts in large nearly-barren samples. Journal of Paleontology, 44, 164-165.

Scott, H.W., 1934. The zoological relationships of the conodonts. Journal of Paleontology, 8, 448-445.

Scott, H.W., 1942. Conodont assemblages from the Heath Formation, Montana. Journal of Paleontology, 16, 293-301.

Scott, J.A., 1987. Sedimentology of the Holkerian Rocks of South Wales. Ph.D. thesis, University of Wales (Aberystwyth).

Seddon, G., 1970. Frasnian conodonts from the Sadler Ridge Bugle Gap area, Canning Basin Western Australia. Journal of the Geological Society of Australia, 16, 723-753.

Seddon, G. and Sweet, W.C., 1971. An ecologic model for conodonts. Journal of Paleontology, 45, 869-880.

Sevastopulo, G.D. and Keegan, J.B., 1980. A technique for revealing the stereom structure of fossil crinoids. Palaeontology, 23, 749-756.

Simpson, J., 1985. The Sedimentology of the Arundian (Dinantian) of Gower and south Dyfed. Ph.D. thesis University of Reading, 1-304.

Simpson, J., 1987. Mud dominated storm deposits from a Lower Carboniferous ramp. Geological Journal, 22, 191-205.

Simpson, J. and Kalvoda, J., 1987. Sedimentology and foraminiferal biostratigraphy of the Arundian (Dinantian) stratotype. In: Hart, M.B. (Ed.), Micropalaeontology of Carbonate Environments. Ellis Horwood Limited, Chichester, 226-237.

Smith, E.G., Rhys, G.H. and Eden R.H., 1967. Geology of the country around Chesterfield, Matlock and Mansfield. Memoir of the Geological Survey of Great Britain 112.

Smith, M.P., 1987. The use of back-scattered electron imaging in the photographic examination of bedding-plane assemblages. In: Austin, R.L. (Ed.), Conodonts: Investigative techniques and Applications. Ellis Horwood Limited, Chichester, 149-151.

Smith, M.P., Briggs, D.E.G. and Aldridge, R.J., 1987. A conodont animal from the lower Silurian of Wisconsin, U.S.A., and the apparatus architecture of panderodontid conodonts. In: Aldridge, R.J. (Ed.), Palaeobiology of conodonts. Ellis Horwood, Chichester, 91-104.

Solakius, N., 1983. Use of the 'petrol method' for extracting foraminifera from various types of sedimentary rocks. In: Costa, L.I. (Ed.), Palynology Micropalaeontology: Laboratories, Equipment and Methods, Norwegian Petroleum Directorate Bulletin, 2, 93-95.

Stanley, E.A., 1958. Some Mississippian conodonts from the high resistivity shale of the Nancy Watson No.1 Well in northeastern Mississippi. Journal of Paleontology, 32, 459-476.

St. Clair, D.W., 1935. The use of acetic acid to obtain insoluble residues. Journal of Sedimentary Petrology, 5, 146-149.

Stewart, I.J., 1981. The structure, stratigraphy and conodont biostratigraphy of the N.E. margin of Bodmin Moor and adjacent areas. Ph.D. thesis University of Exeter.

Stinemayer, E.H., 1965. Microfossil vacuum-needle segregating pick. In: Kummel, B. and Raup, D., (Eds.), Handbook of Paleontological Techniques, Freeman, San Francisco, California, 276-283.

Stone, J.J., 1987. Review of investigative techniques used in the study of conodonts. In: Austin, R.L. (Ed.), Conodonts: Investigative techniques and applications. Ellis Horwood Limited, Chichester, 17-34.

Stone, J.J. and Saunders, R., 1987. Magnetohydrostatic separation of conodonts from residues. In: Austin, R.L. (Ed.), Conodonts: Investigative techniques and applications. Ellis Horwood Limited, Chichester, 69-74.

Sweet, W.C., 1970. Uppermost Permian and Lower Triassic conodonts of the Salt Range and Trans-Indus Ranges, West Pakistan. In: Kummel, B. and Teichert, C. (Eds.), Stratigraphic Boundary problems, Permian and Triassic of West Pakistan. University of Kansas Department of Geology Special Publication, 4, 207-275.

Sweet, W.C., 1988. The Conodonta; Morphology, Taxonomy, Palaeoecology and Evolutionary History of a Long-Extinct Animal Phylum. Oxford Monographs on Geology and Geophysics, 10. Oxford University Press, Oxford, 1-212.

Swift, A., 1987a. The petroleum ether method for the disaggregation of clastic sediments. In: Austin, R.L. (Ed.), Conodonts: Investigative techniques and Applications. Ellis Horwood Limited, Chichester, 44.

Swift, A., 1987b. Conodont concentration using diiodomethane. In: Austin, R.L. (Ed.), Conodonts: Investigative techniques and Applications. Ellis Horwood Limited, Chichester, 66.

Szaniawski, H., 1982. Chaetognath grasping spines recognised among Cambrian protoconodonts. Journal of Paleontology, 56, 806-810.

Szaniawski, H., 1983. Structure of protoconodont elements. Fossils and Strata, 15, 21-28.

Szaniawski, H., 1987. Preliminary structural comparisons of protoconodont, paraconodont and euconodont elements. In: Aldridge, R.J. (Ed.), Palaeobiology of conodonts. Ellis Horwood Limited, Chichester, 35-47.

Then, D.R. and Dougherty, B.J., 1983. A new procedure for extracting foraminifera from indurated organic shale. In: Current Research, Part B, Geological Survey of Canada, Paper 83-1B, 413-414.

Thompson, T.L., 1979. A gnathodont lineage of Mississippian conodonts. Lethaia, 12, 227-234.

Thompson, T.L. and Fellows, L.D., 1970. Stratigraphy and conodont biostratigraphy of Kinderhookian and Osagean rocks of Southwestern Missouri and adjacent areas. Report of investigations No. 45, Missouri Geological Survey and Water Resources, Rolla, Missouri, 1-263.

Thompson, T.L. and Goebel, E.D., 1969. Conodonts and stratigraphy of the Meramecian Stage (Upper Mississippian) in Kansas. State Geological Survey of Kansas Bulletin, 192, 1-56.

Tubbs, P.K., 1986. Certificate. Opinion 1415 Polygnathus bilineatus Roundy, 1926 designated as type species of Gnathodus Pander, 1856 (Conodonta). Bulletin of Zoological Nomenclature, 43, 262-263.

Tunbridge, I., 1986. Mid Devonian tectonics and sedimentation in the Bristol Channel area. Journal of the Geological Society, London, 143, 107-115.

Turner, P. and Tarling, D.H., 1975. Implications of new paleomagnetic results from the Carboniferous System of Britain. Journal of the Geological Society of London, 131, 469-488.

Turner, W.M., 1966. An improved method for recovery of bromoform used in mineral separation. United States Geological Survey Professional Paper, 550C, 224-227.

Ulrich, E.O. and Bassler, R.S., 1926. A classification of the tooth-like fossils conodonts with descriptions of American Devonian and Mississippian species. Proceedings of the United States National Museum, 68, 1-63.

Varker, W.J., 1967. Conodonts of the genus Apatognathus Branson and Mehl from the Yoredale series of the north of England. Palaeontology, 10, 124-141.

Varker, W.J., 1987a. A method of extracting conodonts from non-calcareous shale samples using paraffin (kerosene). In: Austin, R.L. (Ed.), Conodonts: Investigative techniques and Applications. Ellis Horwood Limited, Chichester, 43-44.

Varker, W.J., 1987b. Electromagnetic separation of conodonts from residues. In: Austin, R.L. (Ed.), Conodonts: Investigative techniques and Applications. Ellis Horwood Limited, Chichester, 67-69.

Varker, W.J. and Austin, R.L., 1974. The significance of Adetognathus unicornis (Rexroad and Burton) in the Mirk Fell Beds (E_{2a}) of the north of England. Journal of Earth Science, 8, 399-408.

Varker, W.J. and Sevastopulo, G.D., 1985. The Carboniferous System Part 1 - Conodonts of the Dinantian Subsystem from Great Britain and Ireland. In: Higgins, A.C. and Austin R.L., (Eds.), A stratigraphical index of conodonts, Ellis Horwood, Chichester, 167-209.

Vaughan, A., 1905. The palaeontological sequence in the Carboniferous Limestone of the Bristol area. Quarterly Journal of the Geological Society of London, 61, 183-307.

Voges, A., 1959. Conodonten aus dem Unterkarbon I und II (Gattendorfia und Pericyclus Stufe) des Sauerlandes. Paläontologische Zeitschrift, 33, 266-314.

Voges, A., 1960. Die bedeutung der Conodonten für Stratigraphie des Unterkarbons I und II im Sauerland. Fortschritte in der Geologie von Rheinland und Westfalen, Krefeld, 3, 197-228.

von Bitter, P.H., 1972. Environmental control of conodont distribution in the Shawnee Group (Upper Pennsylvanian) of eastern Kansas. University of Kansas Paleontological Contributions, 59, 1-105.

von Bitter, P.H., 1976. Palaeoecology and distribution of the Windsor Group (Viséan - early Namurian) conodonts, Port Hood Island, Nova Scotia, Canada. In: Barnes, C.R. (Ed.), Conodont palaeoecology, Geological Society of Canada Special Paper, 15, 225-242.

von Bitter, P.H. and Merrill, G.K., 1980. Naked species of Gondolella (Conodontophorida) their distribution, taxonomy, and evolutionary significance. Royal Ontario Museum Life Sciences Contributions, 125, 1-49.

von Bitter, P.H. and Millar-Campbell, C., 1984. The use of spikes in monitoring the effectiveness of phosphatic microfossil recovery. Journal of Paleontology, 58, 1193-1195.

von Bitter, P.H., Plint Geberl, H.A. and Miller, H.A.L., 1978. Decolorization of heavy liquids - an economic assessment. Canadian Journal of Earth Sciences, 15, 1872-1875.

von Bitter, P.H., Sandberg, C.A. and Orchard, M.J., 1986. Phylogeny, Speciation, and Palaeoecology of the Early Carboniferous (Mississippian) Conodont Genus Mestognathus. Royal Ontario Museum Life Sciences Contributions, 143, 1-115.

Walliser, O.H., 1964. Conodonten des Silurs. Abhandunglen des Hessischen Landesamtes für Bodenforschung, 41, 1-106.

Wang Yu Xian, 1981. High frequency dielectrical separation of microfossils. Lethaia, 14, 261-268.

Waters, R.A. and Lawrence, D.J.D., 1987. Geology of the South Wales Coalfield Part III the country around Cardiff (third edition). Memoir of the British Geological Survey. Her Majesty's Stationery Office, London, 1-114.

Webers, G.F., 1966. The Middle and Upper Ordovician conodont faunas of Minnesota. Minnesota Geological Survey Special Paper, 4, 1-123.

Webster, G.D., 1969. Chester through Derry Conodonts and stratigraphy of northern Clark and southern Lincoln Counties, Nevada. University of California Publications in Geological Science, 79, 1-121.

Weddige, K. and Ziegler, W., 1979. Evolutionary patterns in the Middle Devonian conodont genera Polygnathus and Icriodus. Geologica et Palaeontologica, 13, 157-165.

Welch, R.G., Hill, W.E. and Ireland, H.A., 1964. A continual extraction technique for insoluble residues and phosphatic microfossils. Transactions of the Kansas Academy of Science, 67, 553-555.

Westrop, S.R., 1986. Taphonomic versus ecologic controls on taxonomic relative abundance patterns in tempestites. Lethaia, 19, 123-132.

Wicher, C.A., 1942. Praktikum der augewandten Mikropaläontologie. Bomtrager, Berlin.

Wright, V.P., 1981. The stratigraphy and sedimentology of the Llanelly Formation between Blorenge and Penderyn, South Wales. Ph.D. thesis University of Wales.

Wright, V.P., 1982. Uralloporella Korde from the Lower Carboniferous of South Wales. Bulletin of the British Museum of Natural History (Geology), 36, 151-155.

Wright, V.P., 1986. Facies sequences on a carbonate ramp: the Carboniferous limestones of South Wales. Sedimentology, 33, 221-241.

Wright, V.P., Faulkner, T. and Pickard, N., 1987. Early Carboniferous ramp and shelf carbonates and algae, South Wales. In: Riding, R., (Ed.), Fourth International Symposium on Fossil Algae, Cardiff 1987, Post-Symposium Field Excursion Guide, 1-43.

Young, J.Z., 1981. The life of vertebrates (third edition). Oxford University Press, Oxford, 1-645.

Youngquist, W.L. and Miller, A.K, 1949. Conodonts from the Late Mississippian Pella Beds of south central Iowa. Journal of Paleontology, 23, 617-622.

Zengji, W., 1987. Lower Carboniferous Stratigraphy and Coral Fossil Sequence in the Amunike Mountains of the North Qaidam Basin. Bulletin of the institute of Geology, Chinese Academy of Geological Sciences, 16, 91-133.

Zhang Youqiu, 1987. The tower method: an improved method for conodont recovery from calcareous rocks. In: Austin, R.L. (Ed.), Conodonts: Investigative techniques and Applications. Ellis Horwood Limited, Chichester, 37-39.

Ziegler, W., 1960. Die Conodonten aus den Geröllen des Zechsteinkonglomerates von Rossensay (südwestlich Rheinberg/Niederrhein). Fortschritte in der Geologie von Rheinland and Westfalen, 6, 1-15.

Ziegler, W., 1971. Conodont stratigraphy of the European Devonian. In; Sweet, W.C. and Bergström, S.M., (Eds.), Symposium on Conodont Biostratigraphy. Geological Society of America Memoir, 127, 227-284.

Ziegler, W., 1971b. (Review of Rhodes Austin and Druce 1969) Zentralblatt für Geologie und Paläontolologie, 2, 365-369.

Ziegler, W. (Ed.), 1973. Catalogue of Conodonts. I. Schweizerbartsche, Stuttgart, 1-504.

Ziegler, W. (Ed.), 1973. Catalogue of Conodonts. II. Schweizerbartsche, Stuttgart, 1-404.

Ziegler, W. (Ed.), 1977. Catalogue of Conodonts. III. Schweizerbartsche, Stuttgart, 1-574.

Ziegler, W. (Ed.), 1981. Catalogue of Conodonts. IV. Schweizerbartsche, Stuttgart, 1-445.

Ziegler, W. and Lane, H.R., 1987. Cycles in conodont evolution from Devonian to mid-Carboniferous. In: Aldridge, R.J. (Ed.), Palaeobiology of conodonts. Ellis Horwood, Chichester, 147-163.

Ziegler, W. and Lindström, M., 1981. Chemical and mineralogical properties. In: Clarke et al (Eds.), Treatise on Invertebrate Paleontology Part W, 52-56.

Ziegler, W., Lindström, M. and McTavish, R., 1971. Monochloracetic acid and conodonts - a warning. Nature, 230, 584-585.

Zingula, R.P., 1968. A new breakthrough in sample washing. Journal of Paleontology, 42, 1092.

Zittel, K.A. and Rohon, J.V., 1886. Uber Conodonten. Sitzungsberichte, Bayerischen Akademie der Wissenschaften zu München, Klasse für Mathematik -Naturwissenschaften, 16, 108-136.