

ARCHITECTURE, GROWTH, AND FUNCTION OF
OZARKODINID CONODONTS

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Doctor of Philosophy
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by

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Architecture, growth, and function of ozarkodinid conodonts

by

Philip Conrad James Donoghue

ABSTRACT

Analysis of natural assemblages reveals that the architecture of the ozarkodinid conodont feeding apparatus remained conservative throughout two hundred million years of evolution. The apparatus was differentiated into an anterior array which performed a rasping and/or slicing function and its supporting structures were probably homologous to the dental cartilages of the living agnathans. The taphonomy of the apparatus indicates that the majority of natural assemblages represent carcasses that came to rest at a high angle to the sea floor, suggesting the presence of soupy substrates.

Analysis of conodont hard tissue histology has led to a new model of element growth. This is used to reinterpret the affinity of the hard tissues themselves as opposed to the competing methodology which interprets the hard tissues first. Conodont elements are composed from numerous odontodes, and individual elements can be considered as odontocomplexes. Analysis of pattern formation in conodont element growth provides a new means of understanding these structures. The pattern of growth exhibited by many conodont elements is similar to that of the dentigerous jaw bones of acanthodians, and to that of lungfish toothplates. The periodic addition of odontodes to conodont elements provides a mechanism by which the paradox of growth and function may be resolved. The identification of internal discontinuities as representing episodes of function in the growth record of conodont elements indicates that the animal retained its feeding array throughout life rather than periodically shedding and replacing component elements.

The functional morphology of pairs of elements dissected from natural assemblages reveals that, even though conodonts lacked jaws, some groups evolved a level of dental occlusion unrivalled before the rise of mammals, occurring in conodonts at least several tens of millions of years earlier. Comparison with the functional morphology of other taxa indicates that this level of occlusion was maintained by an additional unpreserved structure, comparable in function but not homologous to a jaw.

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INTRODUCTION

Conodonts are an extinct group of exclusively marine organisms that are almost exclusively represented in their extensive fossil record by microscopic toothlike structures known as conodont elements. One hundred and forty years have now passed since their first discovery (Pander 1856), yet all significant advances in conodont palaeobiology have been made within the last thirty years. The earliest of these fundamental advances was a progression from the wholly artificial single-element taxonomy that had persisted from the time of Pander, to the more rigorous multielement taxonomy that has now become standard.

Conodont palaeobiology has also matured from its moribund state so apparent in the latest edition of the *Treatise on Invertebrate Paleontology* (Clark *et al.* 1981). The discovery in the early 1980s of soft tissue remains of the conodont animal (Briggs *et al.* 1983) has completely revolutionised the subject from one that was interesting, but esoteric, to one that is fundamental to our understanding of the early evolution of the vertebrates. Acceptance of the vertebrate, or at least, craniate affinity of the conodont animal is now widespread (Forey and Janvier 1993, 1994; Janvier 1995, 1996a, b) and thanks to the discovery of further specimens that include remains of the conodont animal's soft tissues (Aldridge *et al.* 1986, 1993; Aldridge and Theron 1993; Gabbott *et al.* 1995) affinity can be substantiated solely on soft tissue characters. However, some workers remain adamant in their perception of conodonts as cephalochordates (Nicoll 1995; Kemp and Nicoll 1995a, b; 1996). This remaining hostility to the vertebrate hypothesis appears to stem from the misconception that the affinities of conodonts are based on the identification of uniquely vertebrate hard tissues in conodont elements (Sansom *et al.* 1992). Sansom and his colleagues identified cellular dermal bone, enamel, globular calcified cartilage, and more recently, dentine (Sansom *et al.* 1994) as components of the conodont mineralised skeleton, though these interpretations have themselves been based on the assumption that conodonts are at least chordates, which is in turn based on characters of the soft tissue anatomy. Kemp and Nicoll have therefore attempted to refute the vertebrate interpretation of conodont affinity, by deconstructing the work of Sansom *et al.* Nevertheless, there are many others who doubt the interpretations of Sansom *et al.* (Fåhræus and Fåhræus van Ree 1993; Forey and Janvier 1993, 1994; Janvier 1995, 1996a, b) while accepting that conodonts are vertebrates. Indeed Krejsa and colleagues (Krejsa *et al.* 1990a, b; Krejsa and Leaffer 1993; Slavkin and Diekwisch 1996) have attempted to draw homology between the toothlets of hagfish and conodont elements, based on comparative histology.

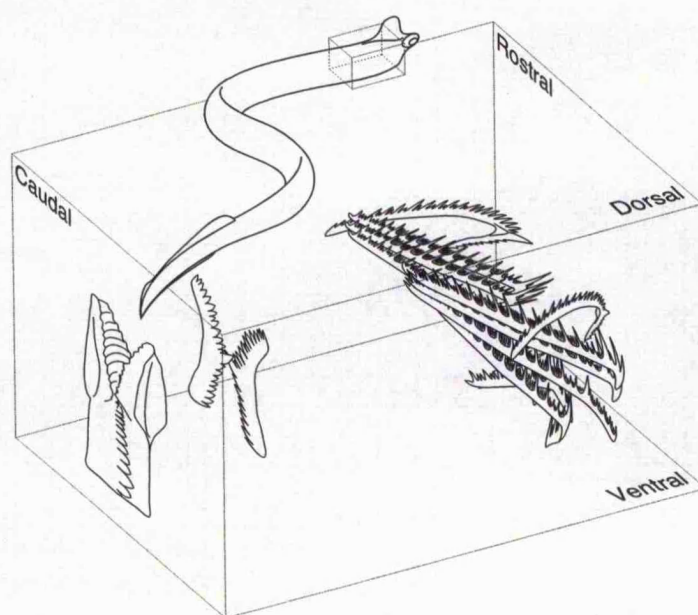
Although the affinity debate appears to be drawing to a close, there are many other points of contention that persist in conodont palaeobiology. Amongst these, the question of conodont element function is of paramount importance, and debate on this issue has seen something of a revival since it was separated from the question of affinity (see Bengtson 1980 for a perspective before this). Of the two competing hypotheses of function; support to a filtering device in a microphage (e.g. Lindström 1964, 1973, 1974; Nicoll 1977, 1985, 1987, 1995), versus tooth-function in a macrophage (e.g. Jeppsson 1979; Aldridge and Briggs 1986; Purnell and von Bitter 1992), the tooth hypothesis appears to be favoured (Purnell 1995). However, although we have some understanding of what functions individual elements may have performed, our understanding of exactly *how* they performed these functions is based largely on conjecture.

The original objectives of my PhD were to attempt to resolve some of the remaining controversies in conodont palaeobiology, through study of the Ozarkodinida, the most derived and most diverse of all the conodont orders. Despite their derived nature, ozarkodinids are important because of their rich fossil record which includes (probably) all the conodont animals with preserved soft tissue from the Granton Shrimp Bed (Briggs *et al.* 1983; Aldridge *et al.* 1986, 1993), and the majority of bedding plane assemblages, fossils which preserve evidence of the

original three dimensional architecture of the conodont feeding apparatus. Furthermore, the notational scheme on which homologies are identified between distantly related groups of conodonts is ultimately based on ozarkodinids (Purnell 1993). In summary, much of what we know about conodont palaeobiology is based on ozarkodinids, and so they provide an ideal database with which to resolve current controversies.

Individual objectives included investigation of the architecture, growth, function and cladistic relationships of the Ozarkodinida, but so many of the individual projects spiralled into much larger studies, encompassing not only the ozarkodinid order, but also conodonts of other orders, that some aspects had to be put aside, or have not been included as part of this thesis due to the constraints of time and space. I have therefore restricted the thesis to ozarkodinid apparatus architecture, function of P elements, and conodont element growth in general.

In chapter one, Mark Purnell and I have produced a new three-dimensional architectural model of the apparatus of *Idiognathodus*, the taxon most abundantly represented in bedding plane assemblages. Our model is a considerable improvement on its rivals, and our work has shown that the apparatus architecture is representative not only of *Idiognathodus*, but also all other ozarkodinids represented by bedding plane assemblages. Paradoxically, ozarkodinids, the most diverse of all seven conodont orders, possibly of all jawless fish, were evidently an extremely conservative group.



Text-fig. 1.
Architecture of
the conodont
feeding
apparatus and
its position in
the head of the
conodont
animal. The
new
orientational
terms are
included.

In chapter two I reconsider conodont hard tissue histology based on a review of ozarkodinids, prioniodinids, prioniodontids, and representatives of some of the four remaining orders. I attempt to extend our understanding of conodont element growth from the simplistic model proposed by Müller and Nogami (1971, 1972) to a more realistic level that considers interaction of the component tissues; the pattern of formation is an important factor in this reconsideration.

Chapter three continues the theme of growth by considering whether conodonts were permanent, as in the dentition of lungfish and some acanthodians, or deciduous, as in most other craniates. This question is of relevance to our whole perception of the conodont fossil record, as well as resolving the apparent paradox between growth and function in conodont elements (Bengtson 1976, 1983a; Jeppsson 1979). Function is the topic of chapter four which is a study based on elements dissected from a bedding plane assemblage. Because of this data base, we can be

Introduction

sure that the elements worked together when the animal was alive, and their functional morphology holds important clues to the mode of operation of homologous elements in all ozarkodinids.

Orientational terms used in this thesis for conodont elements do not follow convention (e.g. Clark *et al.* 1981). The new terms relate to the original orientation of the elements when the animal was alive. The conventional anterior and posterior orientation of P elements translates to ventral and dorsal respectively; the conventional anterior and posterior orientation of S elements remains the same, but to prevent confusion between the two schemes, anterior translates to rostral, and posterior to caudal (Text-fig. 1).

The structure of this thesis is such that individual chapters are in a format suitable for immediate publication. Chapter one has been prepared for publication in *Philosophical Transactions of the Royal Society, London, Series B* and is co-authored by Mark Purnell. Chapter two has also been formatted according to the style required by *Philosophical Transactions of the Royal Society, London, Series B*. Chapter three has been formatted according to the style required by *Lethaia*, and chapter four is formatted according to the guidelines for manuscript preparation in the journal *Paleobiology*.

A few other publications have arisen during the course of my PhD. These are listed below.

Aldridge, R. J. & Donoghue, P. C. J. *in press*: Conodonts: a sister group to the hagfish? *In*: Jørgensen, J. M., Weber, R. E., Lomholt, J. P. and Malte, H. (eds) *The Biology of Hagfish*. Chapman and Hall.

Purnell, M. A., Aldridge, R. J., Donoghue, P. C. J. & Gabbott, S. E. 1995: Conodonts and the first vertebrates. *Endeavour* 19, 20-27.

Zhang, S., Aldridge, R. J. & Donoghue, P. C. J. *in press*: An Early Triassic conodont with periodic growth? *Journal of Micropalaeontology*.

CHAPTER 1

Architecture, functional morphology, and taphonomy of the skeletal apparatus of ozarkodinid conodonts

SUMMARY

Ozarkodinid conodonts were one of the most successful groups of agnathan vertebrates ever to have lived. Natural assemblages of their skeletal elements are the remains of individual animals, fossilized after postmortem collapse of the oropharyngeal feeding apparatus onto a two-dimensional plane. From analysis of element arrangement in natural assemblages from the Pennsylvanian of Illinois, we have produced a precise, scale model of the feeding apparatus of *Idiognathodus*. At the front lay an axial Sa element, flanked by two groups of four close-set, elongate Sb and Sc elements which were inclined obliquely inwards and forwards; above these elements lay a pair of arched and inward pointing M elements. Behind the S-M array lay transversely oriented and bilaterally opposed Pb and Pa elements. This reconstruction of skeletal architecture differs from previous hypotheses, but detailed comparisons with all known natural assemblages of taxa assigned to the order Ozarkodinida confirm that the arrangement of elements in the model accurately reflects the apparatus architecture of this major group of extinct agnathans.

Based on our model, we propose that the anterior S and M elements of ozarkodinid conodonts were attached to cartilaginous plates. In order for the animal to feed, these plates were first everted, and then drawn back and upward over the anterior edge of an underlying cartilage. These movements produced a highly effective grasping action, the cusps and denticles of the elements converging to grab and impale any food item that lay anterior of the open array. According to this hypothesis, the anterior part of the conodont apparatus is comparable to, and possibly homologous with, the lingual apparatus of extant agnathans; the elements themselves, however, have no direct homologues. Our model also sheds new light on the taphonomy of the conodont skeleton, and on problems of homology and notation of elements and apparatuses.

1. INTRODUCTION

For more than a century, questions of conodont palaeobiology were considered interesting, but esoteric. The last few years, however, have seen a revolution in our understanding of conodont anatomy, affinities and functional morphology, and this has led to a dramatic shift in focus. Conodonts are now widely thought to be vertebrates or craniates, and have an important role to play in understanding the origins and early diversification of the clade (e.g. Sansom *et al.* 1992; Aldridge *et al.* 1993; Purnell *et al.* 1995; Janvier 1996a). Not only are they among the first craniates to appear in the fossil record, they are also far more diverse than any other group of jawless fish. With this new focus, analysis of conodont functional morphology takes on a new significance.

Recent work has established that many conodonts, including some primitive taxa with coniform elements, were macrophagous, probably predatory, organisms, and that those conodonts with more complex apparatuses used their phosphatic elements to grasp, slice and crush their food (Purnell and von Bitter 1992; Purnell 1995). The strongest evidence for these conclusions comes from microwear analysis of surface features on conodonts elements (Purnell 1995), but this study, and all rigorous analysis of conodont functional morphology, relies to some extent on a sound understanding of the arrangement of the elements in the conodont apparatus. Indeed, one of the key steps in the initial recognition of element wear patterns in ozarkodinid conodonts (*sensu* Sweet 1988) was the realisation that their Pa elements occlude with the left hand element behind that on the right, an observation made in the preparation of a new, precise model of ozarkodinid skeletal architecture. This model has been widely

illustrated (e.g. Purnell and Donoghue 1995; Purnell *et al.* 1995; Palmer 1995, 1996; Abrams 1996) but the evidence upon which it is based, and our analysis of ozarkodinid skeletal architecture have not been presented. Our aim here is to rectify this situation, by providing a discussion of our methodology, the details of ozarkodinid architecture, and the wider significance of our results.

The development of ideas about conodont skeletal architecture (see figure 1) has closely paralleled hypotheses of biological affinity and functional morphology (see Aldridge 1987 for a review). Understanding of architecture underpins analysis of function, but many studies (e.g. Schmidt 1934; Lindström 1964, 1973, 1974; Nicoll 1995) have confused the two by using scenarios of function to construct and constrain models of element arrangement. This lack of methodological rigour has contributed to the diversity of alternative models of skeletal arrangement that have been proposed, some of which are little more than pure speculation (see §2 below). Part of the blame, however, also lies in a paucity of good fossil material and a consequent lack of morphological constraint. Until the fossilized remains of the conodont body were found it was not possible to determine anterior-posterior and dorso-ventral axes with certainty, but the fossils that provide the means to unravelling the primary, *in vivo* spatial arrangement of conodont elements were first described more than sixty years ago (Schmidt 1934; Scott 1934).

(a) *Natural assemblages*

Because conodonts were primarily soft bodied organisms, their fossil record consists almost entirely of the dissociated skeletal elements of their feeding apparatus which became scattered in the sediment on the death and decay of the animals. Fortunately, however, there are fossils that preserve together numbers of different conodont elements, either as associations on bedding-planes or as clusters of elements fused together by diagenetic minerals. More than 1000 of these “bedding-plane assemblages” and “fused clusters” are now known, and several conodont orders are represented in collections from around the world. This figure is, however, somewhat misleading, as a few Upper Carboniferous localities have yielded hundreds of assemblages of only a few taxa. The majority of assemblages and clusters belong to taxa assigned to the order Ozarkodinida, and the hundreds of specimens known represent a range of biostratigraphic histories (see Appendix for a review). Some are undoubtedly accumulations of elements which represent the faecal matter or stomach ejecta of animals that preyed upon conodonts. These may contain elements belonging to more than one individual and more than one taxon (e.g. Hinde 1879; Schmidt and Müller 1964, figure 9) and generally they preserve very little of the original arrangement of the elements. On the other hand, many clusters and bedding-plane assemblages represent the remains of a single dead conodont. The amount of architectural information preserved, however, varies. At one end of the preservational spectrum the remains have become completely disarticulated and strewn over the bedding surface (e.g. Higgins 1981; Norby and Rexroad 1985) by current activity, scavenging, bioturbation, or other factors such as explosive release of gases from the decomposing conodont carcass. At the other, the only post mortem processes to have affected the apparatus are passive gravitational collapse as the soft tissues of the conodont body decayed (e.g. figures 2-13). In such assemblages, post mortem movement is limited to minor rotations of element long axes as they came to rest parallel to the sediment surface. Only clusters and assemblages towards this end of the preservational spectrum are of use in reconstructing apparatus architecture. For convenience we will refer to them as natural assemblages.

Diagenetic history apart, bedding-plane assemblages and fused clusters do not reflect different styles of preservation or record different information; the only significant difference between the two arises from the methods used to obtain the material. Bedding-plane assemblages are found on natural bedding-planes or bedding-

parallel split-surfaces of black shales and occasionally other lithologies; their elements may or may not be diagenetically bonded. Fused clusters, however, are recovered by acid dissolution of limestones and dolomites, and they can only preserve together those elements that were in physical contact at the time of formation of the diagenetic mineral that binds them. Adjacent elements that were not in contact, which would be preserved in a bedding-plane assemblage, are removed from the cluster along with the rock matrix. Fused clusters, therefore, tend to be less complete, but they do not record any information regarding original element arrangement that is not preserved in bedding-plane assemblages. Collections of fused clusters also tend to have a higher proportion of faecal associations, simply because the process of coprolite formation often brings elements into closer juxtaposition.

Compared to normal collections of disjunct conodont elements, natural assemblages are extremely rare, but despite this they are of paramount importance in conodont palaeontology. Conodonts have no close living relatives, and without homologous structures in extant organisms to aid interpretation, natural assemblages provide the only evidence for the original arrangement of the components of the conodont skeleton. Thereby, they serve as references in the development of conodont taxonomy and anatomical notation, and provide templates for reconstructing the apparatuses of the vast majority of taxa that are known only from dissociated remains. They are also fundamental in the recognition of homologies between taxa and in the interpretation of evolutionary pathways. Analysis of natural assemblages is the only rigorous method of reconstructing the three dimensional architecture of the conodont feeding apparatus.

2. ARCHITECTURAL RECONSTRUCTIONS OF THE CONODONT APPARATUS

Recent classifications of conodonts recognize up to seven orders (Sweet 1988; Dzik 1991; Aldridge and Smith 1993). Four have apparatuses composed of morphologically simple elements, and the architecture of some of these, including taxa assigned by Sweet (1988) to the orders Bellodellida and Panderodontida, has recently been reviewed by Sanson *et al.* (1994). Of the three orders characterised by more complex element morphology, the architecture of prioniodontids was addressed by Aldridge *et al.* (1995), and an analysis of prioniodinid apparatuses is in preparation (MAP). The third order, the Ozarkodinida (*sensu* Sweet 1988), is the focus of this paper. Representatives of this group dominate conodont faunas through most of the Palaeozoic, in terms of both abundance and diversity, and most of bedding-plane assemblages and clusters are ozarkodinids. It is not surprising, therefore, that almost all attempts at reconstructing the conodont apparatus have dealt primarily with ozarkodinid taxa.

Most analyses of conodont apparatus arrangement have been based on the pattern of element distribution in bedding-plane assemblages and clusters which are thought to retain something of the original spatial relationships of the elements. There are exceptions to this, however. The radically different approach adopted by Lindström (1964, 1973, 1974) was based primarily on his functional interpretation of the conodont apparatus as a lophophore, with spatial constraints imposed by the dimensions of the conodont eater *Typhloesus*. Lindström's reconstructions are not considered further here. Similarly, Nicoll's (1995) reconstructions of architecture are derived from his predilections regarding conodont affinity and function, an approach summarized in his statement (p. 247) "The conodont apparatus morphology has thus been placed in an amphioxus-like body . . . and this is used to explain and interpret the anatomical relationships of the elements."

(a) Linear reconstructions

Analyses that have relied on data from bedding-plane assemblages and clusters have conformed to two distinct methodologies. Both recognise that the extremely rare natural assemblages that preserve bilaterally symmetrical arrangements of elements (e.g. figures 2, 3) record primary architectural information, but the two approaches differ in the way they treat asymmetric assemblages (e.g. figures 4-13). Most analyses have assumed that deviations from symmetry reflect post mortem movement of the elements, and that recurrent asymmetric patterns are produced by rotations and translations of elements into their final resting place by compression and decomposition or by systematic muscle relaxation-contraction effects. This approach dates back to the discovery of the first natural assemblages (Scott 1934; Schmidt 1934). Schmidt (1934) proposed that *Gnathodus* bore a linear arrangement of 14 elements with the long axes of the elements approximately parallel to one another (figure 1a). In this model, the M elements flank the S elements, the denticles of which are directed downwards, inwards and towards the P elements. Schmidt's hypothesis of element arrangement was clearly based to a large extent on the specimen illustrated in figures 14 and 15, but it was also influenced by his interpretation of the conodont apparatus as the mandibles, hyoid and gill arches of a placoderm fish. For this reason he oriented the apparatus with the Pa elements at the front. Apart from this error, however, and the omission of the Sa element, Schmidt's reconstruction was ahead of its time and had no real rival until the work of Rhodes (1952) nearly twenty years later. The intervening period saw several publications documenting new conodont assemblages (see Appendix), but, with the exception of Scott (1942) and Schmidt (1950), these did not consider element arrangement in any detail. Scott (1942) drew his conclusions from a collection of around 180 assemblages, but only a very few appear to retain any trace of primary element arrangement, and there is very little evidence to support his hypothesis of the conodont apparatus. Schmidt (1950) augmented his 1934 reconstruction of *Gnathodus* with extra pairs of Pa elements and extra M elements, surmising that these elements had not been evident in the assemblages he described in 1934 because they lay in a different plane from the other elements of the apparatus. However, the additional elements resemble those of *Lochrien* and it seems very likely that his revised arrangement was based on an assemblage of two apparatuses.

Perhaps the most influential reconstruction of the conodont apparatus was that proposed by Rhodes (1952) for the apparatus of *Idiognathodus* (= *Scottella*, = *Scottognathus*) (figure 1b). Rhodes explicitly stated that this was intended to indicate the general form and number of the component elements and that the relative arrangement of the elements was diagrammatic, but the linear arrangement was clearly based on one of the natural assemblages of Du Bois (1943, plate 25, figure 14; refigured by Rhodes 1954; figures 2, 3 herein) and gave an impression of three-dimensionality. The reconstruction did not include an Sa element nor did Rhodes recognize different morphologies of S element. His model was reillustrated in both conodont Treatises (Hass 1962; Clark *et al.* 1981) and provided a skeletal template for a number of subsequent reconstructions and hypotheses of conodont function. For example, Collinson *et al.* (1972), Avcin (1974) and Norby (1976) adopted Rhodes's linear arrangement with only minor modifications, such as shifting the M elements away from the axis and grouping the S elements into two opposed pairs (Collinson *et al.* 1972), or suggesting a more cylindrical disposition of elements with cusps directed towards the midline of the apparatus, and with an axial Sa element present (Avcin 1974; Norby 1976).

Schmidt and Müller (1964) considered their well preserved bedding-plane assemblages (e.g. figures 16-19) to be a better approximation of the original arrangement in the conodont animal than most previously described material. They recognised morphological differentiation within the S elements and advocated a linear apparatus pattern similar to that of Schmidt (1934), but with the P elements in opposition. A similar conclusion was reached

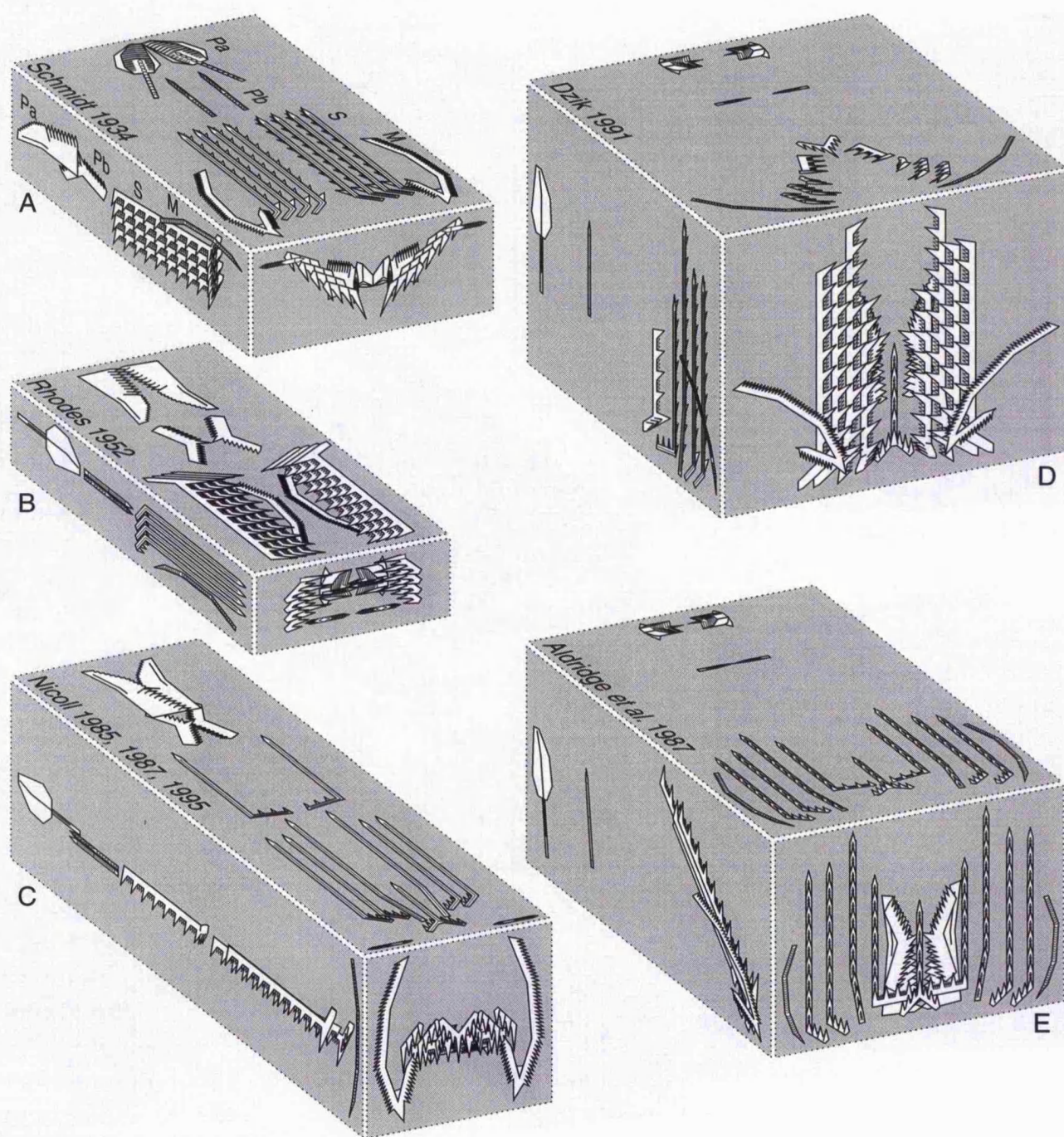


Figure 1. Hypotheses of element arrangement in ozarkodinid conodonts. Front, side and top views of the apparatus are projected onto the sides of each box; element morphology is diagrammatic, but based on *Idiognathodus*; A also shows P, M, S element notation. A, linear arrangement of Schmidt 1934, Pa elements anterior. B, linear arrangement of Rhodes (1952), neither anterior-posterior nor dorso-ventral axes were indicated by Rhodes. C, linear arrangement of Nicoll (1985, 1987, 1995, Nicoll and Rexroad 1987), M elements anterior, S element denticles directed ventrally, Sb₁ elements (his Sd₁) set back from other S elements. Nicoll did not reconstruct *Idiognathodus*, and it is not clear how he would orientate M elements of *Idiognathodus* morphology. D, vertical arrangement Dzik (1991) (modified from Dzik 1976, 1986); M elements anterior, posterior of all elements, by conventional designation, is dorsal. E, arrangement of Aldridge et al. (1987); S and M elements anterior.

by Jeppsson (1971), based on a review of the evidence from bedding-plane assemblages and clusters, and recently Walliser (1994) has also proposed a very similar linear model based on a re-examination of the material of Schmidt and Müller (1964). Nicoll (1977) also proposed a linear model, but arranged the elements as three groups. His later model (figure 1c; 1985, 1987, 1995; Nicoll and Rexroad 1987; "Peraios" style of Nicoll 1995) was also linear, but suggested a more posterior location for one pair of S elements in taxa which bore an Sa element with a posterior processes.

The emphasis placed on symmetrical assemblages, the interpretation of asymmetric assemblages as "unnatural", and the consequent need to invoke systematic post mortem effects to explain recurrent asymmetric patterns represent significant weaknesses in the approach to apparatus reconstruction adopted by many of these authors. Several authors, however, realised that different apparatus patterns reflected different orientations of collapse of the original three-dimensional structure. For example, based on their interpretation that their collections contained only a few more laterally than dorso-ventrally collapsed apparatuses, Schmidt and Müller (1964) concluded that the conodont animal was neither dorso-ventrally nor laterally flattened. Avcin (1976) recognised that different attitudes of repose of the conodont carcass would produce different assemblage configurations, but ruled out dorso-ventral collapse as impossible, given the extreme lateral flattening of what he mistakenly took to be the conodont animal (i.e., *Typhloesus*).

(b) Three-dimensional reconstructions

Observations such as these paved the way for a more rigorous approach to reconstructing apparatus architecture. This methodology differs from that outlined above in that its aim is to produce a single model of apparatus architecture that can account for a variety of natural assemblage patterns without recourse to *ad hoc* hypotheses of post mortem muscle relaxation and contraction effects. Norby (1976, 1979), for example, realised the difficulties of producing asymmetric bedding-plane assemblage patterns from a linear model of element arrangement and suggested that the elements in the apparatus may have been oriented side by side, with their long axes vertical. Dzik (1976) noted that the natural assemblages illustrated by Rhodes (1952, plate 126, figure 11; figures 2, 3 herein) and Mashkova (1972, plate 1; figures 20, 21 herein) were dorso-ventrally and laterally flattened respectively, and proposed a similar arrangement of elements with their long axes vertical and cusps opposed across the midline of the apparatus as the only one that could account for both assemblage patterns. Dzik's later hypothesis of skeletal architecture (1986, 1991, also discussed in Dzik 1994) modified his earlier arrangement a little in order to better account for observed natural assemblage patterns; his 1991 model is illustrated in figure 1d and is discussed in more detail below (§3).

This approach was further developed by Aldridge *et al.* (1987) through incorporation of a physical modelling technique derived from that of Briggs and Williams (1981). Aldridge *et al.* (1987) took the apparatus of the first-discovered conodont animal specimen (IGSE 13822) as the primary data for a physical model of element arrangement (figure 1e) which they then tested by attempting to simulate photographically a variety of recurrent patterns of apparatus collapse, both symmetrical and asymmetrical. The architectural model they proposed was followed in several subsequent papers (e.g. Purnell and von Bitter 1992; Aldridge *et al.* 1993, 1994, 1995; Purnell 1993a, 1994). This physical modelling method has since been successfully used to reconstruct the apparatus of the giant conodont *Promissum pulchrum* (Aldridge *et al.* 1995), and our new model of ozarkodinid architecture is based on similar techniques, the details of which are discussed below (see §3(a)).

3. PROBLEMS, MATERIALS AND METHODS

Rigorous architectural interpretation of bedding-plane assemblages and clusters is based on the recognition that, firstly, some of these element associations are faecal or disarticulated accumulations that preserve little or nothing of primary architecture, and secondly, that the remaining natural assemblages represent collapse of the original three-dimensional apparatus onto a two dimensional bedding-plane. Different patterns of element arrangement in natural assemblages therefore represent different orientations of apparatus collapse, the limited number of recurring patterns reflecting the attitude of the dead conodont on the sea floor (cf. Dzik 1986). A conodont carcass lying on its belly produced one characteristic pattern (figures 22, 23), a carcass on its side another (figure 4, 5), and a carcass lying head down (or up) in the sediment produced another (figures 6, 7). All these orientations of collapse are possible, as are all the intermediate orientations, but they are not all equally likely, and the majority of natural assemblages reflect collapses in which the conodont carcass lay in an intermediate orientation (see §8).

Clearly, any single model that can account for all recurrent natural assemblage patterns is superior to architectural hypotheses that require *ad hoc* post mortem movements of elements. Acceptance of this premise makes testing of reconstructions simple: if they cannot account for the details of element arrangement observed in natural assemblages, they must be rejected or modified. All linear models (e.g. Schmidt 1934; Rhodes 1952; Jeppsson 1971; Nicoll 1977, 1985, 1987, 1995; Walliser 1994; figure 1a-c herein) fail this test because they cannot account for the asymmetrical patterns observed in the majority of natural assemblages. The models proposed by Aldridge *et al.* (1987) and Dzik (1991) (figure 1d, e) are in much closer accord with observed patterns, but there are still a number of discrepancies.

Although the overall pattern of element arrangement and orientation in their model corresponds well with natural assemblage patterns, Aldridge *et al.* (1987) were aware of a number of limitations. They noted that the elements of their model were more widely spaced than in nature, and their comparisons with natural assemblages clearly demonstrated this. They also stated (p. 74) that "details of the model, especially the relative positions of the ramiform elements, remain to be refined. In particular, the M elements [in natural assemblages] commonly display an independence from the S elements, suggesting that they may have been operated by different muscles". Dzik (1991, p. 274) also pointed out that the orientation of the S elements in this model, with their cusps directed anteriorly, was "a poor fit with natural assemblages"; in particular, it is difficult to account for the consistent inward inclination of S element denticles in collapses approaching dorso-ventral orientations (e.g. figures 2, 3a, 14, 15a). Dzik's own model (figure 1d), however, is not without its problems: the vertical orientation of the S elements is not matched by lateral or oblique lateral collapse patterns (e.g. figures 4, 5a, 8, 9a, 10, 11a, 12, 13a), and his hypothesis that the elements of the symmetry transition series were arranged with their cusps in direct opposition across the axis, in a structure the shape of an anteriorly open V with a vertical closure, also places elements in positions that are not observed in natural assemblages. Aldridge *et al.* (1987) and Dzik (1991) identified many of the important general features of ozarkodinid architecture, such as the orientation of the P elements, and the anterior posterior spatial differentiation within the apparatus. It is the difficulties outlined above, however, together with the acquisition of new material and re-examination of existing collections, that prompted us to produce our new model of ozarkodinid architecture.

(a) Materials and methods

All published bedding-plane assemblage and cluster collections are listed in the Appendix along with notes on their preservation, completeness and collapse patterns. This list does not include prioniodontid or coniform taxa. As part of this study we have re-examined most collections of natural assemblages including those of Du Bois (1943), Rhodes (1952), Schmidt and Müller (1964), Rexroad and Nicoll (1964), Pollock (1969), Mashkova (1972), Avcin (1974), Norby (1976), Puchkov *et al.* (1982), Briggs *et al.* (1983), Nicoll (1985), Aldridge and Briggs (1986), Aldridge *et al.* (1987), Nicoll and Rexroad (1987), Aldridge *et al.* (1993), and Purnell (1993a). We have also examined new or unpublished Carboniferous material from Bailey Falls and Wolf Covered Bridge in Illinois, USA, the Heath Shale Formation and its Bear Gulch Member, in Montana, USA (see Purnell 1993b, 1994 for stratigraphic and locality details), and the Devonian Cleveland Shale of Ohio, USA.

Natural assemblages of *Idiognathodus* (*sensu* Baeseman 1973; Grayson *et al.* 1991) outnumber those of all other taxa, and the morphology of all the elements of its apparatus is well known (see e.g. Grayson *et al.* 1991). Our architectural reconstruction is, therefore, based primarily on *Idiognathodus*. In order to produce the most accurate reconstruction possible, we used regressions derived from measurements of *Idiognathodus* bedding-plane assemblages (Purnell 1993a, 1994) to calculate the size of elements in an apparatus with Pa elements 2 mm long and produced 1:50 scale models of all of the elements. These elements, made using epoxy putty modelling combined with moulding and casting techniques, were then used to produce our three dimensional model. The configuration of the elements in the model was determined by an iterative process analogous to the techniques of numerical forward modelling. An initial arrangement was produced and then visually compared with the arrangements of elements in the natural assemblages of *Idiognathodus* that formed the database of the analysis. This process revealed a number of discrepancies between the positions of elements in the preliminary model and those observed in the fossils; the positions of the elements in the model were adjusted accordingly, and the process of testing was repeated. This continued until the model converged on a solution which minimized the differences between the observed and modelled positions and orientations of the elements. Final testing was achieved by producing collapse patterns of element distribution from the model without any further adjustment. In nature, assemblages were produced as elements fell onto the sea floor under the influence of gravity as the conodont carcass decayed. Rather than reproducing this physically, however, collapse of the model was simulated by photographing it from a variety of directions, each corresponding to a particular orientation of apparatus collapse. The results of this final testing are reproduced here as figures 3, 5, 7, 9, 11, and 13. We were also able to calculate the orientation of the principal axes of the conodont apparatus and the conodont head as it lay on the sea floor prior to collapse (i.e., x = anterior-posterior axis, y = dorso-ventral axis, z = left-right axis). This was achieved by measuring the attitude of the focal plane of the camera relative to the axes of the apparatus while producing the simulated collapse. The focal plane represented the bedding-plane, and stereographic rotation of this plane and the axes of the apparatus to restore 'bedding' to horizontal yielded the original orientation of the apparatus. Independent repetition of some measurements indicated that calculations of orientation using this technique are reproducible to within a few degrees. It is important to note that natural assemblage collections do not record the original way up of specimens, and part and counterpart (when both are known) are generally designated according to quality of preservation. Thus, it is generally impossible to determine whether it was the left or right side, or ventral or dorsal surface of the body which lay on the sea floor at the time of collapse.

Modelling techniques similar to these have previously been used to great effect on conodonts (Aldridge *et al.* 1987, 1995), but they are not without minor drawbacks. The process of simulating collapse photographically

does not reproduce the slight reorientations of elements that occur as they come to lie on a horizontal plane, and in some orientations the viewing angle causes elements to appear foreshortened. The discrepancies that arise as a result of these effects are generally very minor, but they are indicated below. Due to the limitations of page space the assemblages and simulated collapse patterns illustrated in figures 2-13 are just examples which demonstrate the range of different collapse patterns observed in *Idiognathodus*. The model can, however, account for the patterns of element arrangement seen in other natural assemblages (see Appendix). Furthermore, in order to evaluate the model as a general hypothesis of the skeletal architecture of ozarkodinid conodonts we have also attempted to simulate the collapse patterns observed in a variety of ozarkodinid taxa other than *Idiognathodus* (figures 14-25; see also notes in Appendix).

4. ARCHITECTURE OF THE APPARATUS OF *IDIOGNATHODUS*

The Scottish conodont animals provide the basic constraints on ozarkodinid apparatus orientation, and these indicate unequivocally that the S and M elements were at the front of the apparatus and that the posterior P elements were oriented with their long axes normal to the long axis of the conodont body (Aldridge *et al.* 1987). Dorsal and ventral have been difficult to determine with certainty (Aldridge *et al.* 1987), but recognition of cartilaginous eye capsules, possible otic structures, and an equivocal dorsal nerve cord (Aldridge *et al.* 1993) all indicate that the apparatus was oriented such that the 'posterior' of the P elements (according to conventional designation) was directed dorsally. In our description of the apparatus of *Idiognathodus*, a plane parallel to the long axis of the animal and orthogonal to the sagittal plane is taken as horizontal. The whole model (1:50 scale), measured from the tip of the cusp of the Sa element to the blade of the Pa element, is 25 cm long, and an animal with 2 mm long Pa elements would, therefore, have had an apparatus 5 mm long. The model of the apparatus is to scale, and all linear dimensions could be given as absolute values. We give them as proportions of total apparatus length, however, because the elements of the apparatus of *Idiognathodus* grew isometrically (Purnell 1993a, 1994), and assuming the same to be true of the whole apparatus, dimensions expressed as proportions are applicable to *Idiognathodus* apparatuses of any size. At its widest (between the distal tips of the M elements), the apparatus is 60% of length, and its maximum dorso-ventral depth, between the most ventral ends of the anterior processes of the Sb₁ elements and the distal tips of the Sc₂ elements, is 50% of length. Note that our usage of element notation and the problems of element orientation are discussed below (§9(b)).

Detailed description of the elements of *Idiognathodus* is beyond the scope of this paper, but brief clarification of the morphology of the elements occupying S positions is necessary. The alate Sa element is the shortest of the S elements, its posterior process approximately half the length of that of the Sc elements. The Sb₁ elements are bipennate, lack a pronounced cusp, and have a fairly long anterior process that curves sharply inwards through about 90°; the posterior process is about three-quarters the length of that of the Sb₂ and Sc elements. The Sb₂ elements are bipennate, lack a pronounced cusp, and have a fairly long anterior process that curves gently inwards and downwards. The Sc elements are bipennate, with a pronounced cusp and a short incurved and downcurved anterior process bearing recurved elongate denticles. The anterior process of the Sc₁ element is more tightly incurved than that of the Sc₂, and in some specimens the aboral edge of the anterior process of the Sc₂ is recurved and more hooklike than that of the Sc₁. Posterior inclination of denticles on the posterior processes of the elements decreases from an angle of ~50° (with respect to the posterior process) in Sb₁ elements to ~60°-65° in Sc elements. The denticles of Sb₁ elements are also more strongly incurved.

In addition to the photographs which simulate collapse patterns, we include a stereo pair (figure 26) and an anterior view (figure 27) of our model which illustrate details of architecture not evident in other photographs. The Sa element is the most anterior of the S elements and lies on the sagittal plane with its posterior process approximately horizontal and its cusp vertical (figures 5, 19, 26, 27). It is flanked by four pairs of symmetrically arranged S elements; in sequence, away from the axis these pairs are the Sb₁, Sb₂, Sc₁ and Sc₂ elements. The cusps of the Sb₁ elements are set back ~10% of apparatus length from the Sa cusp and lie ~4% of apparatus length from the sagittal plane. The Sb₂ cusps are ~5% behind the Sa, and ~5.5% from the sagittal plane. The two Sc elements on each side are tightly grouped, their cusps slightly behind that of the Sa, and the cusp of the Sc₂ ~9% of apparatus length from the sagittal plane. Posteriorly, the posterior processes of the Sb and Sc elements terminate ~4 - 5% of apparatus length from the sagittal plane; the posterior processes of the Sb₁ elements are parallel to the sagittal plane, but those of the other elements diverge anteriorly, the Sb₂ elements at ~5°, the Sc elements at ~15° with respect to the sagittal plane.

The vertical disposition of the elements is measured relative to an horizontal datum along the base of the posterior process of the Sa element. The Sb₁ elements are the most ventral in the apparatus (figures 5, 19, 26, 27), and the other elements have progressively more dorsal locations away from the axis. The basal cavity beneath the cusp of each Sb₁ element is ~6% of apparatus length below the datum, that of each Sb₂ element is very slightly above the datum, that of each Sc₁ element ~4% above, and that of each Sc₂ element 10% above. The posterior tips of the Sc₂ elements terminate ~35% of apparatus length above the datum, and apart from the horizontal Sa element, all the S elements are oriented with their posterior process tilted forwards. Relative to the horizontal, this angle decreases from ~45° in the Sb₁ elements though ~35° in the Sb₂ elements to ~30° in the Sc elements. These elements are also inclined inwards; the plane in which the denticles of the posterior process lie is inclined at ~45° to the sagittal plane in Sb₁ elements and increases through to ~60° in Sc elements (figures 7, 26, 27).

The M elements are located above the S elements, the basal cavity of each ~20% of apparatus length above the datum, and ~14% from the sagittal plane; the cusp tips ~9% away from the sagittal plane. The orientation of the M elements is very different to that of the S elements. Each lies with its lateral processes in a plane that is approximately vertical in anterior aspect, but which curves gently inwards when viewed from above. At the posterior of the M element, this plane lies at an average angle of ~30° to the sagittal plane, increasing to 50° at the cusps. Viewed from the side (figures 5, 19), the M elements are pitched gently forwards, but the cusps themselves are directed downwards at ~20° from horizontal.

The Pb elements lie 72% of apparatus length behind the Sa cusp, and the Pa elements at the back of the apparatus, ~28% behind the Pb elements. The element on the left side of each pair is the more posterior of the two (figures 6-9, 13, 16, 17). The long axes of the P elements are approximately vertical, and the oral surfaces of the elements are directed inwards at 90° to the sagittal plane. The dorsalmost tips of the elements lie ~30% of apparatus length above the Sa datum. The Pb elements extend ventrally to ~2% above, and the Pa elements to 10% below the datum.

This reconstruction of apparatus architecture differs from that proposed by Aldridge *et al.* (1987; figure 1e) primarily in the arrangement of the S and M elements, an aspect of their model which they themselves considered in need of further refinement. Their reconstruction placed the S elements in parallel, with approximately equal forward inclination, with no vertical displacement from one element to the next, and with no inward inclination. The M elements flanked the S array, and had a similar general orientation, the long axis parallel to those of the S elements. It is also in the orientations of the S and M elements that our reconstruction differs from Dzik's

hypothesis (1991; figure 1*d*). He considered the S elements to be vertical, their long axes parallel, and their cusp directed inwards at 90° to the sagittal plane; he placed the M elements at the front of the apparatus.

5. SIMULATIONS OF *IDIOGNATHODUS* COLLAPSE PATTERNS

The model of apparatus architecture described above stands or falls according to how closely it can simulate the patterns of element distribution in natural assemblages of *Idiognathodus*. Documentation of the match between the model and assemblages is, therefore, a crucial aspect of this paper. The specimen in figures 2 and 3*a* is the most widely illustrated natural assemblage (originally figured by Du Bois 1943, plate 25, figure 14; see Appendix for subsequent illustrations), primarily because of its clear bilateral symmetry. Previous attempts to simulate the collapse of this assemblage (e.g. Aldridge *et al.* 1987, figure 4.12; Purnell *et al.* 1995, figure 6) have, however, incorrectly identified the left and right sides of the apparatus, and have therefore produced incorrect simulations. As preserved on the specimen part (figure 2) the apparatus has collapsed obliquely, from below and in front towards top and behind. This orientation cannot be simulated photographically (it would require a completely transparent base-board), so our simulation is of the whole apparatus as drawn in the camera lucida (figure 3*a*) with the counterpart on the bottom. Simulating collapse of the apparatus with the principle axes of the model (and the conodont head) oriented at $x=59^\circ$, $y=30^\circ$, $z=8^\circ$ with respect to horizontal, produces the pattern observed in the assemblage. Details such as the overlap between the Pa and Pb elements, the orientation of the S element denticles inwards and towards anterior, the location of the Sc element cusps, and the position of the preserved sinistral M element are all accurately matched in the simulation (figure 3*b*). The main visual differences between the simulation and the specimen arise from the foreshortening of elements caused by the oblique angle of photography; in reality the long axes of elements came to lie on the sea floor during collapse, but this cannot be simulated photographically. Du Bois (1943, plate 25, figure 4) figured another *Idiognathodus* assemblage exhibiting a similar pattern of element arrangement, but reflecting a slightly more posterior angle of collapse ($x=71^\circ$, $y=17^\circ$, $z=9^\circ$).

Figure 4 and figure 5*a* illustrate a lateral collapse, simulated by orienting the model with principle axes at $x=0^\circ$, $y=8^\circ$, $z=82^\circ$ (figure 5*b*). In this orientation, the P elements could probably have fallen either way, but they have come to rest with the more anterior dextral element in front of the sinistral elements. This photograph accurately simulates the relative juxtapositions and orientations of the S and M elements, as shown clearly by the Sa, Sb and M elements. The slightly steeper forward inclination of the S elements in the assemblage probably reflects post mortem reorientation of element long axes as they came to lie on the sea floor. *Idiognathodus* assemblages with a similar pattern of element arrangement, reflecting similar collapse orientation have been figured by Du Bois (1943, plate 25, figure 17; plate 25, figures 3 & 11, a slightly more posterior collapse, $x=29^\circ$, $y=3^\circ$, $z=61^\circ$) and Avcin (1974, plate 2, figure 12).

Although the lack of a counterpart and probable burial of some elements beneath others means that only eight elements of the apparatus are evident in the assemblage shown in figures 6 and 7*a*, the pattern of element arrangement exhibited by the specimen is accurately simulated by photographing the model from behind, to the left and slightly below, equivalent to the principle axes being oriented at $x=67^\circ$, $y=14^\circ$, $z=18^\circ$ at the time of collapse (figure 7*b*). Similar *Idiognathodus* assemblages have been figured by Du Bois (1943, plate 25, figure 5, $x=67^\circ$, $y=10^\circ$, $z=21^\circ$; figure 13, $x=64^\circ$, $y=5^\circ$, $z=26^\circ$) and Avcin (1974, plate 2, figure 19, $x=71^\circ$, $y=9^\circ$, $z=17^\circ$, reillustrated by Aldridge *et al.* 1987, figure 4.4).

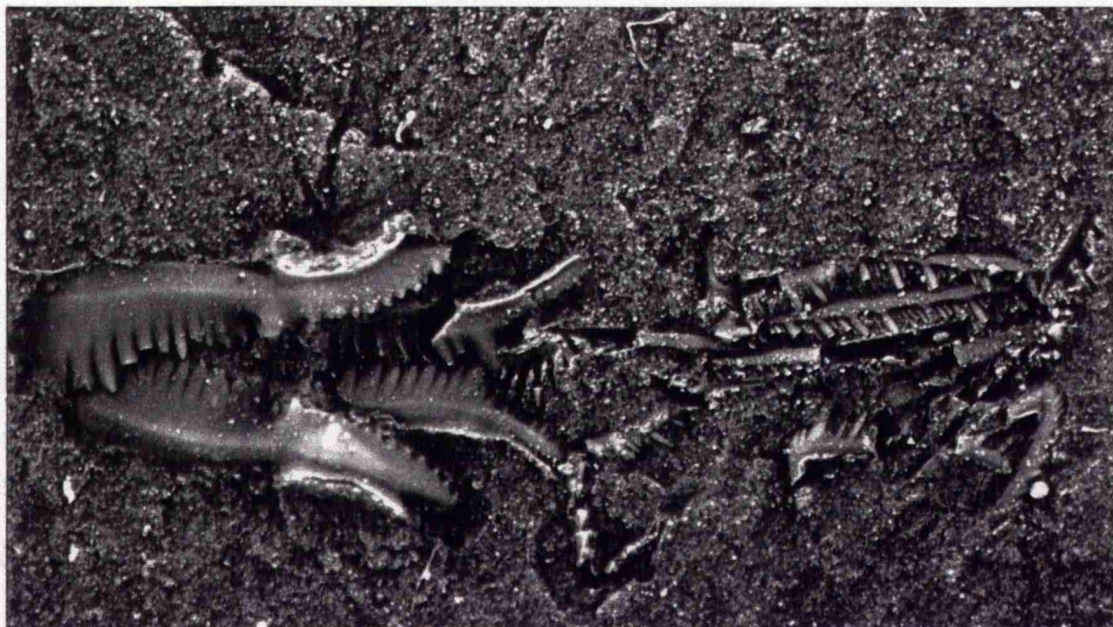


Figure 2. Natural assemblage of *Idiongnathodus* from the Pennsylvanian Modesto Formation, Bailey Falls, Illinois, USA; specimen UI X-1480, originally figured by Du Bois (1943; see Appendix for subsequent illustrations). All four P elements, the remains of at least 6 S elements, and one M element are preserved in the part; counterpart not illustrated. See figure 3A for scale.

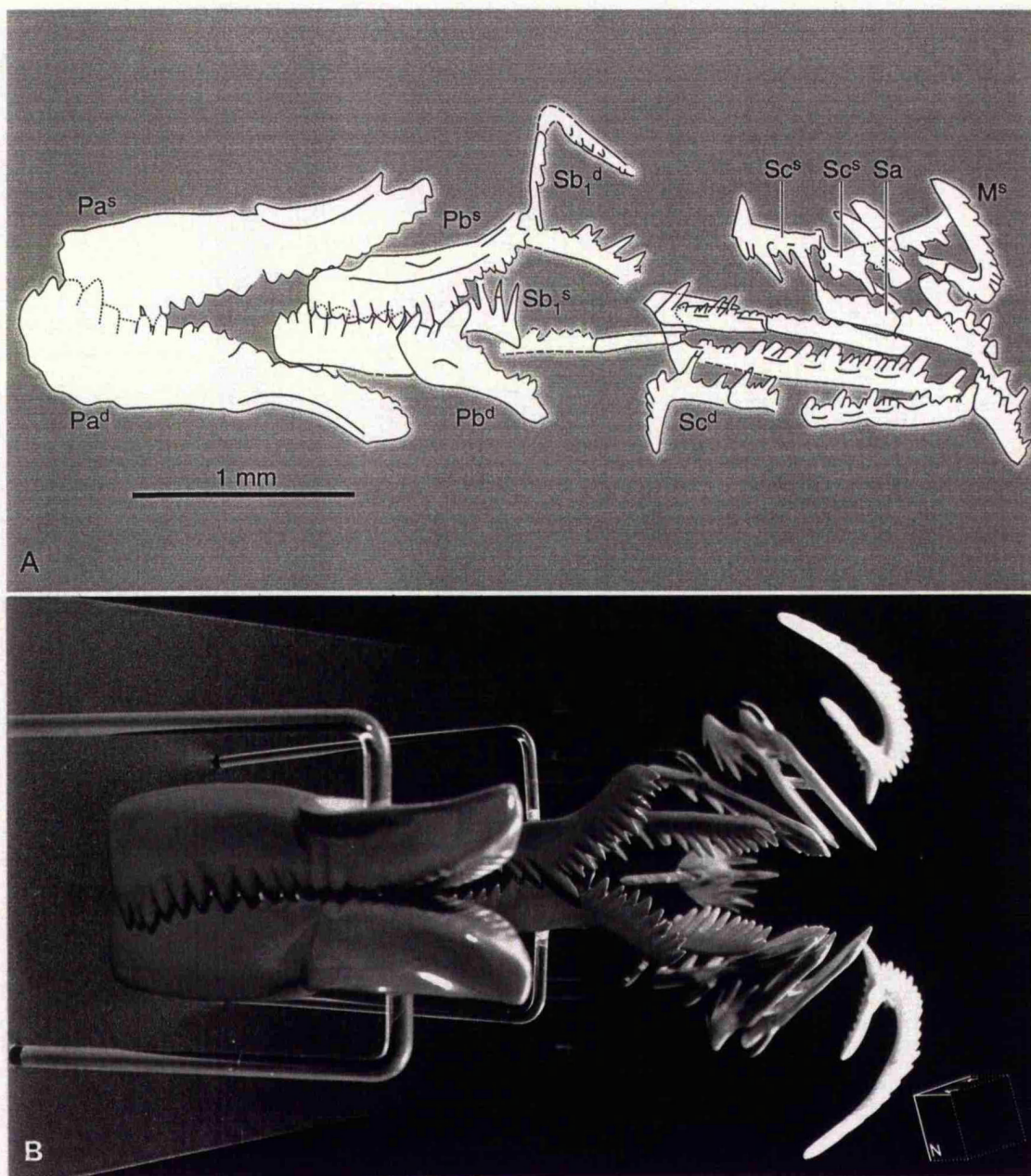


Figure 3. A, composite camera lucida drawing of specimen UI X-1480, counterpart and part (counterpart on bottom). B, photograph of model taken from above, behind and slightly to left to simulate collapse pattern of UI X-1480; small cube indicates orientation of principle axes of apparatus relative to horizontal sea floor at time of collapse, $x=59^\circ$, $y=30^\circ$, $z=8^\circ$.

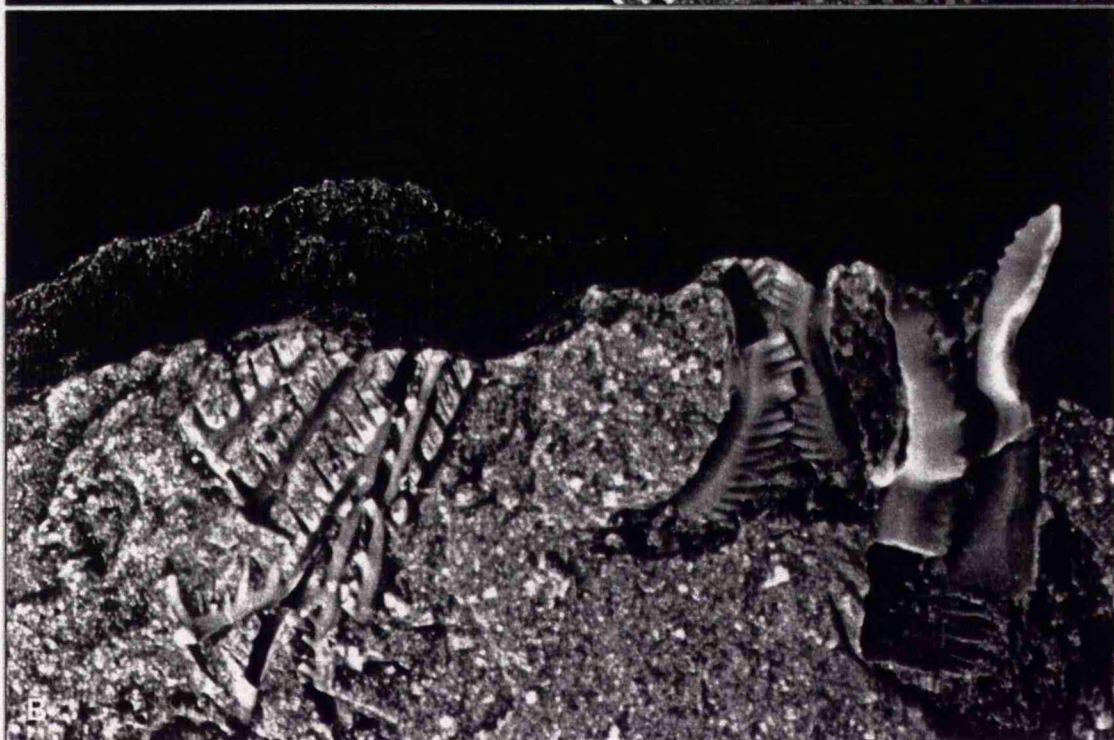
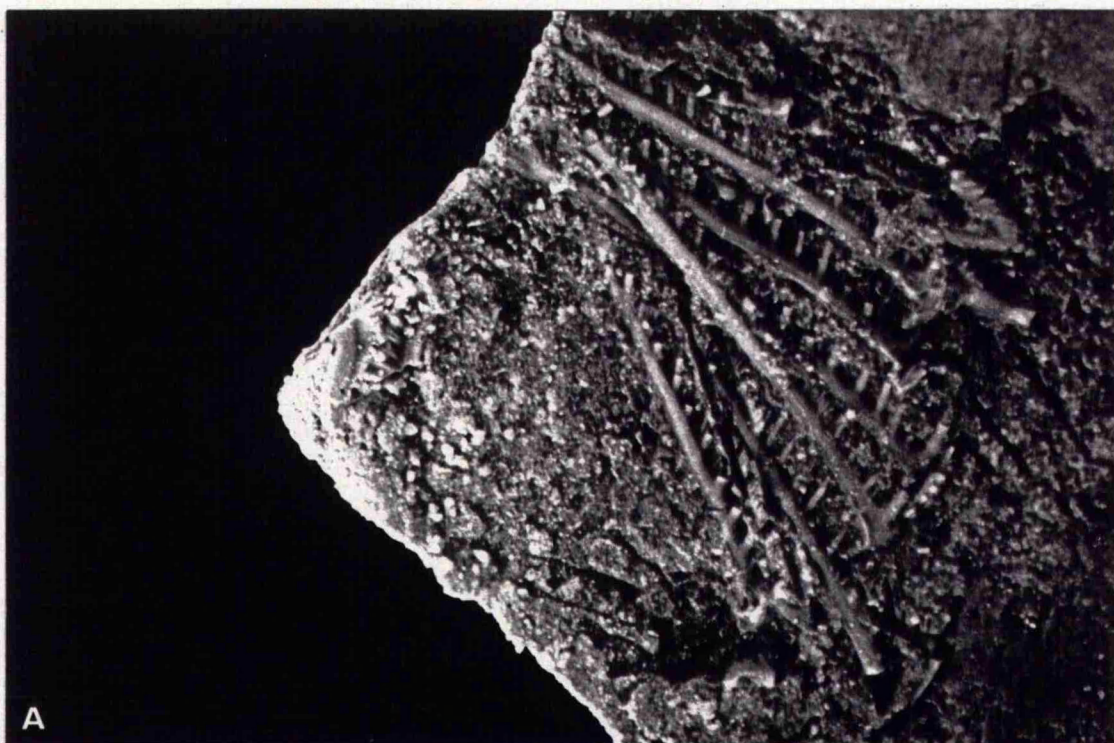


Figure 4. Natural assemblage of *Idiognathodus* from the Pennsylvanian Modesto Formation, Bailey Falls, Illinois, USA; specimen pcjd5. A, part; B, counterpart; see figure 5A for scale.

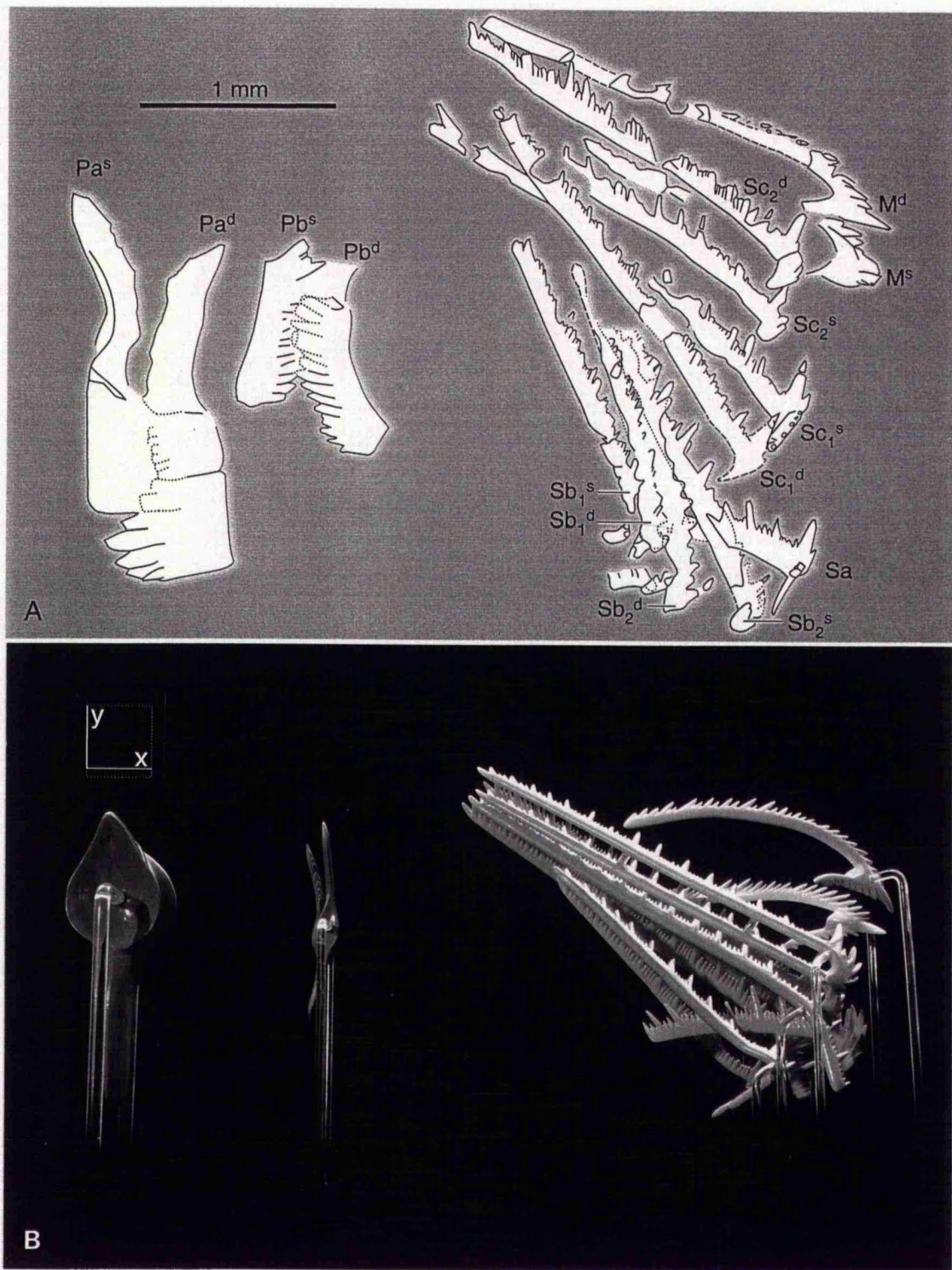


Figure 5. A, composite camera lucida drawing of specimen pcjd5, counterpart and part (counterpart on bottom). B, photograph of model taken from right side and slightly below to simulate collapse pattern of pcjd5; small cube indicates orientation of principle axes of apparatus relative to sea floor at time of collapse, $x=0^\circ$, $y=8^\circ$, $z=82^\circ$.

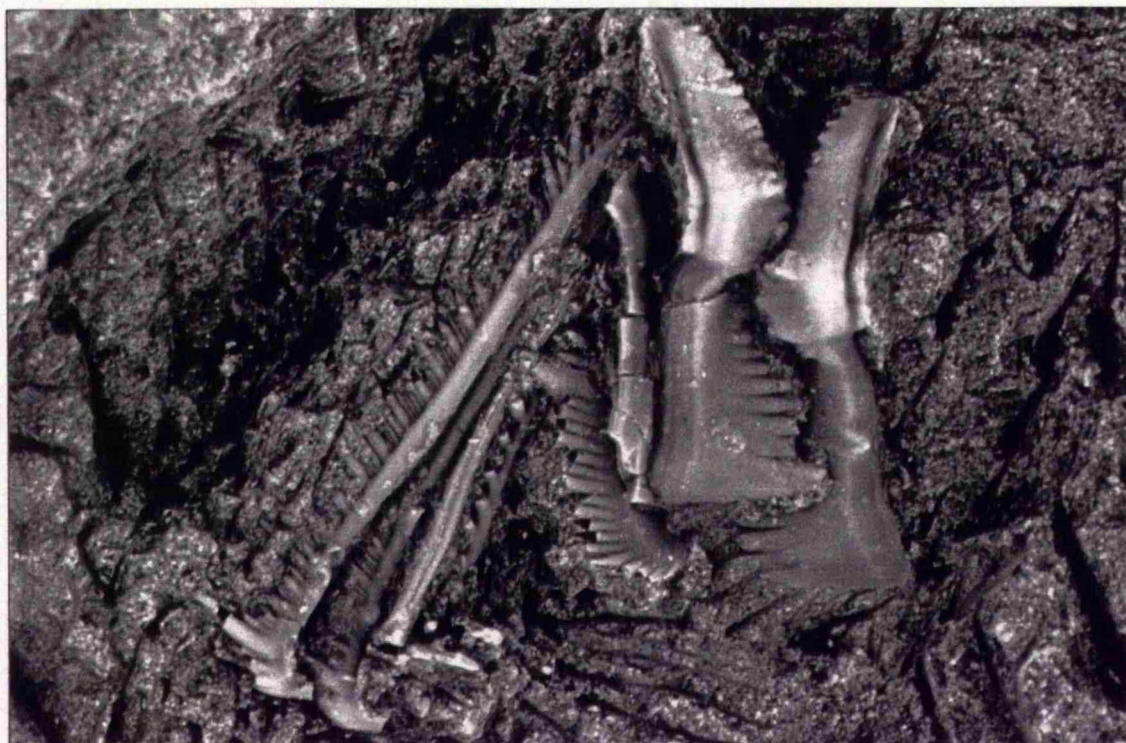


Figure 6. Natural assemblage of *Idiognathodus* from the Pennsylvanian Modesto Formation, Bailey Falls, Illinois, USA; specimen pcjd3. P elements and four S elements are preserved on the part; no counterpart. See figure 7A for scale.

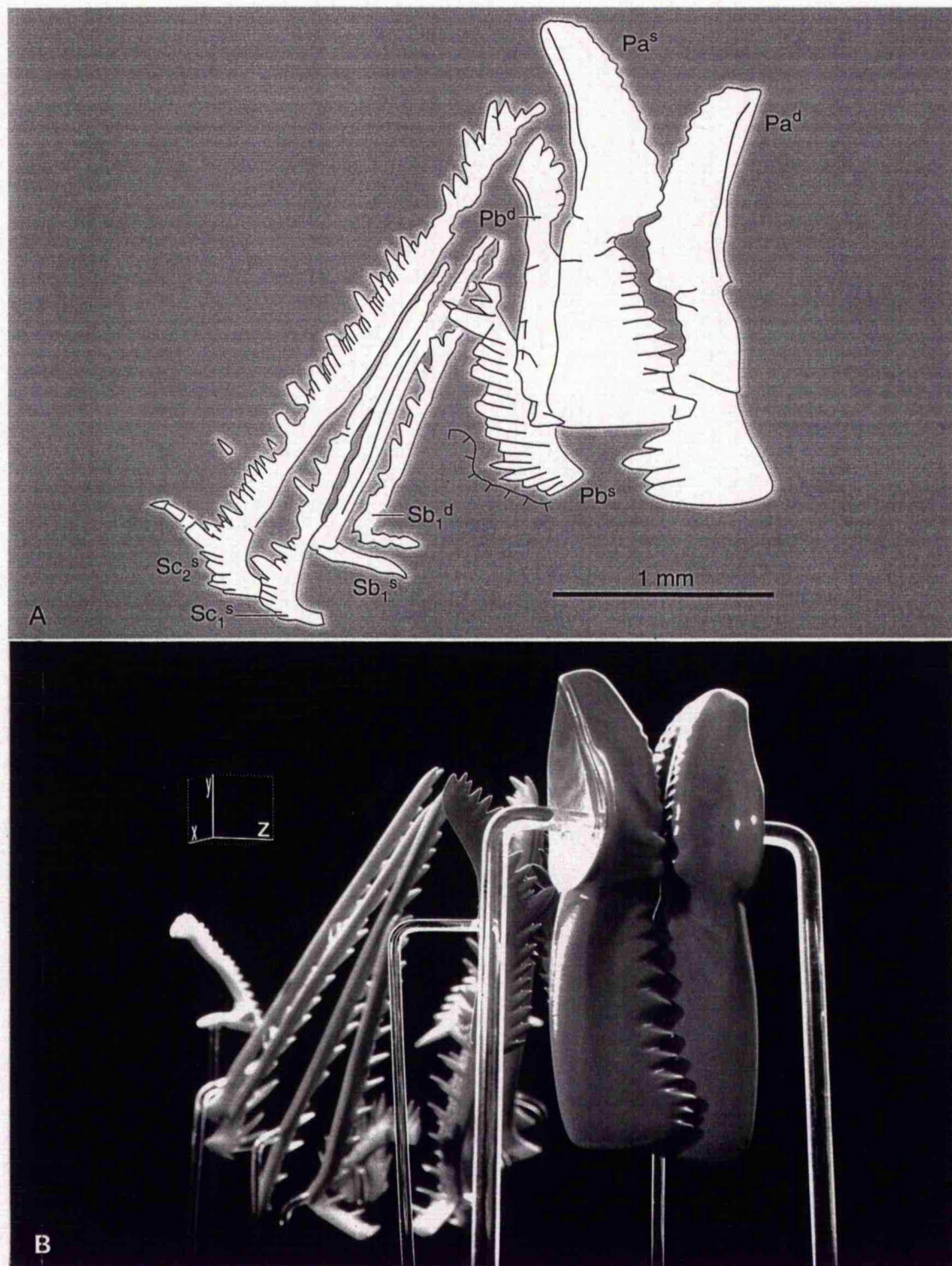


Figure 7. A, camera lucida drawing of specimen pcjd3. B, photograph of model taken from behind, left and slightly below to simulate collapse pattern of pcjd3; small cube indicates orientation of principle axes of apparatus relative to horizontal sea floor at time of collapse, $x=67^\circ$, $y=14^\circ$, $z=18^\circ$.

The assemblage illustrated in figures 8 and 9a is accurately simulated by photographing the model from behind and to the right, the principle axes of the apparatus oriented at $x=43^\circ$, $y=4^\circ$, $z=47^\circ$ (figure 9b). The dextral Sb elements are not preserved on the specimen (which lacks a counterpart), but the correspondence between positions and orientations of the remainder of the elements in the fossil and the model is very close. The sinistral M element underlies all the S elements and its distal extremity can be seen protruding from behind, towards the Pb elements in both the assemblage and the model. The dextral M element, oriented at the time of collapse with its long axis almost 90° to the sea floor, has broken part way down the process, the two parts coming to lie parallel to bedding in the orientations one would predict from their orientations in the model. The spaces between the Pa and Pb elements, and between the dextral Pb and the sinistral M element evident in the simulation were closed up as the elements came to lie on the sea floor. At this angle of collapse, all the S elements have their denticles directed anteriorly, with the possible exception of the dextral Sb1 element, the anterior process of which may have brought the element to lie with its denticles facing into the sea floor or posteriorly. Du Bois (1943) figured two other *Idiognathodus* assemblages with similar collapse patterns (plate 25, figures 3 & 11, $x=29^\circ$, $y=3^\circ$, $z=61^\circ$; figure 12, $x=62^\circ$, $y=5^\circ$, $z=28^\circ$).

The pattern of element position and orientation preserved in the specimen shown in figures 10 and 11a is matched almost exactly by simulating oblique collapse from above, right, and slightly behind, with the principle axes at $x=12^\circ$, $y=43^\circ$, $z=44^\circ$ (figure 11b). The unusual arrangement of the M elements, at first sight anomalous in having the sinistral M parallel to the S elements, but the dextral M lying across them, is faithfully reproduced in the simulation. The locations of the S elements, those on the sinistral side lying above and behind their dextral counterparts, is reproduced accurately, with the sinistral Sb2 element, for example, located in the space between the sinistral Sc1 and the dextral Sc2 in both the fossil and the simulation. The P elements are lying with the sinistral member of each pair offset above and behind the other. A similar orientation of collapse is recorded by the specimen figured by Avcin (1974, plate 1, figure 8, plate 2, figure 1, $x=1^\circ$, $y=40^\circ$, $z=50^\circ$; refigured by Aldridge *et al.* 1987, figure 4.8A).

A photograph of the model from front, left and below, with principle axes at $x=33^\circ$, $y=19^\circ$, $z=49^\circ$ relative to sea floor at the time of collapse (figure 13b) simulates the pattern seen in figures 12 and 13a. The sinistral S and M elements lie above and behind their dextral counterparts, with the cusp region of the Sa element overlying the cusps of the dextral Sb2 and Sc elements. Identification of the Sb2, Sc1 and Sc2 elements on the dextral side of this assemblage is based on their stacking order, as breakage of the anterior processes renders morphologically based determination impossible. The sinistral Pb and Pa elements lie above and behind the dextral elements of the pair. The assemblage figured by Aldridge and Briggs (1986, figure 5) exhibits a similar pattern of apparatus collapse ($x=36^\circ$, $y=8^\circ$, $z=53^\circ$).

These illustrations serve only as examples. Our model can also account for the patterns of element arrangement seen in other natural assemblages of *Idiognathodus* (see Appendix), but the figured examples alone demonstrate that our apparatus model passes the test of being able to simulate the range of different element arrangements in natural assemblages of *Idiognathodus*. Furthermore, the fidelity with which photographs of our reconstruction reproduce the patterns exhibited by fossils which reflect different orientations of collapse provides compelling evidence that our model is accurate. Given the number of variables involved, and the complexity of the apparatus, it is inconceivable that a significantly different apparatus architecture could produce equally accurate simulations. We are, therefore, confident that the arrangement of elements in our model is extremely close to the *in vivo* skeletal architecture of *Idiognathodus*. But it is also our aim with this paper to evaluate the model as a general

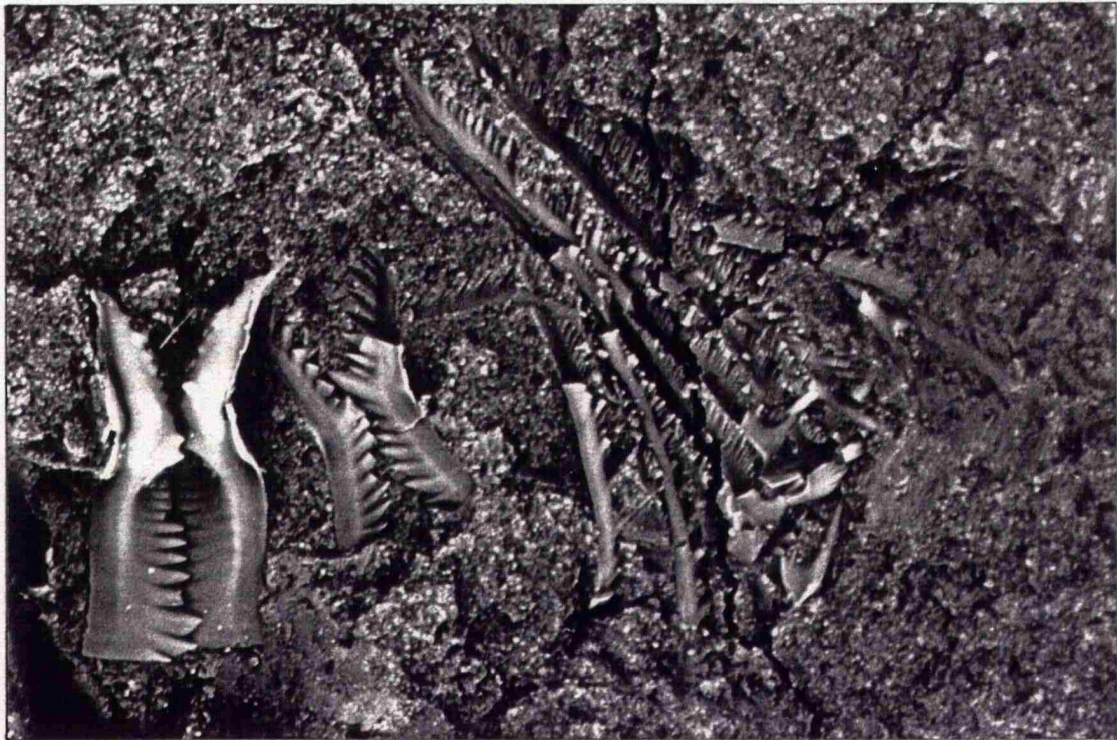


Figure 8. Natural assemblage of *Idiongnathodus* from the Pennsylvanian Modesto Formation, Bailey Falls, Illinois, USA; specimen UI X-6377, originally figured by Du Bois (1943; see Appendix for subsequent illustrations). All four P elements, the remains of seven S elements, and both M elements are preserved on the part; no counterpart. See figure 9A for scale.

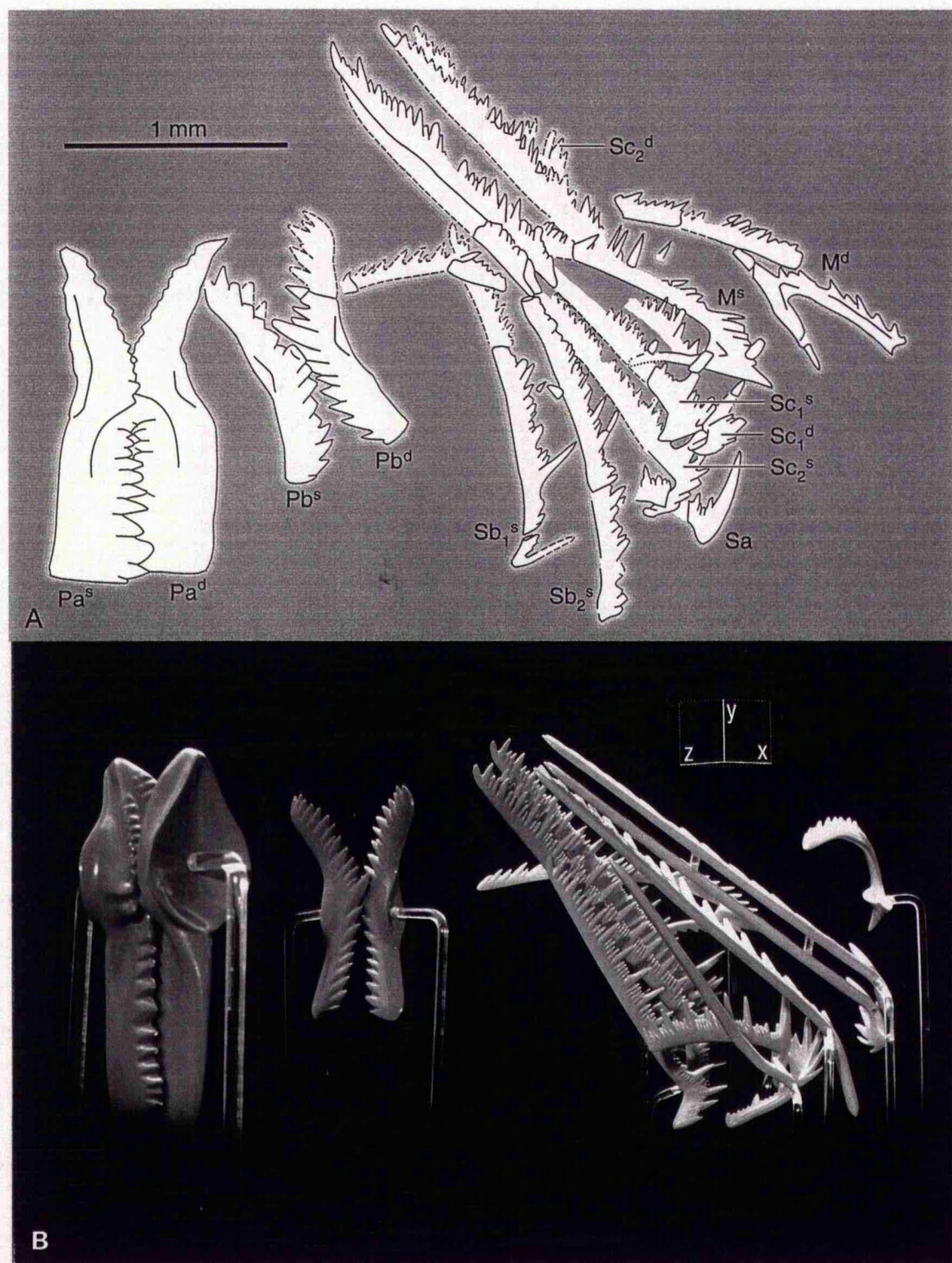


Figure 9. A, camera lucida drawing of specimen UI X-6377. B, photograph of model taken from behind, right to simulate collapse pattern of UI X-6377; small cube indicates orientation of principle axes of apparatus relative to horizontal sea floor at time of collapse, $x=43^\circ$, $y=4^\circ$, $z=47^\circ$.

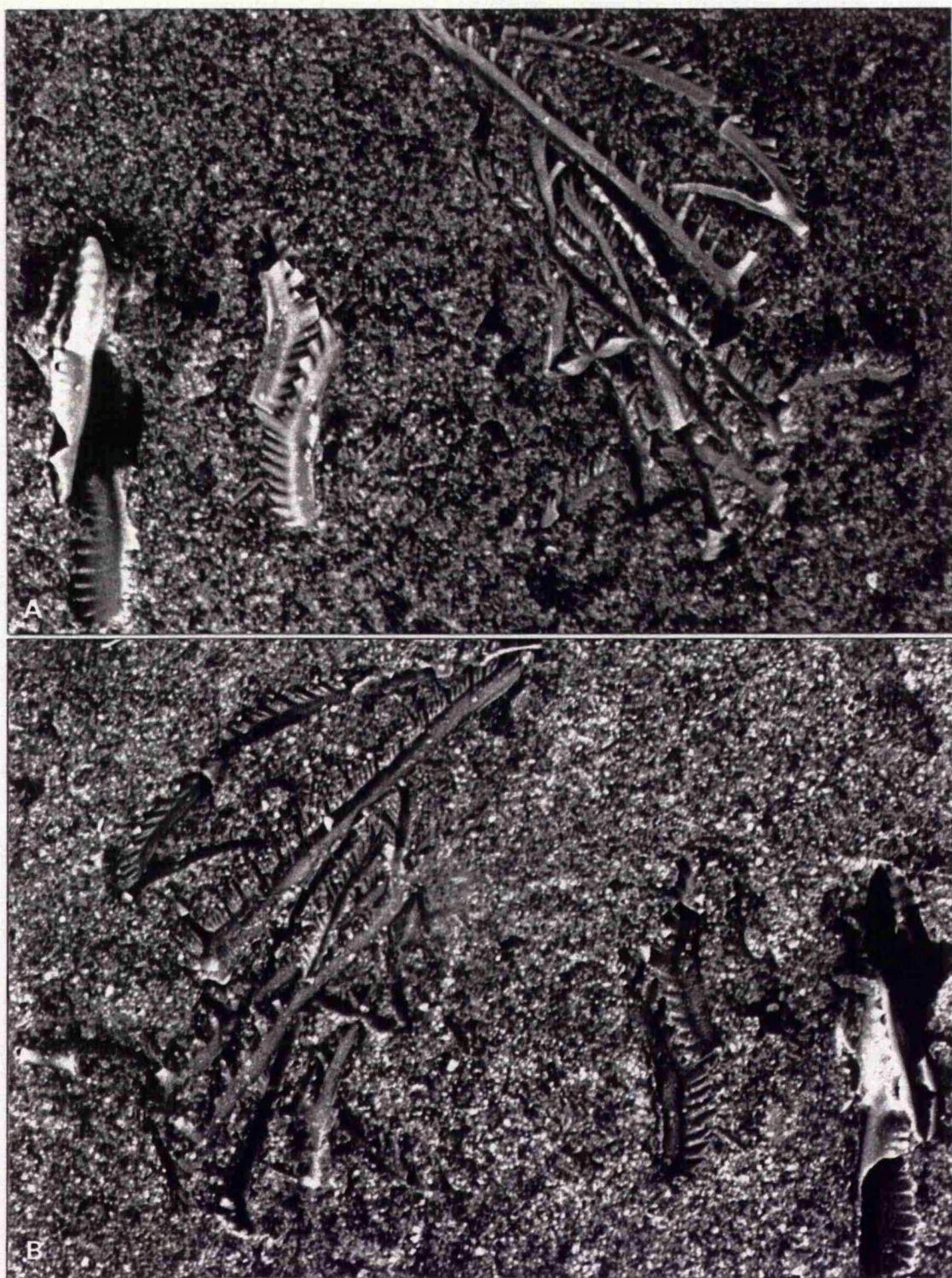


Figure 10. Natural assemblage of *Idiognathodus* from the Pennsylvanian Modesto Formation, Bailey Falls, Illinois, USA; specimen 1059002. A, part; B, counterpart; see figure 11A for scale.

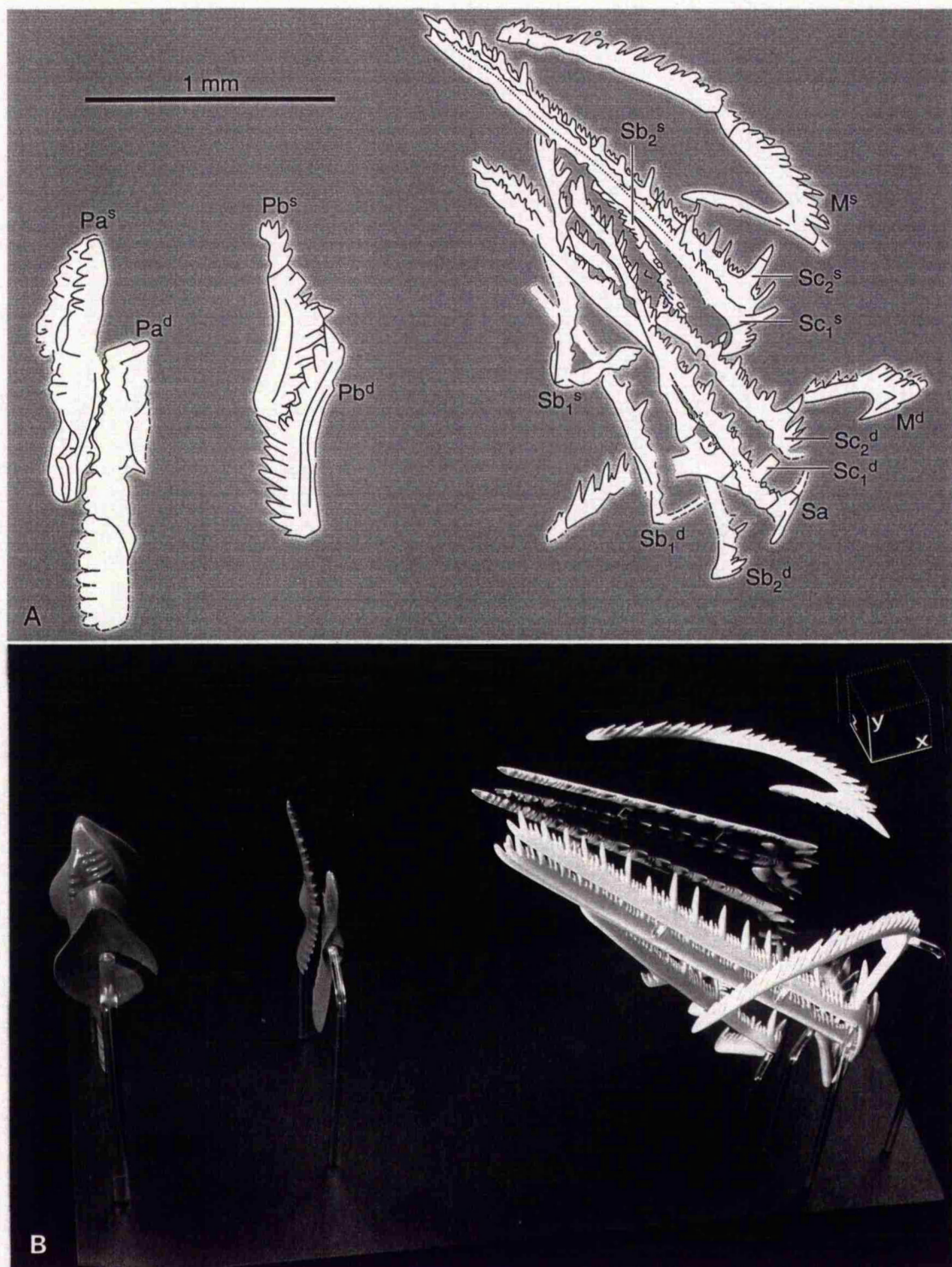




Figure 12. Natural assemblage of *Idiongnathodus* from the Pennsylvanian Modesto Formation, Bailey Falls, Illinois, USA; specimen pcjd8. A, part; B, counterpart; see figure 13A for scale.

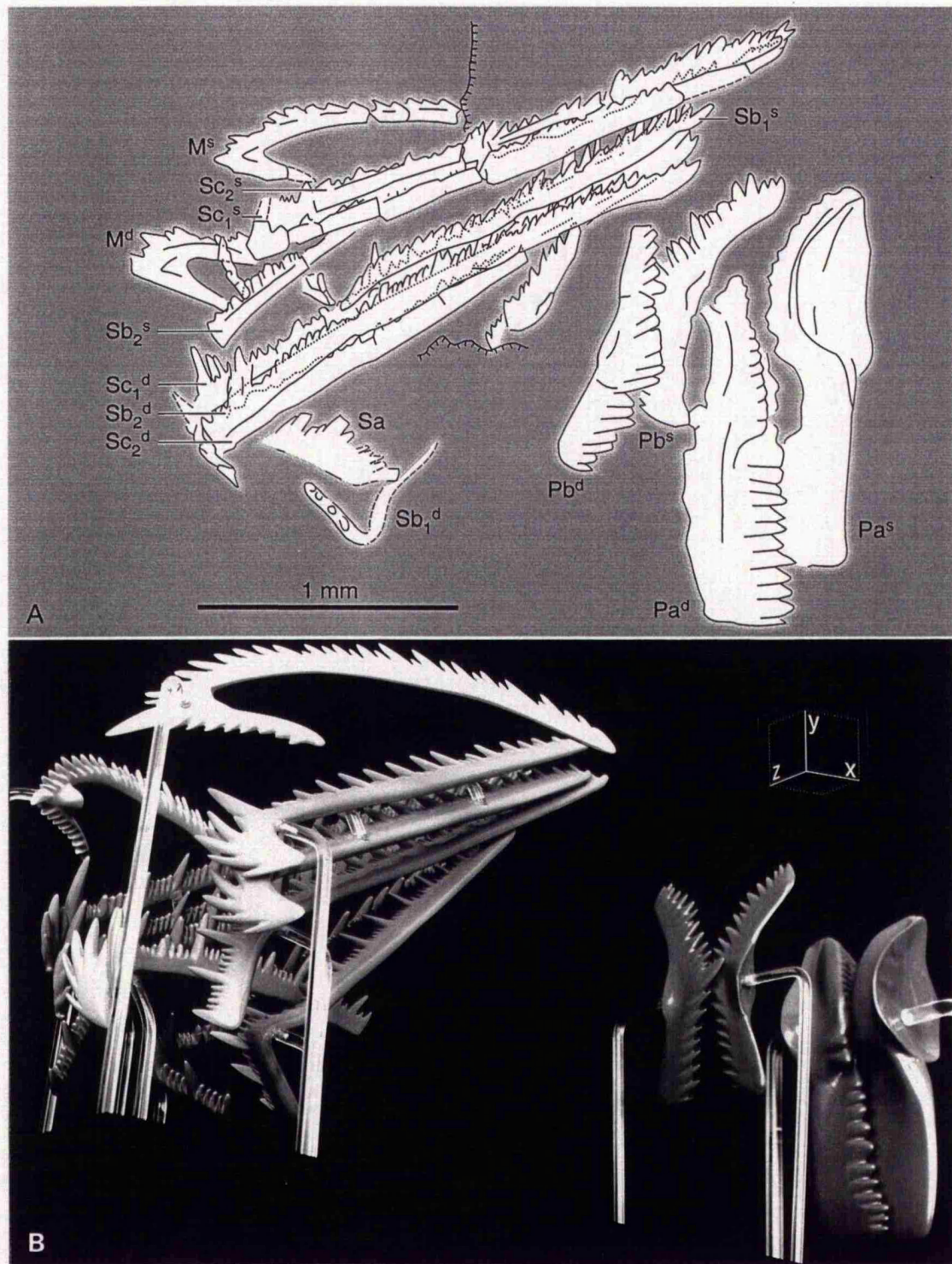


Figure 13. A, composite camera lucida drawing of specimen pcjd8, part and counterpart (part on bottom). B, photograph of model taken from front, left and below to simulate collapse pattern of pcjd8; small cube indicates orientation of principle axes of apparatus relative to horizontal sea floor at time of collapse, $x=33^\circ$, $y=19^\circ$, $z=49^\circ$.

hypothesis of the skeletal architecture of ozarkodinid conodonts, and we have therefore attempted to simulate the collapse patterns observed in a variety of other ozarkodinid taxa.

6. COLLAPSE PATTERNS OF OTHER TAXA AND A GENERAL MODEL OF ARCHITECTURE

(a) Collapse patterns of other ozarkodinid taxa

Schmidt (1934) was the first to illustrate complete natural assemblages of conodonts, and although the specimen illustrated in figures 14 and 15a is lost, it is significant because of its strong influence on early models of apparatus arrangement. It is a specimen of *Gnathodus* (probably *G. bilineatus*), and although the pattern of element arrangement is very uncommon, a photograph of the model from front, left and above, with principle axes of the apparatus at $x=30^\circ$, $y=60^\circ$, $z=4^\circ$ relative to the sea floor, accurately simulates the assemblage (figure 15b). Figures 16 and 17a also illustrate an assemblage of *G. bilineatus*, and this pattern of element arrangement, similar to that shown by the specimen of *Idiognathodus* in figures 12 and 13, is accurately reproduced by a photograph taken from front, left and below, simulating collapse with principle axes at $x=33^\circ$, $y=14^\circ$, $z=54^\circ$.

Natural assemblages of *Gnathodus* have been illustrated by a number of authors, and these can also be simulated by photographs of the model. For example, the element arrangement in a specimen figured by Schmidt (1934, figure 3, plate 6 figure 3) is similar to that simulated in figure 25b (but from behind, so that the Pa elements have collapsed forwards; $x=27^\circ$, $y=59^\circ$, $z=14^\circ$). The arrangement of a specimen figured by Norby (1976, plate 8, figure 5) is similar to that in figure 23 ($x=37^\circ$, $y=38^\circ$, $z=31^\circ$); another of his assemblages (Norby 1976, plate 8, figure 2; also figured by Sweet 1988, p. 2) is similar to that simulated in figure 3b, but with a slight offset and a higher angle of collapse ($x=65^\circ$, $y=18^\circ$, $z=17^\circ$), so that it approaches an orientation similar to that shown in figure 7b. Two specimens (Norby 1976, plate 8, figure 1, plate 8, figure 7), although partially disrupted, are comparable to the arrangement simulated in figure 7b, as is a specimen figured by Varker (1994, plate 1, figure 7; $x=74^\circ$, $y=16^\circ$, $z=3^\circ$). Varker (1994, plate 1, figure 4) also figured a specimen with a collapse orientation between that of figures 3b and 25b ($x=56^\circ$, $y=21^\circ$, $z=25^\circ$). Figure 6 of Schmidt and Müller (1964; $x=37^\circ$, $y=1^\circ$, $z=53^\circ$) is similar to the arrangement simulated in figure 9b, and Purnell (1994, figure 2B) figured one of Norby's specimens, the arrangement of which is very close to that simulated in figure 25b (see Appendix for further examples).

From the accuracy with which the model can simulate these natural assemblages it is evident that the apparatus architecture of *Gnathodus* did not differ in any significant respect from that of *Idiognathodus*. This close similarity lends support to the hypothesis that these taxa are close phylogenetic relatives (Grayson *et al.* 1991).

Natural assemblages of *Lochriea* are less common than *Idiognathodus* or *Gnathodus*. *Lochriea* is a more distant relative of *Idiognathodus*, but the model can match collapse patterns observed in *Lochriea* assemblages. The specimen from the Schmidt and Müller (1964) collection illustrated in figures 18 and 19a, for example, is reproduced by photographing the model from the side and very slightly in front, simulating collapse with principle axes at $x=10^\circ$, $y=3^\circ$, $z=80^\circ$. An interesting feature of this apparatus is that the S elements on the dextral side exhibit slight deviations from their primary positions, whereas those on the sinistral side do not, strongly suggesting that this apparatus collapsed onto its left side. Norby (1976) illustrated several assemblages of *Lochriea*, at least two of which are collapses without significant disruption. The arrangements of elements in these specimens (Norby 1976, plate 14, figures 8, 9) are very similar to the collapse patterns simulated in figures 21b and 25b respectively (see Appendix).

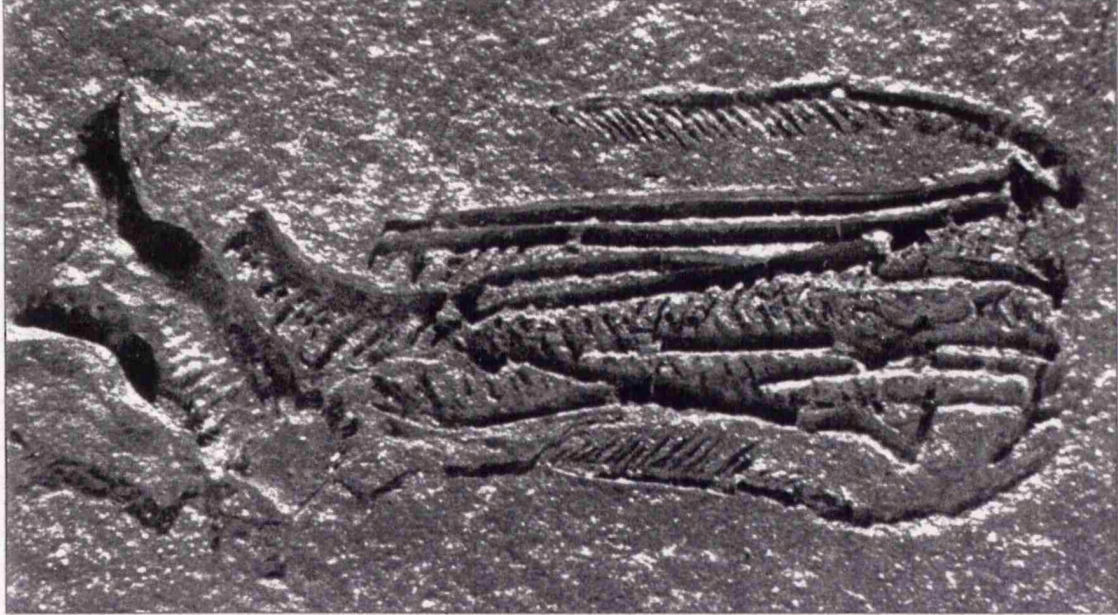


Figure 14. Natural assemblage of *Gnathodus* from the lower Namurian, Hemer, Germany; specimen lost during World War II, originally figured by Schmidt (1934; see Appendix for subsequent illustrations). Molds of all fifteen elements of the apparatus are preserved on the part; counterpart not illustrated. Photograph reproduced with permission from Schmidt 1934, pl. 6, fig. 1. See figure 15A for scale.

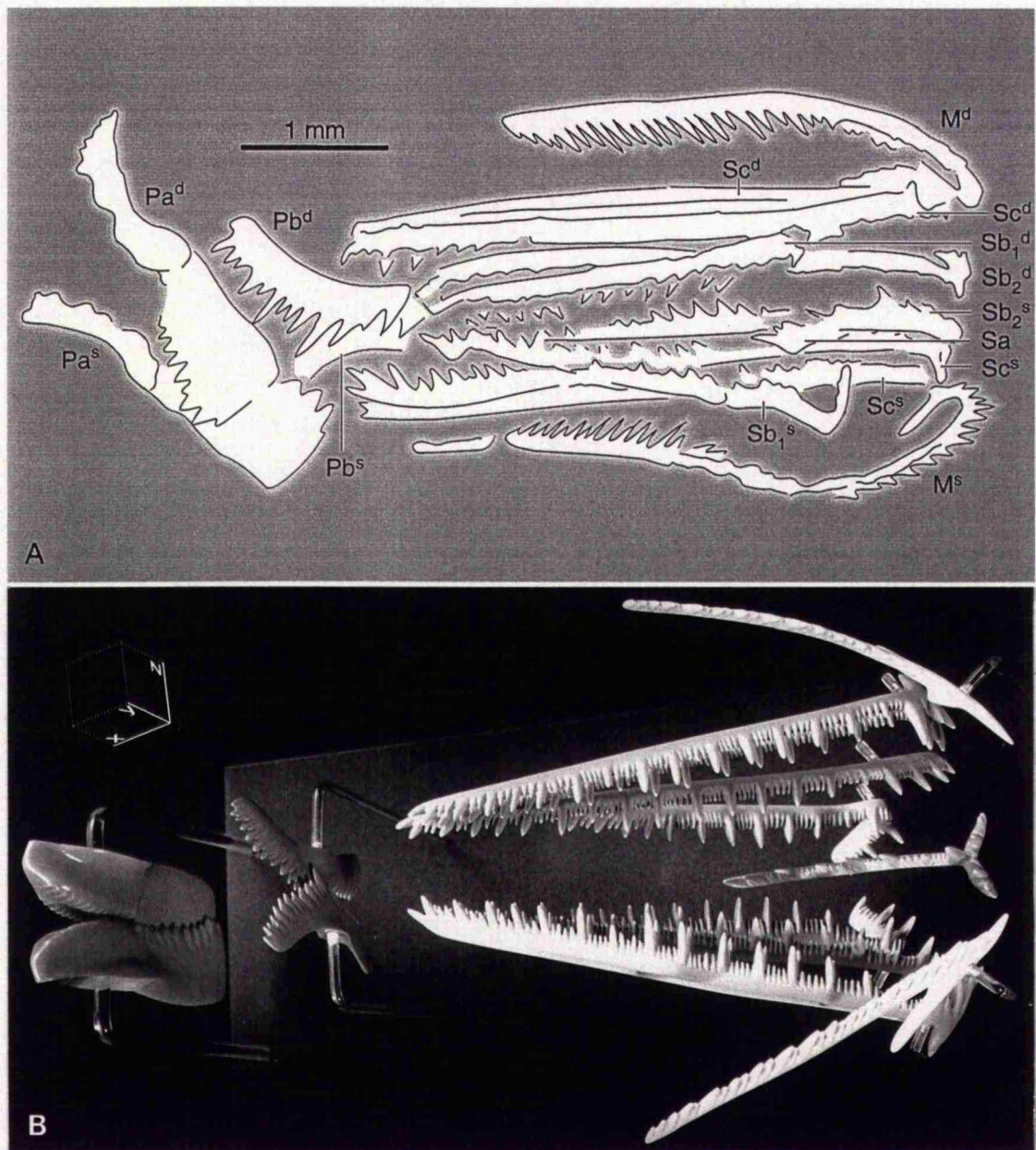


Figure 15. A, drawing of specimen Schmidt's *Gnathodus* specimen, part. B, photograph of model taken from front, left and above to simulate collapse pattern of Schmidt's specimen; small cube indicates orientation of principle axes of apparatus relative to horizontal sea floor at time of collapse, $x=30^\circ$, $y=60^\circ$, $z=4^\circ$. Note that sinistral and dextral in apparatus and model do not correspond; exact match would require photograph to be taken through base board of model.

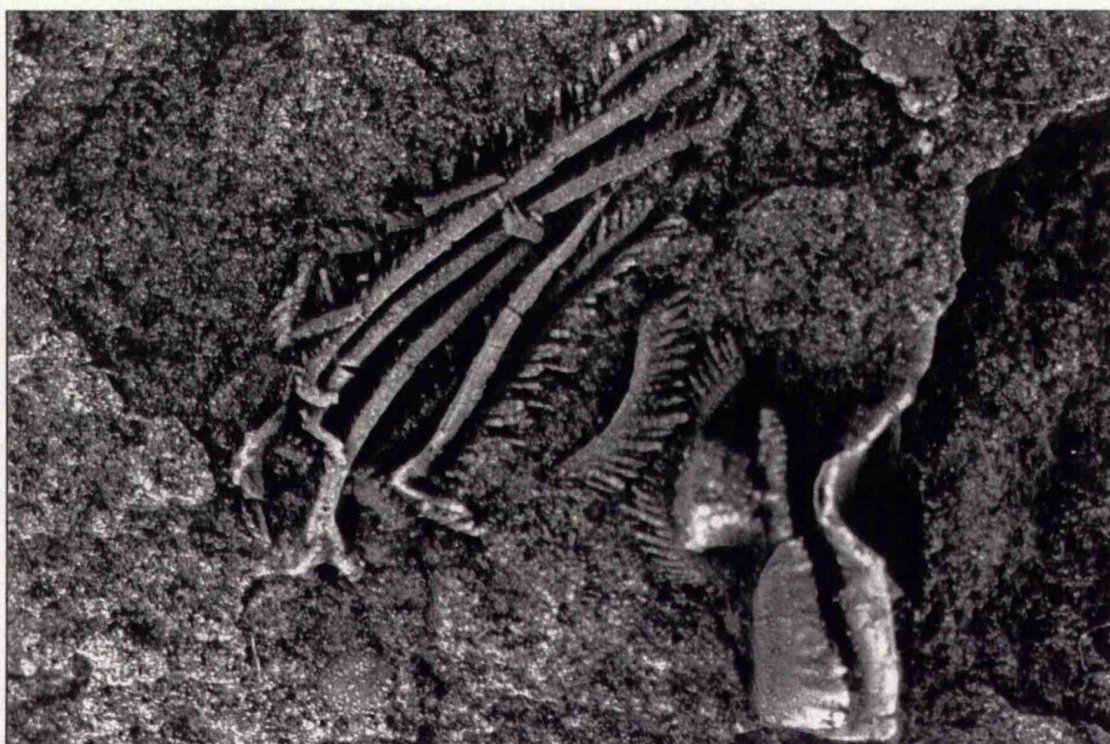
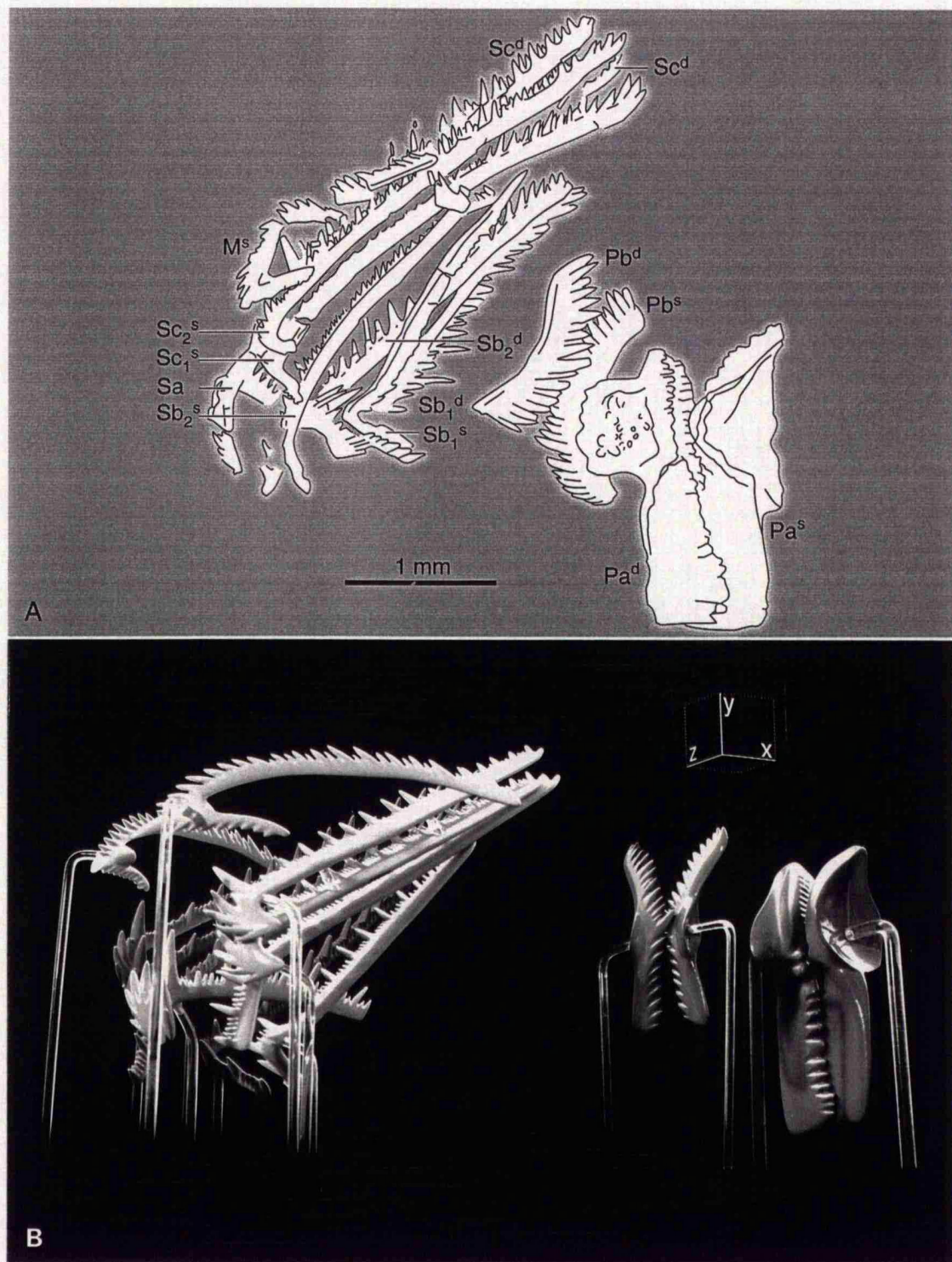


Figure 16. Natural assemblage of *Gnathodus* from the lower Namurian, Hemer, Germany; specimen IMGP Gö 600-44, originally illustrated by Schmidt and Müller (1964; see Appendix for subsequent illustrations). Silicon rubber cast of part preserving molds of all elements except dextral M; counterpart not illustrated. Cast coated with ammonium chloride. See figure 17A for scale.



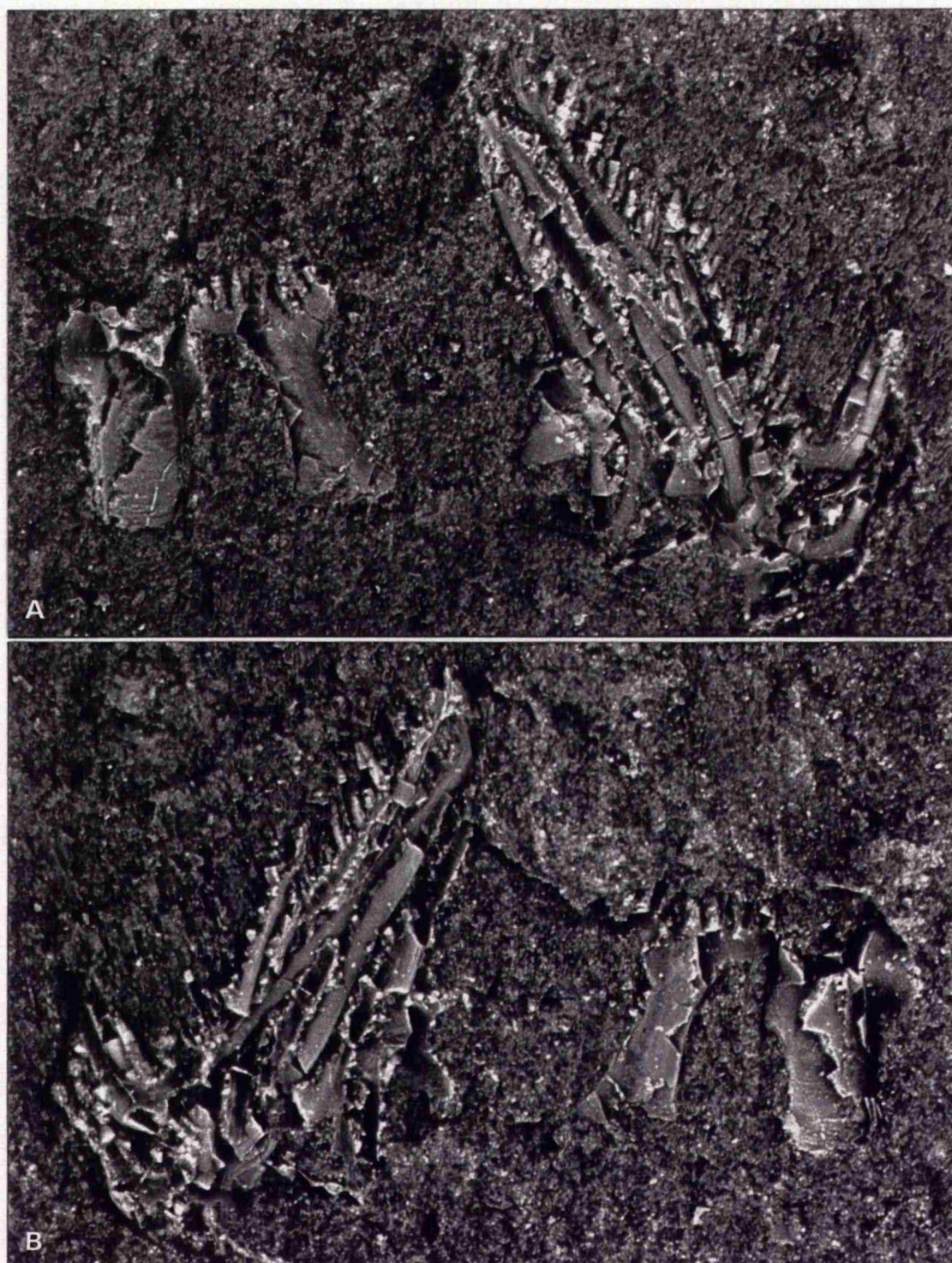


Figure 18. Natural assemblage of *Lochriea* from the Namurian, Hemer, Germany; specimen IMGP Gö 600-36 from collection of Schmidt and Müller (1964). A, part; B, counterpart; see figure 19A for scale.

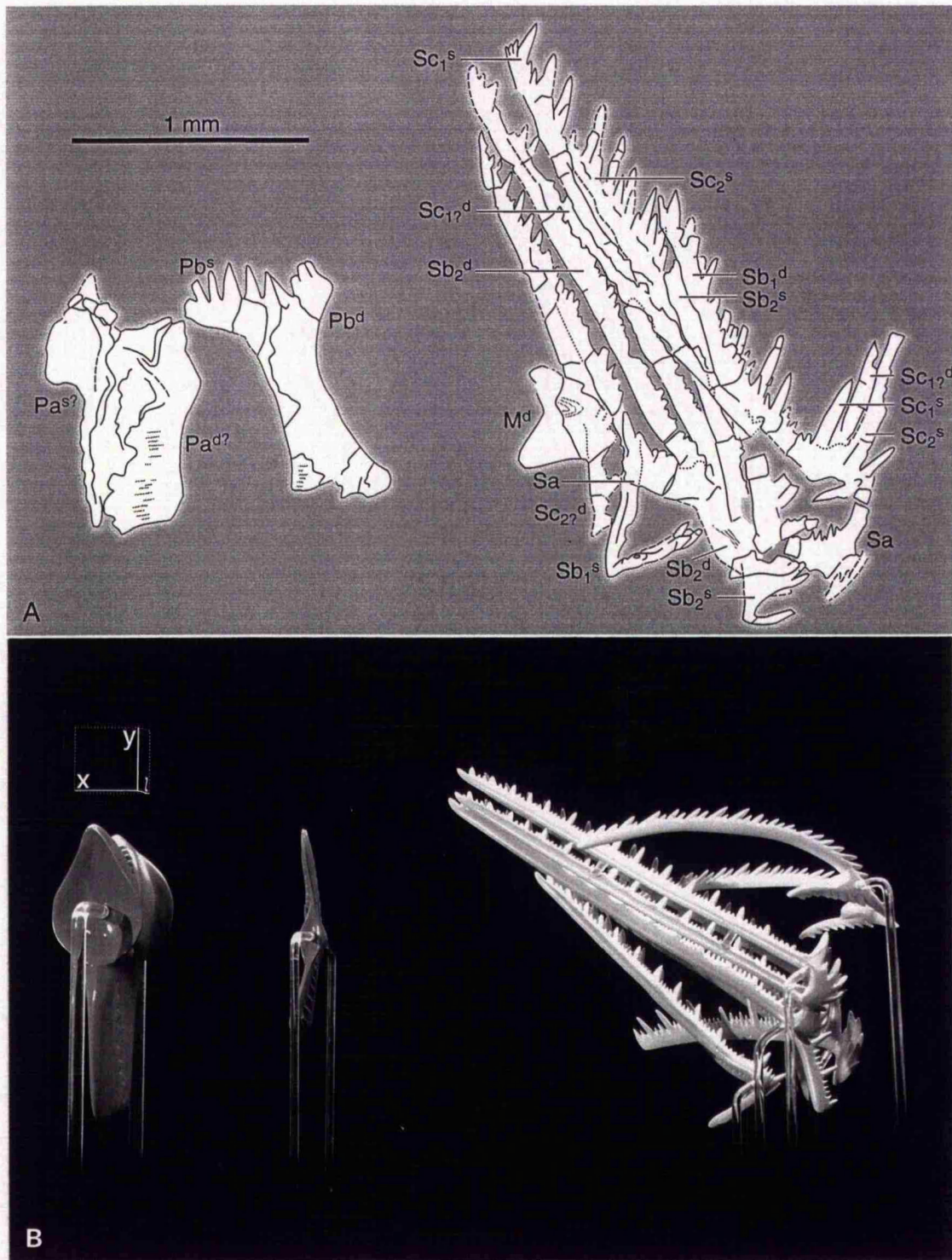


Figure 19. A, composite camera lucida drawing of *Lochriea* specimen IMGP Gö 600-36, counterpart and part (counterpart on bottom). B, photograph of model taken from right side and slightly in front to simulate collapse pattern of IMGP Gö 600-36; small cube indicates orientation of principle axes of apparatus relative to horizontal sea floor at time of collapse, $x=10^\circ$, $y=3^\circ$, $z=80^\circ$.

The ability of the model to simulate natural assemblages of *Lochriea* indicates that the apparatus architecture of *Lochriea* is very similar to that of *Idiognathodus* and *Gnathodus*. Some differences do exist, however, the most significant being the more posterior and slightly more ventral location of the M elements in *Lochriea*. The morphology of M elements in *Lochriea* is very different to that of *Idiognathodus*, and these differences in shape and position suggest that the function of these elements in these taxa was different.

The hypothesis that *Ozarkodina* represents the rootstock from which many members of the Ozarkodinida evolved (Sweet 1988) gives its architecture particular significance. A natural assemblage from the Lower Devonian of Tadjikistan (figures 20, 21) was originally figured by Mashkova (1972) but has subsequently been reillustrated many times (see Appendix). The importance of this specimen for understanding the architecture of ozarkodinid conodonts has long been recognised, and it has been reinterpreted by numerous authors (Dzik 1976, 1986, 1991; Carls 1977; Jeppsson 1979; Aldridge 1987; Nicoll and Rexroad 1987). Our identification of the elements in the assemblage (figure 21a) is based on a re-examination of the original material and differs in detail from all those previously suggested; we identify all the dextral S elements and the Sa element, with only the sinistral Sb elements missing from the assemblage (except for what is probably the posterior process of one of them). Although in terms of element morphology there are clear differences between *Idiognathodus* and *Ozarkodina*, the arrangement of elements is reproduced with good accuracy by photographing the model from the front and below (figure 21b), simulating collapse with principle axes at $x=50^\circ$, $y=20^\circ$, $z=33^\circ$ relative to the sea floor (an orientation similar to that shown in 13b). Clearly the architecture of the apparatus was extremely similar to that of *Idiognathodus*, although the orientation of the posterior processes of the M elements in the assemblage suggests that they may have been more parallel to the S elements than in *Idiognathodus*.

Although incomplete, the natural assemblages of *Ozarkodina* from the Upper Silurian of Indiana (Pollock 1969; Nicoll and Rexroad 1987) also allow the similarities between *Ozarkodina* and other ozarkodinids to be assessed. These assemblages belong to a different species to that illustrated by Mashkova (1972), and have shorter Sb elements, of modified digyrate morphology, rather than the elongate bipennate Sb elements borne by all the taxa discussed so far. In assemblages reflecting lateral and oblique-lateral collapse (e.g. Pollock 1969, plate 111, figures 3, 4, 5, 16; Nicoll and Rexroad 1987, plate 3.4, figures 1, 3, 5) these shorter Sb elements are aligned sub-parallel to the Sc elements, and their original orientation seems to have been similar to the bipennate elements of *Idiognathodus*, with their 'inner lateral' processes (conventional orientation) directed posteriorly and dorsally. The arrangement of elements in several of the assemblages illustrated by Pollock (1969, plate 111, figures 3, 4, 5) is closely simulated by figure 6; another of Pollock's specimens (plate 111, figure 16) exhibits a similar pattern, but reflects collapse from the behind-right rather than left. One of the specimens figured by Nicoll and Rexroad (1987, plate 3.4, figures 1, 3, 5) reflects lateral collapse in an orientation very close to that simulated in figure 5b. The Appendix lists more assemblages of *Ozarkodina* with indications of collapse orientations determined from the model.

Sweet (1988) suggested that many Late Palaeozoic ozarkodinids were descended from *Bispathodus*. The apparatus of this genus is, therefore, of considerable interest, yet natural assemblages of *Bispathodus* have not previously been illustrated. The specimen figured (figures 22, 23a) lies within, and was eaten by a shark (*Cladoseleache*) but it is clearly a natural assemblage of the finest quality, with minimal post-mortem disruption of the apparatus. A photograph of the model from above and in front (figure 23b), simulating collapse with principle axes at $x=10^\circ$, $y=71^\circ$, $z=16^\circ$ matches the assemblage closely. In true collapse the long axes of the P elements would have come to lie parallel to the sea floor, bringing them into the positions seen in the specimen; similarly, the apparent angle of inclination of the S elements would steepen. The greater disruption of S elements on the sinistral

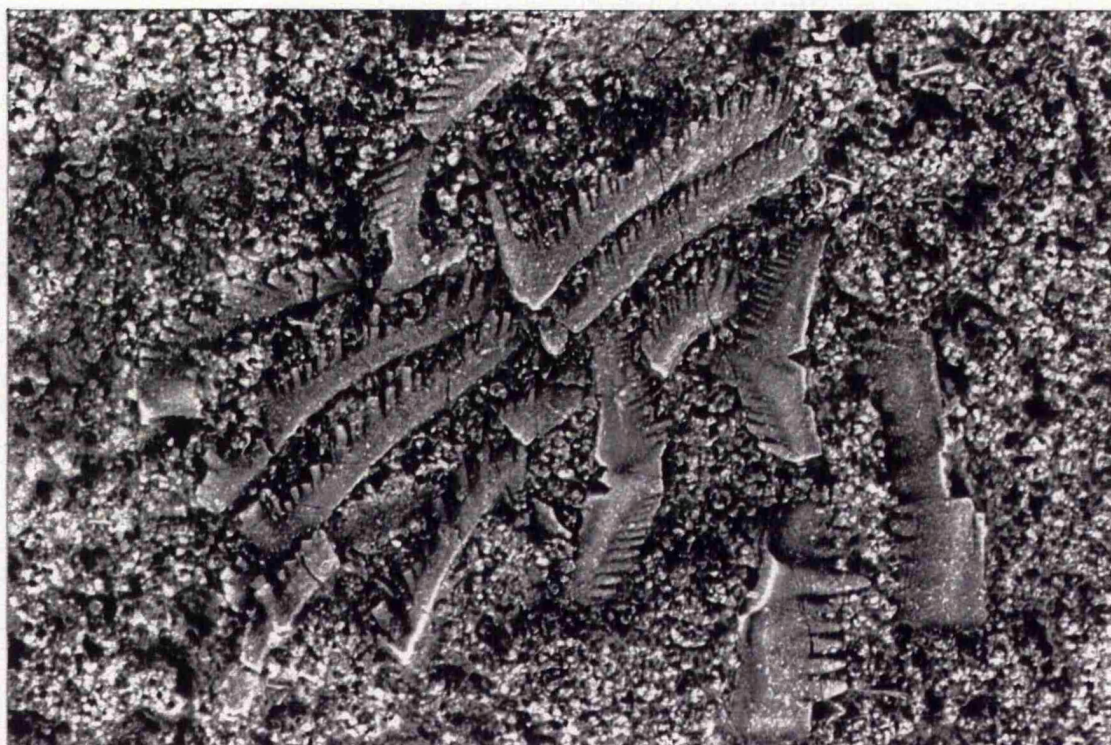


Figure 20. Natural assemblage of *Ozarkodina* from the Lower Devonian, Tadjikistan; specimen CGM 1/10499, originally figured by Mashkova (1972; see Appendix for subsequent illustrations). All P and M elements and 7 S elements are preserved on the part; no counterpart. See figure 21A for scale.

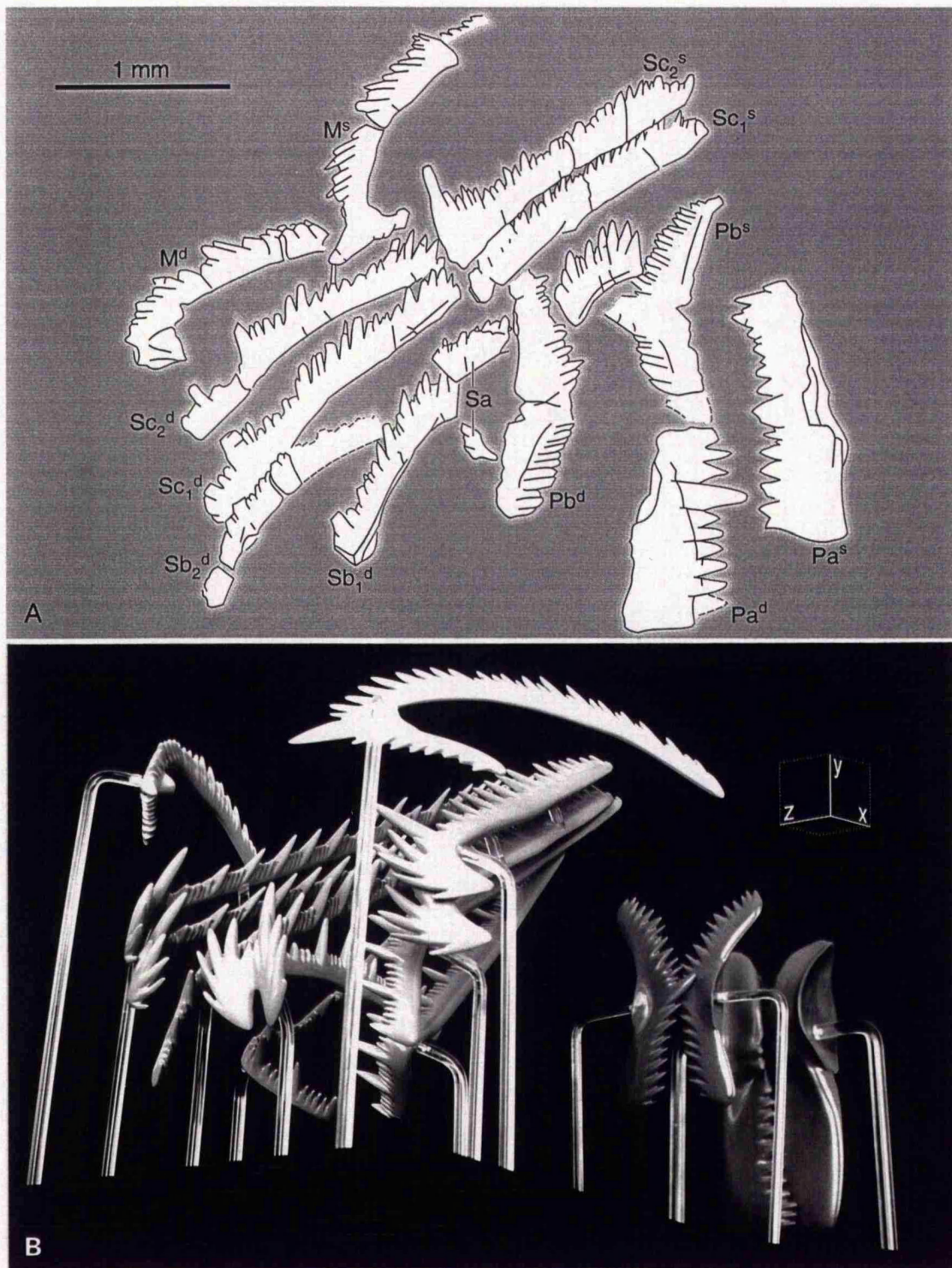


Figure 21. A, camera lucida drawing of specimen *Ozarkodina* CGM 1/10499. B, photograph of model taken from front, left and below to simulate collapse pattern of CGM 1/10499; small cube indicates orientation of principle axes of apparatus relative to horizontal sea floor at time of collapse, $x=50^\circ$, $y=20^\circ$, $z=33^\circ$.

side of the apparatus suggests that collapse was onto the right side; among the dextral S elements the only disruption evident has affected the Sb₁ element, the incurved anterior process of which has caused the element to rotate so that its denticles face those of the other dextral S elements. The vertical stacking of the sinistral S elements produced in this orientation of collapse (see figure 23*b*) is clearly unstable, and in the assemblage the Sb elements have been displaced outwards from the base of the pile. The accuracy and precision with which the pattern of collapse in this assemblage is simulated by the model provides strong evidence that the apparatus architecture of *Bispathodus* did not differ in any significant respect from that of *Idiognathodus*. An extremely similar pattern of apparatus collapse in *Gnathodus* has previously been illustrated by Norby (1976, plate 8, figure 5).

Adetognathus has never been reported as a natural assemblage and the specimen illustrated here (figures 24, 25*a*) has not been figured previously. There is some disruption of the apparatus, particularly affecting the P elements and the sinistral M element, but photographing the model from above and behind (figure 25*b*) simulating collapse with the principle axes at $x=40^\circ$, $y=20^\circ$, $z=43^\circ$ relative to the sea floor accurately simulates the assemblage. There are, therefore, no significant differences in architecture between *Adetognathus* and *Idiognathodus*.

Natural assemblages of a number of other ozarkodinid taxa have previously been figured by several authors, and although we do not reillustrate them, their patterns of apparatus collapse can be simulated by photographs of the model. A full listing appears in the Appendix, but we discuss a few examples here. The specimen of *Hemilistrana* illustrated by Habetin and Knobloch (1981, figure 72) and Dzik (1991, figure 1), although partially disrupted, exhibits a similar collapse pattern to that shown in figure 25*b*, but reflects a higher and more posterior angle of collapse ($x=46^\circ$, $y=28^\circ$, $z=30^\circ$). Two of the assemblages of *Polygnathus* illustrated by Nicoll (1985, figures 3A, 3B) are incomplete, but reflect a lateral collapse orientation similar to that simulated in figure 19*b*. Of particular significance because of their palaeobiological importance are the apparatuses of the conodont animal specimens assigned to *Clydagnathus windsorensis* (Globensky). The specimen illustrated by Briggs *et al.* (1983, figures 1B, 2A, B, C, 3A, B; refigured many times -see Appendix) exhibits an oblique collapse pattern similar to figure 11*b*; the cluster figured by Briggs *et al.* (1983, figure 6) exhibits a lateral collapse pattern similar to figure 19*b*; Aldridge *et al.* (1993, figures 4, 6) illustrated an apparatus with a collapse pattern similar to figure 13*b*, but slightly more lateral ($x=25^\circ$, $y=10^\circ$, $z=63^\circ$); Aldridge *et al.* (1993, figure 9) illustrated an apparatus with an oblique lateral collapse pattern similar to figure 9*b*. There appear to be no significant architectural differences between the apparatuses of *Clydagnathus windsorensis* and *Idiognathodus*.

(b) A general model of ozarkodinid skeletal architecture

Based on all the available natural assemblages, which represent at least five families (*sensu* Sweet 1988) of Silurian, Devonian and Carboniferous age, there is little evidence for significant variation in the apparatus architecture of ozarkodinid conodonts. Apart from subtle differences such as those noted above, the reconstruction based on *Idiognathodus* appears also to be a good model of the skeletal architecture of the apparatus borne by most or all ozarkodinids. The possibility exists that the apparatus of the earliest ozarkodinids was somewhat different to that described above, but there is no evidence to support this hypothesis at present, and the conservatism evident in known material argues against it. Similarly, the possibility that some Permian and Triassic ozarkodinids had apparatuses that differed significantly from that of *Idiognathodus* seems unlikely, but cannot be ruled out altogether.

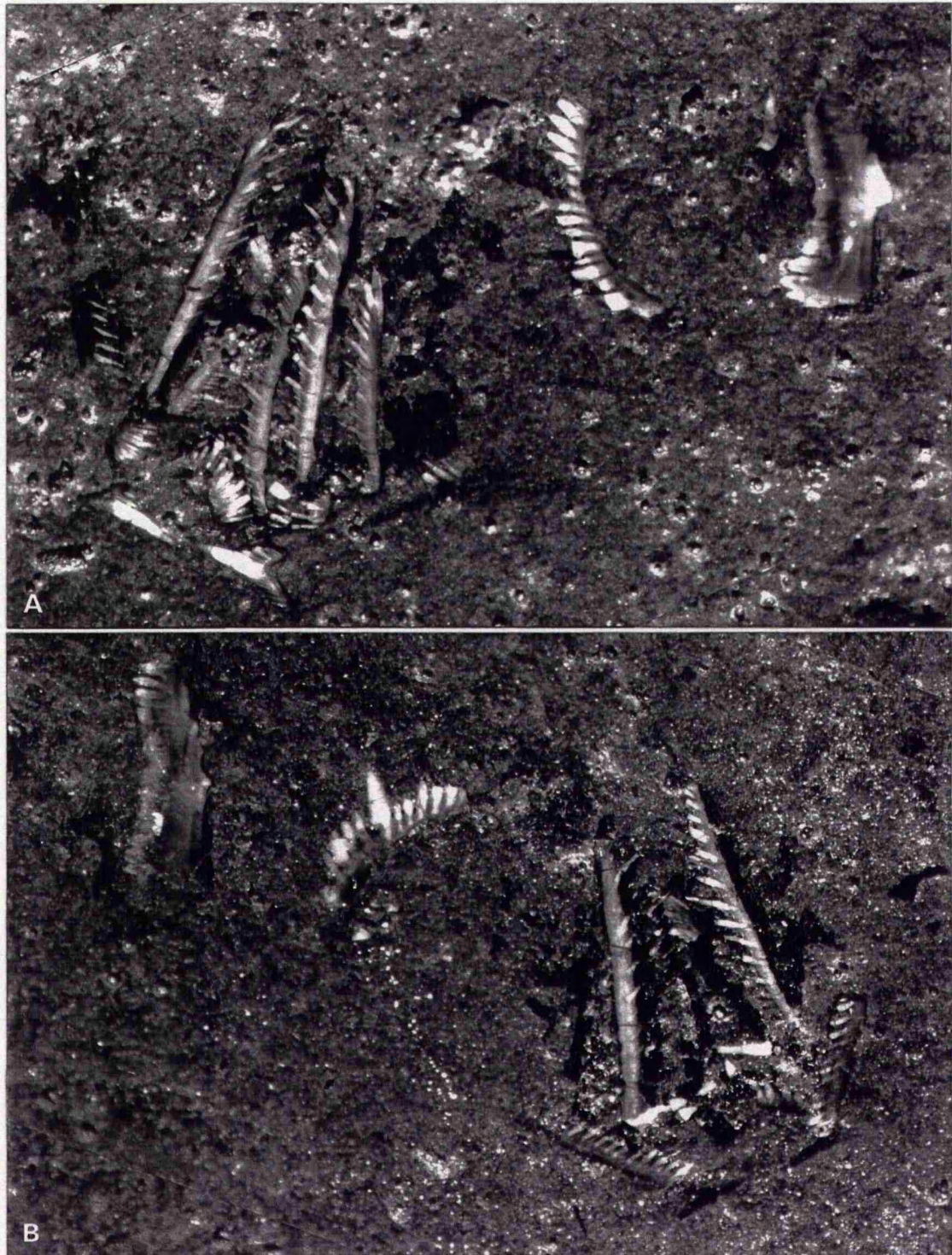


Figure 22. Natural assemblage of *Bispathodus* from the Upper Devonian upper Cleveland Shale, Cleveland, Ohio, USA; specimen CMNH 9201. A, part; B, counterpart; see figure 23A for scale. Specimen photographed under water.

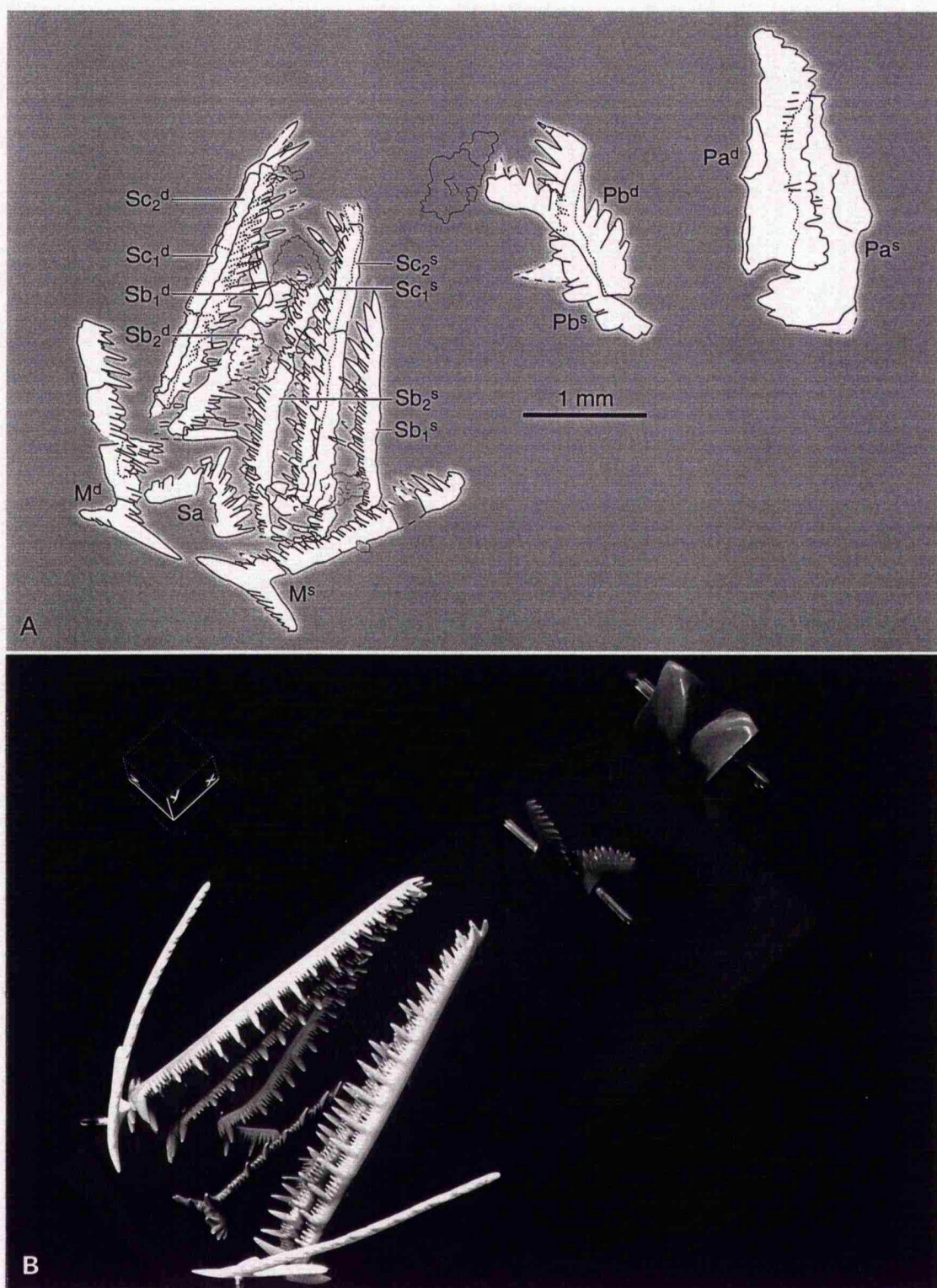


Figure 23. A, composite camera lucida drawing of *Bispathodus* specimen CMNH 9201, counterpart and part (counterpart on bottom). B, photograph of model taken from above, left, and front to simulate collapse pattern of CMNH 9201; small cube indicates orientation of principle axes of apparatus relative to horizontal sea floor at time of collapse, $x=10^\circ$, $y=71^\circ$, $z=16^\circ$.



Figure 24. Natural assemblage of *Adetognathus* from the Namurian Bear Gulch Member, Heath Formation, Montana, USA; specimen ROM 49956. The assemblage preserves remains of all fifteen elements of the apparatus; it is one of five assemblages on a small slab, no counterpart. See figure 25A for scale.

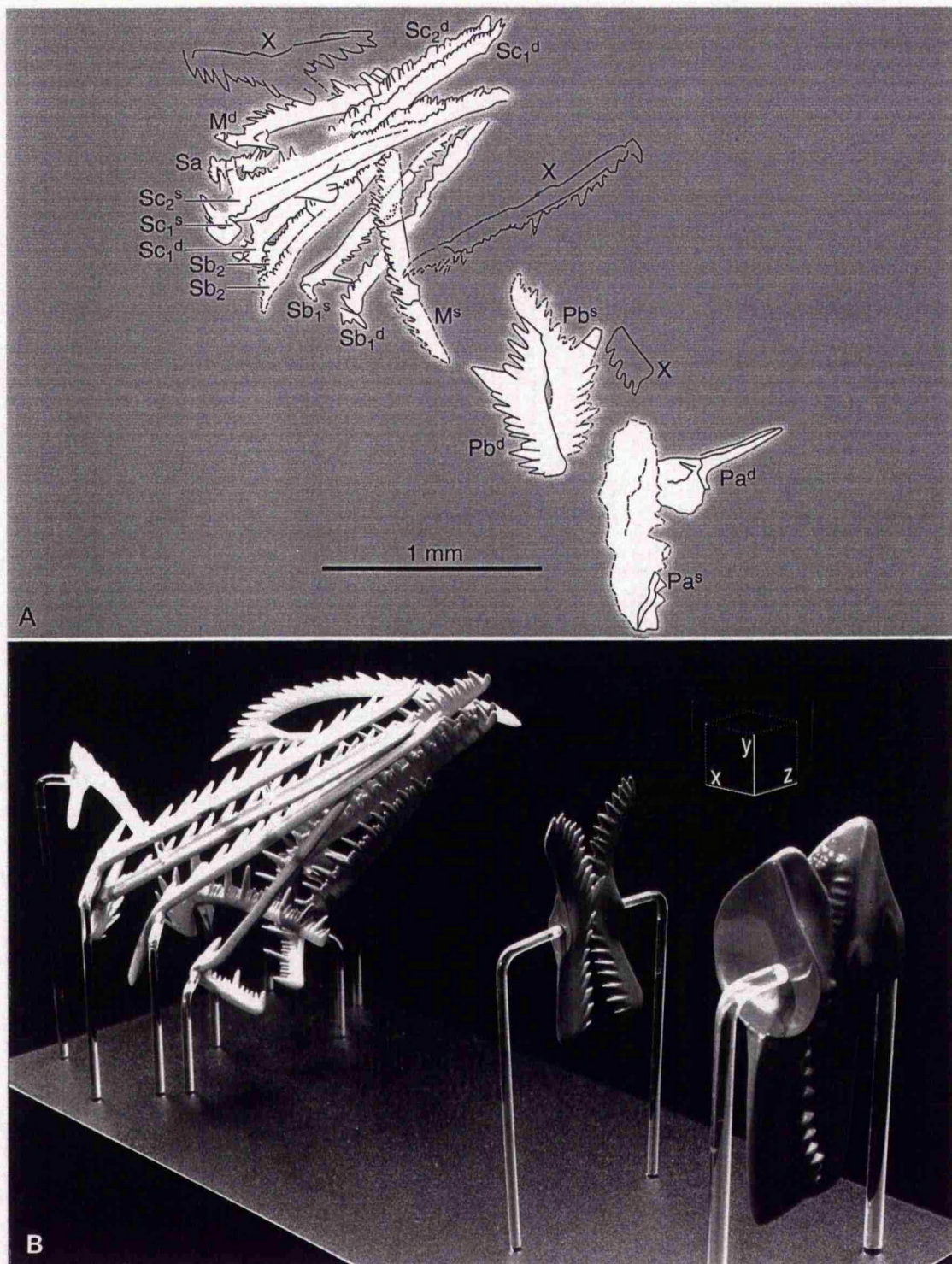


Figure 25. A, camera lucida drawing of *Adetognathus* specimen ROM 49956. B, photograph of model taken from behind, left and above to simulate collapse pattern of ROM 49956; small cube indicates orientation of principle axes of apparatus relative to horizontal sea floor at time of collapse, $x=40^\circ$, $y=20^\circ$, $z=43^\circ$.

7. THE FUNCTION OF THE OZARKODINID APPARATUS

Prior to the discovery of the first conodont animal (Briggs *et al.* 1983), a general lack of biological constraint rendered functional analysis of conodonts effectively impossible (Bengtson 1980). Since then, however, a number of studies of functional morphology have been attempted which considered elements as components of an integrated feeding structure in the head of an eel-like marine animal (e.g. Nicoll 1987, 1995; Purnell and von Bitter 1992; Purnell 1993a, 1994, 1995). Some of these analyses have suggested that the apparatus was a tissue covered filter-feeding device (Nicoll, 1985, 1987, 1995; Nicoll and Rexroad 1987), but this hypothesis is refuted by analysis of apparatus growth rates (Purnell 1993a, 1994) and by the demonstration of shearing microwear on the surfaces of some conodont elements (Purnell 1995). The available evidence indicates that the conodont apparatus had a toothlike function, and in ozarkodinids the S and M elements grasped food which was then crushed and/or sliced by the posterior P elements (Briggs *et al.* 1983; Aldridge and Briggs 1986; Aldridge *et al.* 1987; Purnell and von Bitter 1992; Purnell 1993a, 1994, 1995). Although the evidence of apparatus location, architecture, element morphology, ontogeny and wear patterns are all consistent with the hypothesis that the S and M elements performed a grasping function, there is no direct evidence to indicate how they performed this function. Most detailed analyses have focused on the Pa elements, and although Briggs *et al.* (1983) and subsequent authors have suggested that S and M elements may have operated in a manner broadly analogous to the lingual apparatus of hagfish, statements concerning S and M function are generally vague. In part, this is because it is difficult to envisage how elements arranged in the parallel array proposed by Aldridge *et al.* (1987) actually grasped. Our revised model of apparatus architecture sheds new light on this problem.

A corollary of the hypothesis that the anterior part of the ozarkodinid apparatus was a grasping device is that the S and M element array was not static. Movement of elements during function has been postulated several times (e.g. Jeppsson 1971), and Aldridge *et al.* (1987) suggested that a 90° rotation of each side of the ramiform array was required in order to bring the cusps of the S and M elements into opposition. As we have already noted, previous interpretations of ozarkodinid architecture differ from ours, especially in the orientation of the S and M elements, and these differences have important implications for understanding the function of these elements. Also, the accuracy of the matches between our model and natural assemblages indicates that the arrangement of the elements is extremely close to the original architecture of the apparatus of *Idiognathodus* (and other ozarkodinids). Our model therefore provides both firm physical constraints, and a foundation upon which to construct hypotheses of the mechanics of element motion. Further, biological constraints are also imposed by knowledge of the phylogenetic position of conodonts; the debate continues, but the evidence that conodonts were jawless vertebrates is now compelling (see Aldridge and Purnell 1996 for a recent review). Conodonts share a number of important characters with extant agnathans, but they were clearly a distinct and highly specialised vertebrate clade. The synapomorphy that unites the Conodonta is the phosphatic feeding apparatus, and functional analogies with lampreys and hagfish must, therefore, be drawn with care. Nevertheless, phylogenetic analysis has provided a group of living relatives with which to compare conodonts.

The fact that our model of the ozarkodinid apparatus can simulate the range of collapse patterns observed in natural assemblages indicates that although the elements must have moved during function, they generally lay in the same stable configuration in all dead but undecomposed conodonts. The Sb-Sc elements were arranged as two obliquely opposed sets of closely spaced subparallel elements, their functional surfaces were directed obliquely dorsal, and the aboral surfaces of the elements lay in approximately the same plane. This arrangement strengthens morphological comparisons between the conodont apparatus and the eversible lingual apparatus of extant

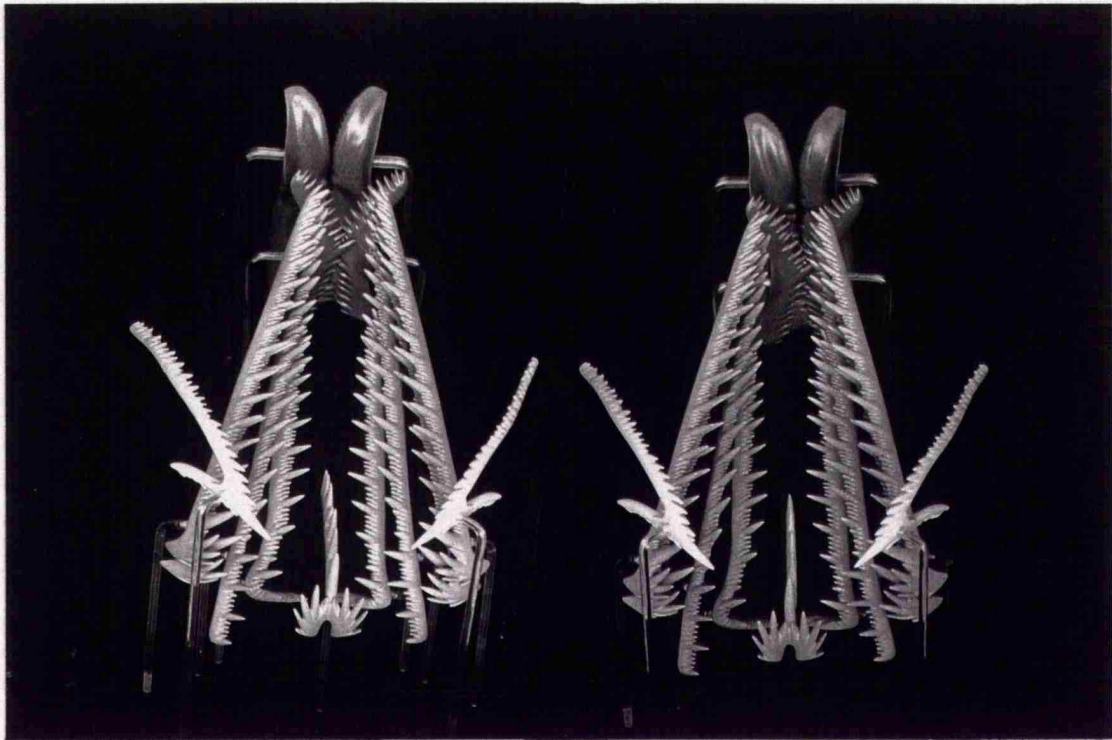


Figure 26. Stereo-pair of model viewed from above front.

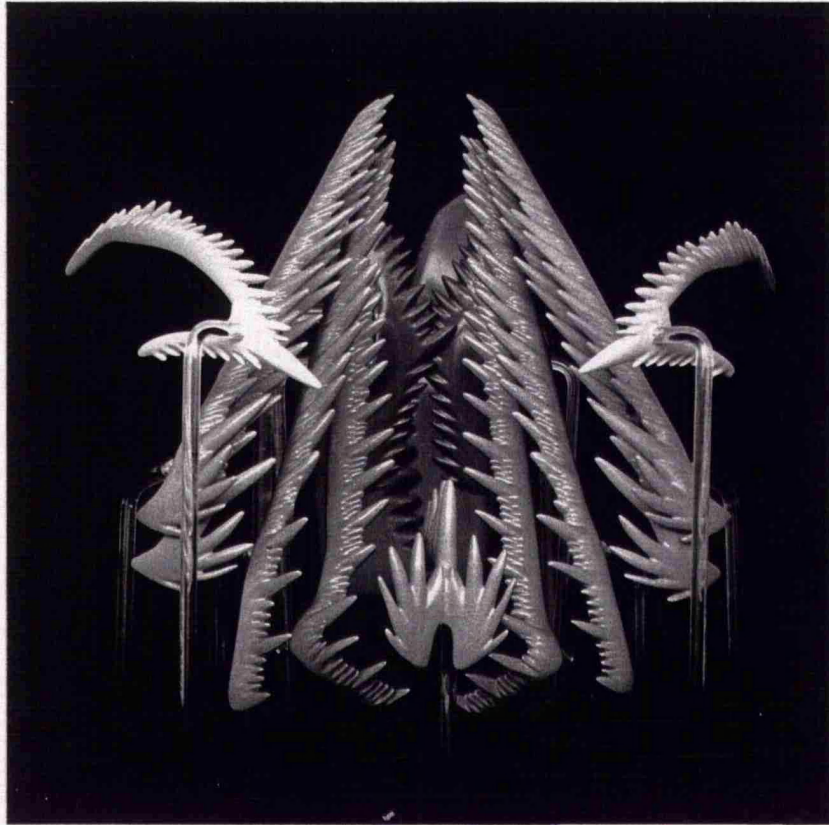


Figure 27. Anterior view of model

agnathans; in both lampreys and hagfish, the keratin biting elements of the lingual apparatus are arranged as oblique sets attached to the dorsal side of a cartilage plate or plates, and we interpret the juxtaposition and orientation of the Sb-Sc elements also to reflect their location on a pair of underlying cartilaginous dental plates. The hypothesis that conodont elements sat on supporting structures is not new (e.g. Kirk 1929; Jeppsson 1979; Smith *et al.* 1987, and references therein), but none of these authors suggested opposable dental plates uniting the Sb-Sc elements as integrated functional units. Without such aboral cartilage support, the control of movement and orientation of each element would have required a separate set of complex musculature; this hypothesis is difficult to reconcile with the lack of space between the elements and is not supported by analogies with other agnathans. The orientation and the position of the Sa element suggests that it did not sit on the same cartilage plate as the Sb-Sc elements, and for this reason we propose separate plates for the sinistral and dextral side of the apparatus, similar to the situation in lampreys, rather than the single flexible dental plate of hagfish (Yalden 1985). The position and orientation of M elements, and the inclination of their denticles are markedly different to S elements and suggest that their motion was also somewhat different. They may have sat on lateral projections of the Sb-Sc plates, capable of a degree of independent articulation, or on separate basal plates. The position of the Sa element, anterior and dorsal of the adjacent Sb elements suggests that it sat on a separate medial ridge or plate of cartilage. Note that we do not equate cartilage support structures with the conodont basal body.

The process of grasping clearly required both opening and closing of the apparatus, and the first step in understanding the operation of the apparatus is to assess the point of the cycle represented by the configuration of elements in the architectural model. The location of the apparatuses in the Granton conodont animal specimens indicates that unless the mouth was in an unusually posterior position, the S and M elements must have moved forward in order to have grasped food. This suggests that our model represents an apparatus near to closure. The orientation of the Sb-Sc element cusps and denticles, in oblique opposition, and the position and orientation of the M elements, curving round above and in front of the S elements, support this interpretation, as does the fact that the position of the P elements would have prevented significant posterior movement of the S elements. It is also pertinent to note that the lingual apparatus of extant agnathans comes to rest in a closed position in dead animals. The Granton fossils also preserve evidence of paired eyes and otic capsules (Aldridge *et al.* 1993), and conodonts must have had a true head and a differentiated brain. This, and the oblique dorsal orientation of the S elements indicate that a significant component of ventral movement was required in order to open the conodont apparatus.

Basic biological constraints demand that movement of the cartilage plates bearing the conodont elements required a system of antagonistic muscles. One end of each of these muscles inserted, probably via a tendon, onto one of the dental plates, and the other end must have been attached to another skeletal cartilage. Retractor muscles could have inserted onto cartilages associated with branchial structures, the braincase, or other hypothetical posterior skeletal structures, but protractors muscles which brought about the necessary anterior and ventral motion of the dental plates must have inserted onto cartilages that were ventral of the elements and their dental plates. The number, size and shape of these skeletal cartilages in conodonts is a matter of speculation, but it is likely, based again on biomechanical constraints and also by analogy with living agnathans, that their shape exerted a fundamental control on the movement of the dental plates. In both lampreys and hagfish, closure of the lingual apparatus (i.e. 'biting') is brought about by retraction of the dental plates into a cartilage described as pulley- or U-shaped (Yalden 1985) and we propose a similar mechanism was responsible for closure of the conodont apparatus (i.e. grasping). The anterior and ventral motions involved in opening of the conodont apparatus, therefore, resulted from pulling of the dental plates forwards out of the laterally confining U-shape, and

pivoting them over the anterior edge of the ventral cartilage into a subvertical position in which the S element denticles were directed anteriorly. The protractor muscles responsible for such motion must have wrapped round the anterior end of the ventral cartilage and inserted somewhere on its ventral side.

This hypothesis of element motion is illustrated in figure 28. Because the apparatus came to rest near to closure, the first stage in the grasping cycle must have been opening of the apparatus, but it is closure that is important for understanding how grasping was achieved, and our illustrations and discussion therefore concentrate on element movements during retraction of the apparatus. The apparatus was, however, opened by reversal of the element movements illustrated. Closure of the apparatus was brought about by the action of retractor muscles inserted onto the dental plate bearing the Sb-Sc, and possibly the M elements. This resulted in a net posterior and inward rotation of the elements as indicated by the arrows on figure 28. This motion need not have been a steady, smooth action; as the dental plates pivoted over the anterior edge of the underlying cartilage the apparatus may have snapped back into the closed position, in manner similar to closure of the hagfish lingual apparatus (Dawson 1963; Krejsa 1990a). The retracted, resting position of the Sa element was anterior and more ventral of the adjacent elements; this, and the shape of the medial cartilage on which we suggest it lay, resulted in a different trajectory as the apparatus closed. Relative to the other S elements it moved up and back, passing through the axial space between the Sb₁ elements. The M elements, during closure, moved backwards and swung inwards.

Although the net effect of retraction of the apparatus was to move the S and M elements backwards, upwards and inwards (figure 28), the mechanism by which food was grasped by the elements is more clearly illustrated by considering their relative rather than their absolute motions (figure 29). During closure, the Sb-Sc elements swing upwards through an arc approximately parallel to the orientation of the cusp and denticles (figure 29a), a motion comparable to the closure of the lower jaw in mammals (e.g. Crompton and Hiimae 1970). At the same time they rotated inwards, again along trajectories approximately parallel to the curvature of the cusp and denticles (figure 29c). Through the same phase of closure the M elements rotated inwards, downwards and slightly forwards (figure 29b). The combined effect of these movements would have produced a highly effective grasping action, the cusps and denticles of the elements converging to grab and impale any food item that lay anterior of the open array. The posterior component of apparatus retraction would have simultaneously drawn food back into the mouth. It is possible the Sb-Sc elements were retracted a little further than the position illustrated (i.e., the configuration of elements in the model) so that the cusps were brought into more direct opposition. However, we envisage a grasping, rather than a biting function for the S and M elements, and this does not require complete closure of the array. It does seem likely, however, that the Sa element continued its backward arc, the posterior process moving through the horizontal to a position of posterior inclination. Through this cycle of retraction, the cusp and lateral processes of the Sa element would have moved from a position close to the cusp of the Sb₁ element when fully everted, past the cusps of each of the other Sb-Sc elements in turn. Thus, at the earliest stages of closure the Sa element would have performed a grasping function, but as retraction continued, food impaled on the Sb-Sc elements would have been lifted off and moved backwards towards the P elements.

It has been suggested that in retracted position, conodont elements may have been withdrawn into enclosing pockets of epithelium (Aldridge *et al.* 1987; cf. Bengtson 1976). However, our hypotheses that the S elements were closely juxtaposed, lay on cartilage dental plates, and were still functional when retracted (cf. Bengtson 1983b), and recent reinterpretations of element histology (Sansom 1996), together indicate that his hypothesis is no longer tenable.

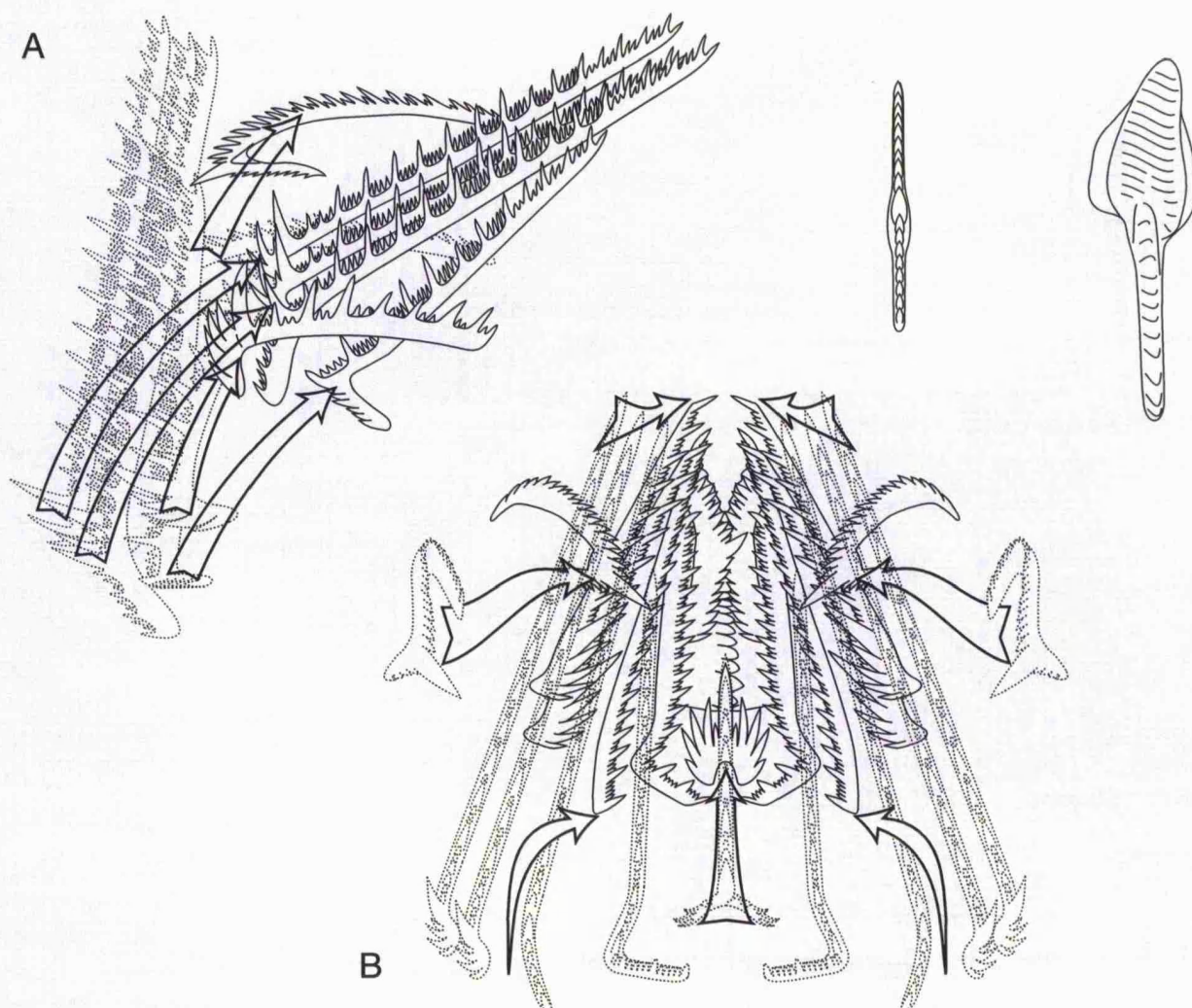


Figure 28. Operation of the anterior array of the ozarkodinid apparatus illustrated by *Idiognathodus*. Elements drawn with dotted lines indicate their position when the apparatus is everted and open; elements drawn with solid lines are in the retracted, closed position. A, lateral view of dextral side of apparatus; arrows indicate net movement of Sa, Sb₁, Sb₂, Sc₂ and M elements during retraction and closure of the anterior array. B, Anterior view of whole apparatus; arrows indicate net movement of S and M elements.

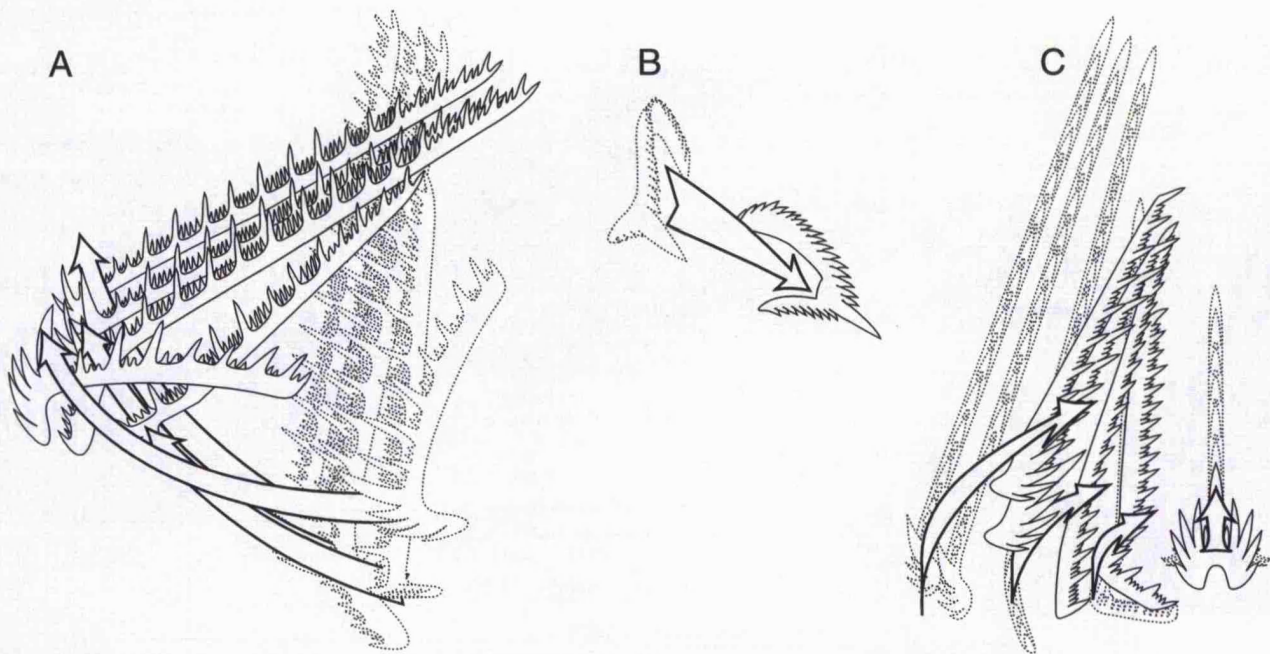


Figure 29. Relative motion of S and M elements during closure of the anterior array. Elements drawn with dotted lines indicate their position when the apparatus is everted and open; elements drawn with solid lines are in the retracted position. A, lateral view of dextral S elements and Sa element; arrows indicate motion of Sa, Sb₁, Sb₂, and Sc₂ elements relative to a fixed point at the distal end of the posterior process of the Sb₁ element. B, anterior view of dextral M element; arrow indicates motion relative to cusp of Sa element. C, Anterior view dextral S elements and Sa element; arrows indicate motion of Sa, Sb₁, Sb₂, and Sc₂ elements relative to a fixed point at the distal end of anterior process of the Sb₁ element.

In ozarkodinid conodonts, food captured by the S and M elements was sliced and crushed by the Pb and Pa elements (e.g. Briggs *et al.* 1983; Purnell and von Bitter 1992; Purnell 1995). Morphology, occlusion, and wear patterns indicate that P elements operated by being rotated against each other across the axis (Nicoll 1987; Weddige 1990; Purnell and von Bitter 1992), and sharp blade-like elements, for example, functioned like a pair of serrated scissors (Purnell and von Bitter 1992; Purnell 1995). The relative movement of these elements is understood, but how motion was produced is not. It is possible that rotation was produced by mechanisms of retraction similar to those proposed for the S and M elements, but the precision with which elements were brought into repeated contact argues against this (Purnell 1995). Rather, it seems more likely that the P elements were located at the entrance to the pharynx (Aldridge *et al.* 1995), and movement was controlled by antagonistic muscles located above and below the elements in the dorsal and ventral walls of the pharynx. Janvier's speculative suggestion that the P elements were "attached to a transversely moving structure derived from a velum of larval lamprey type" (1996a, p. 277) is consistent with their pharyngeal location, but is difficult to test. However, the velum in larval lampreys pushes water into the pharynx, and its primary motion is anterior-posterior (Mallatt 1996). The musculature of this structure would, therefore, require significant remodelling if it was to bring about the axially directed rotational action of ozarkodinid P elements.

The architecture of the conodont apparatus is consistent with a mode of operation analogous to that of extant agnathans, and the possibility that they were similar in detail, as we suggest above, lends strong support to the hypothesis that the anterior portion of the conodont feeding apparatus as a whole is homologous with the lingual apparatus of extant agnathans (cf. Aldridge *et al.* 1986; contra Janvier 1996a p. 267). The conodont elements themselves, however, are certainly not homologous with the keratin 'teeth' of agnathans (contra Krejsa 1990b). The possible homology of the bilaterally operating feeding apparatus supports the hypothesis that it is a synapomorphy of craniates (e.g. Janvier 1981, 1996a; Purnell 1993a), and is not, as has been suggested recently (Mallatt *in press*), a derived feature of extant agnathans. This hypothesis of homology, and the corollary that the S and M elements lay in the conodont mouth, also cause some difficulties for Mallatt's functional scenario for the origin of jaws (1996). Unfortunately, as a plesiomorphic character shared by all craniates, feeding apparatuses homology cannot help to resolve questions of conodont affinity as it provides no indication of the closeness of relationship between one agnathan group and another (contra Yalden 1985). Along with our reconstruction of the ozarkodinid apparatus, however, it does contradict recent suggestions that the apparatus was comparable to the oral plates of 'ostracoderms' (Janvier 1996) or was jaw-like in its arrangement (Gee 1996, p. 67). Similarly, the suggestion that the S and M elements were the pharyngeal denticles of a suction-feeding animal (Janvier 1995, 1996a) can be reconciled neither with our hypotheses of architecture, function, and homology, nor with evidence that agnathans could not generate strong suction (Mallatt 1996).

Our hypothesis of retraction and grasping in ozarkodinid conodonts, although constructed within the framework provided by our model of apparatus architecture and constrained by analogies with living agnathans, is not supported by any direct evidence. It is, however, both plausible and testable. Locations of points of maximum food contact and stress can be predicted, and these should correspond to maximum wear and denticle breakage. It is also possible that microwear analysis will reveal scratches on cusps that will confirm or refute our hypothesis of the relative motions of the elements. Undoubtedly, the conodont head and its various organs were supported by skeletal cartilages which, except for the sclerotic cartilages, have not been preserved in the conodont animal fossils found so far. The possibility of future discoveries of fossils reflecting a different taphonomic history

from the Granton specimens, and which preserve skeletal cartilages, provides a potential test of our hypothesis of the cartilages involved in the function of the conodont apparatus.

8. TAPHONOMY OF THE APPARATUS –ORIENTATIONS OF COLLAPSE

With the possible exception of the panderodontid specimen from Waukesha (Mikulic *et al.* 1985; Smith *et al.* 1987) conodont animal fossils indicate that the body was elongate, eel-like and laterally compressed (Aldridge *et al.* 1993). One would expect, therefore, that most conodont carcasses would come to lie with their long axis parallel to the sea floor, with those lying on their side outnumbering other orientations (Aldridge *et al.* 1987, 1995; Nicoll and Rexroad 1987). Using our stereographic restoration technique we have calculated original collapse orientations of all the natural assemblages of ozarkodinids available to us either as fossils or as published illustrations. The results of this analysis (figure 30) provide some insights into the formation of natural assemblages. Only 8% of assemblages preserve collapse patterns recording orientations approaching dorso-ventral (i.e. $y > 45^\circ$), which accords with intuitive assessments of the likelihood of collapse orientations. But 68% of assemblages exhibit collapse patterns indicating long axis (i.e. x axis) angles in excess of 30° to the sea floor, with 50% indicating orientations of collapse in which x was 45° or more. This is not what one would predict from what is known of conodont body shape, and these counterintuitive results require some explanation.

Thirteen of the natural assemblages in the $>45^\circ$ sector of the graph (figure 30) are fused clusters of *Ozarkodina*. Preservation of fused clusters requires elements to be in contact after collapse, so orientations which produce element overlap are over-represented in cluster collections, whereas those that minimise overlap produce only very partial clusters. This may explain why only one cluster of *Ozarkodina* records collapse with $x < 45^\circ$ (and this cluster lacks P elements due to non-overlap). It is also worth noting here that the lack of Sd elements (i.e. Sb1's) in some of the clusters described by Nicoll (1985) reflects non-overlap resulting from lateral collapse (e.g. figures 5, 17, 19 25), not a more posterior position for the Sb1 elements (contra Nicoll (1985) Nicoll and Rexroad (1987) and Nicoll (1995)). These taphonomic biases involved in cluster formation, however, are not enough to account for the overall distribution of collapse orientations in ozarkodinids because the same pattern emerges from the collapse data for *Idiognathodus*, the most numerous of the assemblages. These data are derived from bedding-plane assemblages, not clusters, yet 71% of *Idiognathodus* assemblages reflect collapse angles in which x exceeded 30° , and in 51% x was more than 45° .

There are a number of possible explanations for x angles in excess of 30° : it seems unlikely to be due to conodont head shape expanding anteriorly to the extent that it comes to rest at high angles to the sea floor, and the possibility that the long axis of the ozarkodinid apparatus did not coincide with the long axis of the animal is ruled out by the apparatuses in the preserved conodont animals. The most likely interpretation is that the sea floor at the time of death of the conodonts animals was soft enough for the carcass to penetrate some way into the sediment, which allowed the head to come to rest in positions that would be gravitationally unstable on a solid surface. Such 'soupy substrates' have been invoked to explain patterns of preservation of larger vertebrate skeletons in black shale environments (Martill 1983). In the case of the *Idiognathodus* collapse data, all the assemblages are from the black shales of the Modesto Formation at Bailey Falls. This unit lacks a significant benthic fauna (Collinson *et al.* 1972), and although this may reflect conditions of reduced oxygen, it is also consistent with a soft substrate. The soft substrate hypothesis is also supported by the high abundance of conodont elements and assemblages in the shale; this may have been produced by the concentration effects linked with the compaction of large volumes low density sediment. It is possible that the commonness of relatively high

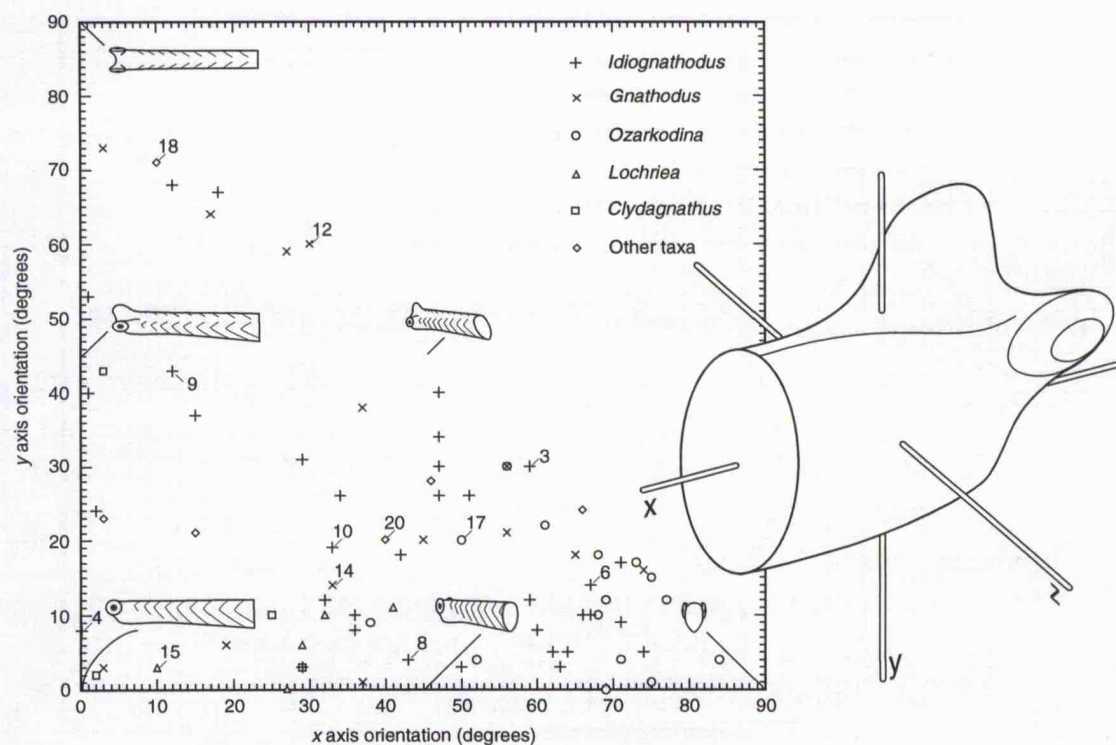


Figure 30. Collapse orientations of ozarkodinid apparatuses determined according to the methods outlined in the text. The orientations of the x and y axes indicate the pitch and roll of the apparatus, the z axis, reflecting the angle of yaw (which has no effect on collapse patterns) is not shown. Points with numeric labels are figures. For details of collections from which data are derived see text and Appendix. Note that *Idiognathodus* data includes unpublished material currently housed at the University of Leicester; *Ozarkodina* data are fused cluster material except for CGM 1/10499 (figure 17); the 'other' category includes *Adetognathus* (figure 20), *Bispathodus* (figure 18), *Hemilistronea* (see Dzik 1991), and three fused clusters of *Polygnathus* (Nicol 1985). n=79.

angles of collapse in *Idiognathodus* is due to the weight of the mineralized conodont apparatus causing dead conodonts to nosedive into the sediment. However, because we are currently unable to differentiate head-up from head-down collapse orientation this hypothesis remains untested.

The hypothesis that substrate density exerted a significant control on carcass orientation in conodonts is supported to some extent by apparatus collapse patterns of *Gnathodus* and *Clydagnathus* (figure 30). We have only analysed 14 natural assemblages of *Gnathodus*, but nine of these (64%) are from lower Namurian black shales from Hemer, Germany and they all exhibit collapse in which α is less than 45° , possibly because the sea floor at the time of deposition of these shales was not soft enough to allow conodont carcasses to penetrate. Only four *Clydagnathus* assemblages have been analysed, but these all come from the Granton Shrimp bed. This unit contains a benthic fauna, and was deposited in a mud-flat environment with possible algal binding of organic rich laminae and evidence of periodic exposure and desiccation (Cater 1987); the substrate was probably quite firm. All the assemblages exhibit collapse in which α axes were inclined at less than 30° , two having α axis inclinations close to zero. These angles that are consistent with carcasses resting on the sea floor with little or no substrate penetration.

9. THE OZARKODINID SKELETAL PLAN, ELEMENT NOTATION, ORIENTATION, AND HOMOLOGIES

(a) Skeletal plan

In contrast to hypotheses of architecture, the broad features of the general skeletal plan of ozarkodinid conodonts have been known for some time, and in recent years this plan (e.g. Aldridge *et al.* 1987, 1995; Smith 1990) or minor variants (e.g. Nicoll 1985, 1987, 1995; Nicoll and Rexroad 1987) has become fairly stabilised. Points of uncertainty and contention remain, however, and our architectural analysis goes some way to resolving these. From the taxonomic and stratigraphic range of the natural assemblages we have studied, it seems certain that the full complement of elements in the ozarkodinid apparatus was 15 elements (cf. Nicoll 1987), and we have encountered no evidence to suggest that elements were lost from this array in any of the taxa preserved as natural assemblages. Architectural analysis also reveals that the arrangement of these 15 elements was extremely similar in all taxa studied, from the Silurian to the Late Carboniferous, and it is reasonable to extrapolate from this that the apparatuses of ozarkodinid conodonts remained essentially unchanged throughout their stratigraphic range. One point that is worth addressing specifically is the number, morphology and position of the S elements. In all the taxa we have analysed there are nine element positions in the symmetrical S array. On each side, the two outermost Sc positions are occupied by morphologically similar elements of bipennate morphology. Between the Sc's and the axial Sa position, the two Sb positions are occupied by elements which are more similar to each other than to the Sc elements, although they are generally less similar to one another than the Sc elements. The two Sb positions are occupied either by bipennate elements or modified digyrate elements; they generally differ from one another in the form and curvature of the process that in conventional terminology is considered anterior or outer lateral.

(b) Homologies and element notation

(i) Notation and homology

Element notation is another area in which our analysis of ozarkodinid architecture may help to resolve some outstanding difficulties. A stable and widely understood notation for conodont elements is crucial to communication of multielement taxonomic concepts and also expresses hypotheses of homology (e.g. Klapper and

Philip 1971; Barnes *et al.* 1979; Sweet 1988; Dzik 1991). Despite its vital importance, notation of the elements in the ozarkodinid apparatus has yet to fully stabilise. With a few exceptions (e.g. Dzik 1991, 1994) the majority of work dealing with ozarkodinid conodonts uses Sweet's P, M, S scheme for naming element positions (Sweet and Schönlaub 1975; Sweet 1981, 1988), but the notation is still applied inconsistently to some elements. For example, the notation 'Sd' has been applied by a number of authors (e.g. Aldridge *et al.* 1987; Nicoll 1985, 1987) to the element we consider to have occupied an Sb position, but according to Sweet (1981, 1988) 'Sd' refers to an axial position occupied by a quadrimate element and should not be applied to ozarkodinids (Sweet 1988; Over 1992). This problem has arisen because Sweet (1981) recognised only three major positions in the S series, the occupants of which were thought to form a transition series of increasing asymmetry away from the Sa. Sweet (1988, p. 25) realised that "there may be more than three morphologically distinct components of the S series and, to describe and locate them, it may be necessary to invent intermediate categories, such as Sa-b, or Sb-c", but we now know that the ozarkodinid apparatus had four S positions on each side of the Sa, and that, based on morphological similarities, the occupants of these positions represent two pairs. We suggest that a solution more in keeping with the primarily locational nature of this notation is to identify these S positions as Sb₁, Sb₂, Sc₁, and Sc₂, as we have done throughout this paper (see also Aldridge *et al.* 1995, figure 1). Over (1992) also suggested using the terms Sb₁ and Sb₂, but we consider his Sb₁ element to be an Sb₂ and vice versa, based on the location of the elements in our model.

Application of element notation and hypotheses of homology are the foundations of biological taxonomy and evolutionary analysis of conodonts. Without hypotheses of homology, analysis of relationships among conodonts is reduced to mere speculation, but recognition of homology in conodonts relies on knowledge of element arrangement (Barnes *et al.* 1979; Purnell 1993b). Except for the very few taxa known from clusters or bedding-plane assemblages, reconstruction of species from their disarticulated components relies on general skeletal blueprints or templates which allow the occupants of homologous element positions to be identified using morphological criteria. Over the last 15 years, most reconstructions of ozarkodinid taxa have relied on the template and criteria provided by Sweet (1981, 1988), but as we note above, this scheme only recognised three major positions in the S series of increasing asymmetry. It now seems clear that the apparatus of most, and possibly all ozarkodinid conodonts contained 15 elements which occupied 2 Pa positions, 2 Pb positions, 2 M positions and nine S positions (from left to right Sc₂, Sc₁, Sb₂, Sb₁, Sa, Sb₁, Sb₂, Sc₁, Sc₂). In none of the taxa preserved as natural assemblages are the S elements arranged as transition series of increasing asymmetry. Perhaps the time has now come to adopt the fifteen element plan as the template for reconstructing ozarkodinid apparatuses. As pointed out by Dzik (1991) one corollary of accepting a standard number of element locations is that terms such as 'septimembrate' or 'octomembrate' are redundant, or reduced to subjective assessments of the morphological thresholds taken as the boundaries between element types.

If it is to have any biological meaning, application of P, M, S notation to the apparatuses of taxa assigned to other orders of conodonts should be based on the recognition of homologies with ozarkodinids. This notational scheme was first *applied* to *Oulodus*, a prioniodinid, but it was based on the recognition of principle categories of elements in natural assemblages (Sweet 1988), and given the material available at the time the scheme was developed, it must have been *derived* primarily from the arrangement of elements in ozarkodinid assemblages (Purnell 1993b). The ozarkodinid apparatus, therefore, can be taken as the standard for the P, M, S scheme (cf. Dzik 1991).

(ii) *Homologies with prioniodinids*

Natural assemblages of taxa assigned to the Prioniodinida and Prioniodontida (*sensu* Sweet 1988), the other two orders with apparatuses composed of complex multidenticulate elements, are much scarcer than those of ozarkodinids. Prioniodinids, for example, are known from a single *Hibbardella angulata* (Hinde) from the Upper Devonian Gogo Formation of Western Australia (Nicol 1977), an incomplete *Idioproniodus* from the lower Namurian of Germany (Schmidt and Müller 1964; Purnell and von Bitter 1996, and ms in prep), a few *Neogondolella* from the Middle Triassic of Switzerland (Rieber 1980; Orchard and Rieber 1996), and a *Kladognathus* assemblage from the Mississippian of the USA (Purnell 1993b). With such limited data, the three-dimensional architecture of prioniodinids cannot yet be determined, and hypotheses of element arrangement and homologies with ozarkodinids remain somewhat preliminary. However, Purnell (1993b) interpreted the apparatuses of *Hibbardella* and *Kladognathus* to have been arranged according to the same basic skeletal plan, which did not differ significantly from that of ozarkodinids. Based on element locations, homologies were recognised with ozarkodinids, and the same element notation that we advocate for ozarkodinids can, therefore, be applied to prioniodinids. The morphology of the occupants of some of the 15 positions in the apparatus is, however, clearly different. This hypothesis of the prioniodinid apparatus stands in marked contrast to the architectural model of *Idioproniodus* proposed by Stone and Geraghty (1994). This was based primarily on the concept of symmetry transition, which we consider a most unreliable indicator of element location in prioniodinids, and is contradicted by data from bedding plane assemblages (Purnell and von Bitter 1996 and ms in prep.).

(iii) *Homologies with prioniodontids*

Natural assemblages of prioniodontids now number in excess of 100, but they are all the same species, *Promissum pulchrum* Kovács-Endrödy. Consequently, the architecture of the apparatus of *Promissum* is known with a high degree of confidence, and although it had more elements, similarities between *Promissum* and ozarkodinids reveal a number of homologies. These were recognised by Aldridge *et al.* (1995), but our improved understanding of the architecture of the ozarkodinid apparatus makes these homologies more secure. The S arrays of both apparatuses contain the same number of elements and, morphology aside, they differ mainly in the position and orientation of the Sa element. This element is horizontal and the most anterior S element in ozarkodinids, but inclined and the most posterior of the S's in *Promissum*. The remainder of the S elements in both apparatuses are inclined forwards with the angle of inclination increasing towards the axis from about 30° in the outermost Sc's; the elements are inclined inwards with the angle increasing away from the axis; and element locations are increasingly dorsal and (except for the Sb₂ element of *Promissum*) anterior away from the axis. Despite the clear homologies between the S elements, Aldridge *et al.* (1995) labelled those of *Promissum* Sb₁, Sd, Sb₂, Sc rather than Sb₁, Sb₂, Sc₁, Sc₂. This was to avoid the terminological confusion of calling quadriramate elements Sb₂, when they have been widely termed Sd in the literature. However, their solution, which reflects the difficulties of separating the locational from the morphological aspects of the P, M, S scheme, is no less confusing; the Sd element of *Promissum* is homologous with the Sb₂ in ozarkodinids, and the Sb₂ of *Promissum* is homologous with the ozarkodinid Sc₁. Regarding the other elements of the apparatus, the location and orientation of the M elements in our revised model of ozarkodinid architecture also strengthens the homology proposed by Aldridge *et al.* (1995), but we can shed no new light on the homologies of *Promissum*'s four pairs of P elements.

The architecture of the *Promissum* apparatus is probably typical of the family Balognathidae (Aldridge *et al.* 1995), but the question remains of the extent to which the skeletal plan of *Promissum* represents a standard for the prioniodontids. Several other bedding plane assemblages of prioniodontid taxa are now known (Nowlan 1993; Stewart 1995), and although these are probably faecal (Stewart 1995; pers. obs.), the number of elements present in these assemblages (Stewart pers. com. 1996; pers. obs.) provides some very preliminary evidence to support the tentative suggestion of Aldridge *et al.* (1995) that some prioniodontid apparatuses may have been less complex than that of *Promissum*. It is possible that the architecture of these apparatuses may have been more similar to that of ozarkodinids. If this proves to be the case, then a 15 element apparatus may be a synapomorphy of ozarkodinids, prioniodinids and prioniodontids. But this speculative hypothesis remains just one possibility; alternatively, a 15 element apparatus may be a plesiomorphic character shared by all members of the Conodonta.

(iv) Orientation of conodont elements

The similarities in element location and orientation that exist between ozarkodinids, prioniodontids (*Promissum*), and possibly prioniodinids, raise the question of the descriptive terminology conventionally applied to conodonts. It has been realised for decades that the terms of orientation applied to conodont elements are entirely arbitrary and may have no relation their true orientation in the animal (e.g. Müller 1956), yet they have persisted. Conventional definitions of element orientations are complex (Sweet 1981, p. W7), but cusp curvature provides the best general guide, the concave side marking 'posterior', the tip 'up', and the upper margin of the base of the element or the posterior process 'horizontal'. In no apparatuses for which the architecture is known do these conventional designations coincide fully or consistently with true biological orientations. This has recently been addressed by Dzik (1994), who proposed a new biologically based system of orientation, derived from his hypothesis of apparatus architecture. However, as we have discussed, there are significant differences between his hypothesis and the element orientations indicated by our analysis of natural assemblages, and we therefore consider some of his terminology to be incorrect. Descriptive terminology based on true orientations is indeed needed, but it must be based on a detailed consideration of the orientations of elements in as many different apparatuses as possible, not just ozarkodinids. The erection of new terminology, therefore, falls outside the scope of this paper.

(v) Homologies with panderodontids

Apart from the apparatuses of conodonts characterised by complex element morphology, the only other order for which an architectural reconstruction has been proposed is the Panderodontida (Sansom *et al.* 1994). This hypothesis is based primarily on two fused clusters and a bedding plane assemblage of *Panderodus* which are variable in their completeness and degree of disarticulation. Sansom *et al.* (1994) introduced a new locational notation for coniform conodonts, based on the spatial differentiation of the elements in their reconstructed apparatus. They recognised the value of identifying homologies between the panderodontid apparatus and the apparatuses of conodonts with more complex element morphology, but it was precisely because such homologies could not be recognised that they introduced a new notational scheme. There are some striking similarities between the spatial differentiation of the panderodontid apparatus and that of ozarkodinids, but the main obstacle to homologizing elements lay in the differences in orientation of the anterior elements (Smith 1990; Sansom *et al.* 1994). The orientation of these elements in panderodontids was compared with that in the ozarkodinid model of Aldridge *et al.* (1987) which had the S elements arranged with their cusps parallel to the sagittal plane, and with no

anterior-posterior displacement. In panderodontids the anterior elements are opposed across the axis and are arranged in an anterior-posterior sequence (Smith *et al.* 1987; Smith 1990; Sansom *et al.* 1994). This is significantly different to the architecture proposed by Aldridge *et al.* (1987), but the S elements in our modified ozarkodinid model are oriented with their cusps inclined obliquely inwards towards the axis, and with significant vertical and horizontal displacement through the array. These changes in our understanding of the ozarkodinid apparatus in themselves significantly reduce the difference between the two apparatuses, but it is also possible that the panderodontid apparatus was more three-dimensional than is suggested by the illustration of Sansom *et al.* (1994, figure 6). With only three or four imperfect clusters and bedding plane assemblages from which to interpret 3D architecture, the possibility that their hypothesis is not entirely correct must remain. It is interesting to speculate on the collapse pattern that would result from a slightly modified model of panderodontid architecture in which the elements occupied positions closer to those of our ozarkodinid model. Based on our experience of collapse patterns, it seems likely that this would produce an assemblage similar to the important Waukesha specimen if collapse was close to anterior-posterior, i.e. a high angle of x , but a low angle of y (see figure 30). This could also account for the posterior position of the axial Ae element in the panderodontid model. The Waukesha specimen provides the only evidence that this element lay at the back of the apparatus (Sansom *et al.* 1994), but its posterior location in the fossil may reflect the orientation of collapse rather than its primary position.

(vi) *Architectural conservatism in conodonts and a standardised notation*

Understanding of apparatus architecture is a prerequisite for the recognition of homologies, an essential step in the interpretation of conodont evolution and in the development of a sound suprageneric classification. We would agree with Sansom *et al.* (1994) that more architectural data are required before current problems can be resolved, and although it would be premature to apply standard P, M, S notation to the panderodontid apparatus, we are more optimistic than Sansom *et al.* (1994) that homologies between coniform apparatuses and those made up of more complex elements can be determined. Our model of the ozarkodinid apparatus goes some way to reducing some of the more significant architectural barriers between these apparatus types and suggests that application of a standard location-based notation to apparatuses belonging to conodont lineages with radically different element morphology may not be too far away. There are many similarities between the apparatuses of prioniodinids, prioniodontids, ozarkodinids and panderodontids; it is possible that the Conodonta were rather more conservative architecturally than current hypotheses suggest.

APPENDIX. PUBLISHED BEDDING PLANE ASSEMBLAGES AND CLUSTERS

We list here published bedding plane assemblages and clusters (not including prioniodontid and coniform taxa) in chronological order, with notes on preservation, completeness and collapse patterns. The term “faecal” is applied to assemblages that may represent stomach ejecta or coprolitic material. Notes on collapse indicate the orientation which would produce the observed pattern of element distribution relative to the axis of the apparatus (N.B. bedding plane assemblage and cluster collections do not record original way up of specimens, therefore “oblique lateral collapse from side, slightly above and behind” for example, could also be “oblique lateral collapse from side, slightly below and in front”). BM, Natural History Museum, London; BU, Lapworth Museum, University of Birmingham, UK; CGM, Central Geological Museum, VSEGEI, St. Petersburg, Russia; CM, Carnegie Museum, Pittsburgh, USA; CPC, Commonwealth Palaeontological Collections, Canberra, Australia; IGSE, British Geological Survey, Edinburgh; IMGP G6, Institut und Museum für Geologie und Paläontologie, University of Göttingen,

Germany; ISGS, Illinois State Geological Survey, USA; IU-IGS, Indiana University - Indiana Geological Survey, USA; MPK, British Geological Survey, Keyworth; RMS, Royal Museum of Scotland; ROM Royal Ontario Museum, Canada; UI, Geology Department, University of Illinois, USA; UM, University of Montana, USA; UN, University of Nottingham; USNM, U. S. National Museum, Washington D. C., USA.

Hinde, 1879: Devonian, Genesee Shale, New York, USA; specimen BM A-4035, A-4036, almost certainly part and counterpart (Aldridge 1987; pers. obs). Large faecal association, no primary architecture preserved, >1 individual, >1 species. Figured by Huddle (1972).

Schmidt 1934: lower Namurian, Hemer, Sauerland, Germany; 7 assemblages of *Gnathodus* illustrated: fig. 1 disarticulated, ?incomplete; fig. 2 disarticulated; fig. 3 and plate 6 fig. 3, oblique collapse from above and behind (cf. figures 22, 23, but more posterior, $x=27^\circ$, $y=59^\circ$, $z=14^\circ$); fig. 4, partial, articulated S and M array; figs 5a, b and pl. 6, fig. 1, oblique axial collapse (see figures 14, 15; reillustrated by Aldridge *et al.* 1987, fig. 4.6A); fig. 6, disarticulated; fig. 7 and plate 6, fig. 2, disarticulated, 2 individuals. All material lost in World War II.

Scott 1934: Mississippian, Quadrant shales, Montana, USA; collection of 75 assemblages, 18 described and figured, including *Lochriea*, *Gnathodus* and *Cavusgnathus*. Most assemblages are incomplete, disarticulated and chaotic; a few retain some evidence of primary architecture (e.g., plate 58, figs 1, 2, 3).

Jones 1935: Pennsylvanian, Nowata Shale, Oklahoma, USA; unpublished thesis collection of >50 assemblages, 17 described and illustrated, six of which are ozarkodinid. Plate V, large faecal assemblage, >1 individual; remainder probably the remains of single individuals, but all incomplete and/or disrupted.

Jones 1938: Pennsylvanian, Seminole Formation, Oklahoma, USA; unpublished thesis collection of 75 assemblages, 15 described and illustrated, including *Gondolella* (prioniodinid) and *Neognathodus*. These are probably the remains of single individuals, but are mostly incomplete and disarticulated; only a few retain traces of primary architecture. Assemblage 2 refigured by von Bitter (1976), assemblage 4 refigured by Merrill and von Bitter (1977).

Burnley 1938: Pennsylvanian, Lexington Coal, Missouri, USA; unpublished thesis collection, assemblage 12 refigured by Merrill and von Bitter (1977, figs 2, 3, 4, 5, 9A, C).

Kraemer 1940: Namurian, Arnsberg, Germany; figured partial and/or scattered individual apparatuses and accumulations of >1 individual, little if any trace of primary architecture (Note: some of Schmidt's material found by Kraemer).

Scott 1942: Mississippian, Heath Formation, Montana, USA; collection of ~180 assemblages, 32 figured; most are incomplete, or disrupted and chaotic; some are remains of >1 individual (e.g., plate 37, fig. 6), only a few retain traces of primary architecture (e.g., plate 38, fig. 10). Plate 37, fig. 4 reillustrated by Clark (1987, fig. 20.2A).

Du Bois 1943: Pennsylvanian, McLeansboro Group, Bailey Falls, Illinois, USA; collection of >75 assemblages, 19 figured (figs 3 & 11 are part and counterpart), mostly *Idiognathodus*, a few *Idioproniodus* (prioniodinid). Pl. 25, 1, 6, 8, 10, 15, 19, 20, UI X-6361, X-6366, X-6368, X-6370, X-1494, X1493, X-6376, partial remains, single individuals, little or no trace of primary architecture, several probably faecal (figs 6, 10, 15, 20); figs 2, 7, 18, UI X-6362, X-6367, X-6375, remains of >1 individual; figs 3 & 11, UI X-6363, lateral collapse from side and slightly posterior, $x=29^\circ$, $y=3^\circ$, $z=61^\circ$ (cf. figures 8, 9, a little more posterior than figures 4, 5); fig. 4, UI X-6364, collapse from behind and slightly above, $x=71^\circ$, $y=17^\circ$, $z=9^\circ$ (angle a little lower than figures 2, 3); fig. 5 (specimen lost), oblique lateral collapse from side and behind, $x=67^\circ$, $y=10^\circ$, $z=21^\circ$ (cf. figures 6, 7, slightly more posterior collapse); fig. 9, UI X-6369, somewhat disarticulated, probably oblique axial collapse; fig. 12, UI X-6371, oblique lateral collapse from side and behind, $x=62^\circ$, $y=5^\circ$, $z=28^\circ$ (cf. figures 8, 9, slightly more posterior collapse); fig. 13, UI X-6372, oblique lateral collapse from side and in front, $x=64^\circ$, $y=5^\circ$, $z=26^\circ$ (cf. figures 6, 7), but collapse from front and below,

rather than rear and above); fig. 14, UI X-1480, oblique dorso-ventral collapse, $x=59^\circ$, $y=30^\circ$, $z=8^\circ$ (see figures 2, 3; refigured by Rhodes 1952, pl. 126, fig. 11, Dzik 1976, fig. 10b, Sweet 1985, fig. 1, Aldridge 1987, fig. 1.6, Aldridge *et al.* 1987, fig. 4.12A, Clark 1987 fig. 20.2B, Sweet 1988, p. 2 (image reversed), Weddige 1989, fig. 5, von Bitter and Merrill 1990, fig. 1A, Purnell *et al.* 1995, fig. 6); fig. 17, UI X-6374, lateral collapse from side and slightly behind, $x=32^\circ$, $y=12^\circ$, $z=55^\circ$ (cf. figures 4, 5); fig. 21, UI X-6377, lateral collapse from side and slightly behind, $x=43^\circ$, $y=4^\circ$, $z=47^\circ$ (see figures 8, 9, refigured by Aldridge 1987, fig. 1.2, Aldridge *et al.* 1987, fig. 4.2A, Weddige 1989, fig. 6, Aldridge 1990, fig. 1, Purnell *et al.* 1995, fig. 5). Du Bois' collection restudied as part of this investigation.

Cooper 1945: Lower Carboniferous, Kentucky, USA; partial apparatus, unfigured.

Schmidt 1950: Namurian, Arnsberg, Germany; sketch figures, several reconstructed assemblages illustrated; fig. 7a, disarticulated remains of 2 individuals.

Rhodes 1952: Pennsylvanian, Illinois and Kentucky, USA; studied >100 bedding plane assemblages of *Idiogonathodus*, *Gondolella* (prioniodinid), and *Idioprioniodus* (prioniodinid), including material of Du Bois (1943); pl. 126, figs 1, 5, 6, 8 and 10, partial remains, 1, 5 and 6 retaining some primary architecture; fig. 9, UI X-1489, complete apparatus, oblique collapse, probably from side, above and behind, but partly disarticulated, $x=36^\circ$, $y=10^\circ$, $z=52^\circ$ (cf. figures 24, 25; refigured by Avcin 1974, pl. 1, fig. 10); fig. 11, refigured UI X-1480 (Du Bois 1943, pl. 25, fig. 14). The remains of *Idioprioniodus* and *Gondolella* (pls. 128 & 129) are partial and/or disarticulated, many probably faecal (e.g., pl. 129, fig. 13, UI X-1505, includes elements of *Gondolella* and *Neognathodus*). Rhodes' collection of assemblages of *Idiogonathodus* restudied as part of this investigation.

Schmidt and Müller 1964: lower Namurian, Hemer, Sauerland, Germany; >50 bedding plane assemblages, 7 prepared by acid dissolution of elements followed by rubber casting, and illustrated by line drawings; figured specimens are remains of single *Gonathodus* apparatuses except: fig. 9, IMGP Gö 600-17, disarticulated, faecal, elements from one or two *Gonathodus* apparatuses and an *Idioprioniodus* (prioniodinid), fig. 10, IMGP Gö 600-16, partial apparatus of *Idioprioniodus*. Fig. 1, IMGP Gö 600-12, lateral collapse from side and slightly below, some disruption of P element articulation, $x=19^\circ$, $y=6^\circ$, $z=70^\circ$ (reillustrated by Huddle 1972, fig. 2, Müller 1978, fig. 12); fig. 3, IMGP Gö 600-22, disrupted, probably faecal; fig. 5, IMGP Gö 600-3, oblique dorso-ventral collapse from above, behind and slightly to left, $x=17^\circ$, $y=64^\circ$, $z=20^\circ$ (angle of collapse forwards has rotated Sb1 elements backwards); fig. 6, IMGP Gö 600-23, lateral collapse, $x=37^\circ$, $y=1^\circ$, $z=53^\circ$ (cf. figures 8, 9; reillustrated by Rietschel 1973, fig. 7); fig. 7, IMGP Gö 600-44, oblique lateral collapse from front left and slightly below, $x=33^\circ$, $y=14^\circ$, $z=54^\circ$ (see figures 16, 17; refigured by Lane and Ziegler 1984, pl. 1). Schmidt and Müller's collection restudied as part of this investigation.

Rexroad and Nicoll 1964: Silurian, northern Indiana, USA; 2 partial fused clusters of *Ozarkodina*, 1 Pa element pair, 1 Pb pair.

Lange 1968: Upper Devonian, Rheinisches Schiefergebirge, Germany; collection of ~70 clusters, 5 figured; fig. 1, very partial prioniodinid cluster; fig. 2, very partial ozarkodinid cluster; pl. 1, complete apparatus of *Palmatolepis*, faecal, but retaining some original juxtaposition of elements (reillustrated by Weddige 1989, fig. 7); pls 3 & 4, cluster of 2 ozarkodinid apparatuses, faecal, but preserving some aspects of primary architecture; pl. 5, cluster of *Belodella* (belodellid).

Austin and Rhodes 1969: single fused cluster, very incomplete apparatus of *Syncladagnathus*, no primary architecture preserved.

Pollock 1969: Silurian, northern Indiana, USA; collection of 54 fused clusters of *Ozarkodina* and *Panderodus* (panderodontid), 25 ozarkodinid clusters figured; most clusters very incomplete remains of single individuals (pl.

110, figs. 1-9, 14-17, pl. 111, figs 1, 2, 6-13, pl. 112, figs 7, 8, 11-16); pl. 111, fig. 3, IU-IGS 11815, partial apparatus, oblique lateral collapse from the posterior, $x=61^\circ$, $y=22^\circ$, $z=19^\circ$ (cf. figures 6, 7, more lateral and from right); pl. 111, figs 4, 5, IU-IGS 11843, partial apparatus, oblique lateral collapse, $x=75^\circ$, $y=1^\circ$, $z=15^\circ$ (cf. figures 6, 7); pl. 111, figs 14, 15, IU-IGS 11803, partial apparatus, S elements only, lateral collapse; pl. 111, fig. 16, IU-IGS 11817, partial apparatus, oblique lateral collapse from behind and slightly below, $x=69^\circ$, $y=0^\circ$, $z=21^\circ$ (cf. figures 6, 7, but from right); pl. 112, figs 1, 2, IU-IGS 11818, almost complete apparatus, axial collapse from below, $x=73^\circ$, $y=17^\circ$, $z=3^\circ$; pl. 112, fig. 3, IU-IGS 11820, partial apparatus, no primary architecture, ?faecal; pl. 112, fig. 4, IU-IGS 11814, partial apparatus, S elements only, axial collapse from below; pl. 112, figs 5, 6, IU-IGS 11807, partial apparatus, S elements only, lateral collapse; pl. 112, figs, 9, 10, IU-IGS 11819, partial apparatus, S elements only, oblique lateral collapse, slightly behind and below.

Scott 1969: Mississippian, Heath Formation, Montana, USA; illustrated nine bedding plane assemblages as sketches, most appear to be *Lochriea*, all probably faecal, no primary architecture (cf. opinion of Scott).

Collinson et al. 1972: figured single disarticulated apparatus of *Idiognathodus*, ISGS 57P-1, from the Avcin thesis collection.

Huddle 1972: figured Hinde's (1879) large faecal assemblage, and reillustrated IMGP Gö 600-12 (Schmidt and Müller 1964, fig. 1).

Mashkova 1972: Lower Devonian, Tadzhikistan; fig. 2, pl. 1, CGM 1/10499, single specimen of *Ozarkodina*, oblique lateral collapse from side and below, $x=50^\circ$, $y=20^\circ$, $z=33^\circ$ (see figures 20, 21; reillustrated by Dzik 1976, fig. 10c, Barskov and Alekseev 1986, pg.68, Weddige 1989, fig. 5, Dzik 1991, fig. 3A, Dzik 1992, fig. 9.16).

Rietschel 1973: fig. 7, reillustrates IMGP Gö 600-23 (Schmidt and Müller 1964, fig. 6).

Scott 1973: Mississippian, Bear Gulch Limestone Member, Montana, USA; pl. 1, figs 1 & 2, pl. 2, figs 1 & 2, USNM 183567, 183568, disarticulated faecal assemblage of *Cavusgnathus* (reillustrated by von Bitter and Merrill 1990, fig. 1A, D); pl. 3, fig. 2, UM 6028, *Kladognathus* (prioniodinid) within a *Typhloesus* (reillustrated by Melton and Scott 1973, fig. 17, Conway Morris 1985, pl. 1, fig. 7, Conway Morris 1989, fig. 1.6, Conway Morris 1990, figs 25, 26, and Purnell 1993, fig. 4).

Melton and Scott 1973: Mississippian, Bear Gulch Limestone Member, Montana, USA; gut contents of *Typhloesus*, fig. 13, UM 6027, disarticulated apparatus of *Kladognathus*; fig. 17, refigured UM 6028 (Scott 1973, pl. 3, fig. 2); fig. 19, UM 6030, sketch of apparatuses of >1 *Adetognathus*, one retaining some primary architecture (also figured by Conway Morris 1985, pl. 2, fig. 2, 1990b, figs 16, 18).

Avcin 1974: Pennsylvanian, Illinois, USA; unpublished thesis, re-examined Du Bois (1943) and Rhodes (1952) collections, plus ~300 new assemblages from Bailey falls locality, ~200 from other localities. ~40 assemblages figured, many partial and/or disarticulated, but several collapsed apparatuses of *Idiognathodus*. Pl. 1, fig. 4, ISGS 57P-180, oblique lateral collapse from side, behind and slightly above, $x=59^\circ$, $y=12^\circ$, $z=29^\circ$ (refigured by Aldridge et al. 1987, fig. 4.9A); pl. 1, fig. 8, pl. 2, fig. 1, ISGS 57P-72I, oblique lateral collapse from side and below, $x=1^\circ$, $y=40^\circ$, $z=50^\circ$ (cf. figures 10, 11; refigured by Aldridge et al. 1987, fig. 4.8A); pl. 1, fig. 10, reillustrated UI X-1489 (Rhodes 1952, pl. 126, fig. 9); pl. 2, fig. 12, ISGS 57P-129(A) I, half apparatus, lateral collapse (cf. figures 4, 5); pl. 2, fig. 19, ISGS 57P-38(A) I, collapse from behind and slightly to side, $x=71^\circ$, $y=9^\circ$, $z=17^\circ$ (cf. figures 6, 7; refigured by Aldridge et al. 1987, fig. 4.4). Avcin's collection of *Idiognathodus* assemblages restudied as part of this investigation.

Behnken 1975: Permian, Minnekahta Member, Goose Egg Formation, South Dakota, USA; three partial clusters of *Ellisonia excavata*, pl. 1, fig. 9, two Sc elements, fig. 10, two ?Pb elements, fig. 14, Sa, Sc and M element.

Higgins 1975: Westphalian, Staffordshire, UK; pl. 6, figs 13, 15, 16, two partial clusters of two elements; pl. 14, fig. 14, (SAD 663 K5) incomplete fused cluster, Pa, S and M elements, ?faecal, but retains some evidence of element juxtaposition

Dzik 1976: fig. 10b, reillustrated UI X-1480 (Du Bois 1943, pl. 25, fig. 14), fig. 10c, reillustrated CGM 1/10499 (Mashkova 1972, fig. 2, pl. 1).

von Bitter 1976: figured several assemblages of *Gondolella* (prioniodinid) and a partial *Idioproniodus* (prioniodinid); all appear to be faecal, partial, or disrupted, with little if any primary architecture preserved. Figs 13A, 13B, 14A, 14B, 15A, 15B, reillustrated UI X-1505, UI X-1506, UI X-1507, UI X-1508, UI X-1503, UI X-1504 (Rhodes 1952, pl. 129, figs 13, 11, 10, 12, 8, 9); fig. 16, reillustration of Assemblages 2 of Jones (1938).

Norby 1976: Mississippian, Heath and Tyler formations, Montana, USA; unpublished thesis collection of ~400 assemblages, 29 assemblages figured. Pl. 4, fig. 1, ISGS 62P-1A, *Gnathodus bilineatus*, partial, probably faecal; pl. 4, fig. 2, ISGS 62P-401A, *Cavusgnathus altus*, disrupted, incomplete (reillustrated by von Bitter and Merrill 1990, fig. 1B); pl. 8, fig. 1, ISGS 62P-21A, *G. bilineatus*, oblique collapse from behind, to one side and below, some disarticulation, $x=56^\circ$, $y=30^\circ$, $z=16^\circ$ (cf. figures 6, 7); pl. 8, fig. 2, ISGS 62P-2A, *G. bilineatus*, collapse from behind, slightly to right, and very slightly above, $x=65^\circ$, $y=18^\circ$, $z=17^\circ$ (cf. figures 2, 3, angle of collapse more axial; refigured by Sweet 1988, p. 2); pl. 8, fig. 3, ISGS 62P-6A-1, *G. bilineatus*, partial, no primary architecture; pl. 8, fig. 4, ISGS 62P-17A, *G. bilineatus*, possibly disrupted axial collapse, or faecal; pl. 8, fig. 5, ISGS 62P-19A, *G. bilineatus*, oblique collapse from above, front left, slight post mortem disruption, $x=37^\circ$, $y=38^\circ$, $z=31^\circ$ (cf. figures 22, 23); pl. 8, fig. 6, pl. 10, fig. 5, ISGS 62P-16A, disarticulated probable faecal assemblage of a *G. bilineatus* and an *Idioproniodus* (prioniodinid) (refigured by Norby and Avcin 1987, pl. 9.1, fig. 7); pl. 8, fig. 7, ISGS 62P-12A, *G. bilineatus*, possible oblique lateral collapse from side and behind (cf. figures 6, 7); pl. 8, fig. 8, ISGS 62P-3A, *G. bilineatus*, incomplete, disrupted, no primary architecture; pl. 8, fig. 9, ISGS 62P-20A, *G. bilineatus*, disarticulated, no primary architecture; pl. 8, fig. 10, ISGS 62P-13A, *G. bilineatus*, disarticulated, remnants of S element juxtaposition; pl. 10, fig. 2, ISGS 62P-604, *Idioproniodus* (prioniodinid), incomplete, no primary architecture (refigured by Norby and Avcin 1987, pl. 9.1, fig. 3); pl. 10, fig. 4, ISGS 62P-605, *Idioproniodus* (prioniodinid), incomplete, no primary architecture (refigured by Norby and Avcin 1987, pl. 9.1, fig. 2); pl. 13, fig. 1, CM 33965, *Lochriea commutata*, disrupted, little if any primary architecture; pl. 13, fig. 2, pl. 14, fig. 6, ISGS 62P-217A, *L. commutata*, disrupted oblique lateral collapse; pl. 13, fig. 3, ISGS 62P-213A, *L. commutata*, faecal, no primary architecture; pl. 14, fig. 1, ISGS 62P-208, *L. commutata*, faecal, no primary architecture; pl. 14, fig. 2, ISGS 62P-601A, faecal assemblage of *G. bilineatus* and *Idioproniodus* (prioniodinid); pl. 14, fig. 3, ISGS 62P-204A, 3 or 4 apparatuses of *L. commutata*, possibly faecal, but some apparatuses retain architectural information (e.g., uppermost apparatus, oblique lateral collapse, only slightly disarticulated, $x=32^\circ$, $y=10^\circ$, $z=57^\circ$); pl. 14, fig. 4, ISGS 62P-205A, *L. commutata*, faecal, no primary architecture; pl. 14, fig. 5, ISGS 62P-206A, *L. commutata*, faecal, 2 apparatuses, no primary architecture; pl. 14, fig. 7, ISGS 62P-207A, *L. commutata*, lateral collapse, post mortem separation of P and S elements; pl. 14, fig. 8, ISGS 62P-216A, *L. commutata*, oblique lateral collapse from the side, slightly in front and slightly above, $x=29^\circ$, $y=6^\circ$, $z=60^\circ$ (cf. figures 20, 21); pl. 14, fig. 9, ISGS 62P-210, *L. commutata*, oblique collapse from behind, above and to one side (cf. figures 24, 25); pl. 19, fig. 1, ISGS 62P-701A, *Vogelgnathus campbelli*, disarticulated, no primary architecture, ?incomplete (<9 S elements; refigured by Norby and Rexroad 1985, fig. 4, pl. 1, figs 1, 2); pl. 19, fig. 2, ISGS 62P-602A, B, faecal assemblage of *Idioproniodus* (prioniodinid) and *G. bilineatus*, partial, no primary architecture; pl. 19, fig. 3, pl. 10, fig. 1, ISGS 62P-603, *Idioproniodus* (prioniodinid), disarticulated, no primary architecture (refigured by Norby and Avcin 1987, pl. 9.1, fig. 1); pl. 19,

fig. 4, pl. 10, fig. 3, ISGS 62P-751, *Kladognathus* (prioniodinid), partial (refigured by Norby and Avcin 1987, pl. 9.1, fig. 4). Most ozarkodinid assemblages in Norby's collection restudied as part of this investigation.

Merrill and von Bitter 1977: Pennsylvanian, USA; *Neognathodus* assemblages; figs 2, 3, 4, 5, 9A, C, refigured assemblage 12 of Burnley (1938), incomplete, disrupted, no primary architecture; figs 6, 7, 8, refigured assemblage 4 of Jones (1938), faecal, very little primary architecture; fig. 1, refigured specimen UI X-1505 (Rhodes 1952, pl. 129, fig. 13), faecal, contains elements from a *Gondolella* and a *Neognathodus* apparatus, no primary architecture.

Nicoll 1977: Upper Devonian, Gogo Formation, Western Australia; articulated apparatus of *Hibbardella angulata* (prioniodinid).

Ramovs 1977: Middle Triassic, central Slovenia; 4 incomplete fused clusters of *Pseudofurnishius* (prioniodinid), one preserving primary architectural information (several refigured by Ramovs 1978).

Müller 1978: fig. 12, reillustrated IMGP Gö 600-12 (Schmidt and Müller 1964, fig. 1).

Ramovs 1978: Middle Triassic, central Slovenia; 92 incomplete fused clusters of *Pseudofurnishius* (prioniodinid), several preserving primary architectural information (some refigured from Ramovs 1977).

Rieber 1980: Middle Triassic, Grenzbitumenzone, Ticino, Switzerland; bedding plane assemblage preserving a complete articulated apparatus of *Neogondolella* (prioniodinid).

Habetin and Knobloch 1981: figure 72, *Hemilistrana*, Zikmundova specimen, some post mortem disarticulation, but reflects oblique collapse from above, left, and behind, $x=46^\circ$, $y=28^\circ$, $z=30^\circ$ (higher and more posterior than figures 24, 25); refigured by Dzik 1991.

Higgins 1981: Westphalian, Staffordshire, UK; *Idiognathoides*, 10 disarticulated, probably faecal assemblages, variable completeness, no primary architecture in figured specimen.

Metcalfe 1981: upper Viséan, North Yorkshire, UK; 3 partial fused clusters of *Gnathodus* S elements preserving some evidence of element juxtaposition.

Mietto 1982: Triassic, Trento, NE Italy; partial fused cluster (Pa pair), *Metapolygnathus* (prioniodinid).

Puchkov et al. 1982: Upper Devonian, northern Urals, Russia; two bedding plane assemblages each preserving an incomplete, disarticulated apparatus of *Palmatolepis*.

Briggs et al. 1983: Lower Carboniferous, Granton Shrimp bed, Edinburgh, UK; figs. 1B, 2A, B, C, 3A, B, IGSE 13821 and 13822, apparatus of *Clydagnathus windsorensis* in head of conodont animal, preservation of apparatus (particularly position of Sb, probably Sb₂ elements, between Sc elements of sinistral and dextral sides, and position of M element) indicates oblique lateral collapse at $\sim 45^\circ$ from axial plane of apparatus, $x=3^\circ$, $y=43^\circ$, $z=47^\circ$ (cf. figures 10, 11). Apparatus refigured by Higgins 1983, p. 107, Briggs 1984, p. 17; Aldridge and Briggs 1986, fig. 8b; Aldridge 1987, fig. 1.9B; Aldridge et al. 1987, fig. 4.2B; Clark 1987, fig. 20.5B, C; Sweet 1988, fig. 3.1B, C; Weddige 1989, fig. 9; Briggs and Crowther 1990, p. 415; Conway Morris 1989, fig. 4; Lane 1992, 10.18; Aldridge et al. 1993, fig. 2. Fig. 6, IGSE 13823, fused cluster of *Clydagnathus windsorensis*, missing P elements, lateral collapse, $x=2^\circ$, $y=2^\circ$, $z=87^\circ$ (cf. figures 18, 19; refigured by Aldridge 1987, fig. 1.4).

Higgins 1983: p. 107, refigured IGSE 13822 (Briggs et al. 1983, figs. 2B, 3B).

Briggs 1984: p. 17, refigured IGSE 13822 (Briggs et al. 1983, figs. 2B, 3B).

Lane and Ziegler 1984: figured IMGP Gö 600-44, fig. 7 of Schmidt and Müller (1964).

Conway Morris 1985: Mississippian, Bear Gulch Limestone Member, Montana, USA; pl. 1, fig. 4, UM 6027, *Kladognathus* (prioniodinid) in *Typhloesus*, no primary architecture (refigured by Conway Morris 1989, fig. 1.5, Conway Morris 1990, fig. 11); pl. 1, fig. 7, refigured UM 6028 (Scott 1973, pl. 3, fig. 2); pl. 1, fig. 9, UM 6029, *Gnathodus bilineatus* in *Typhloesus*, no primary architecture (refigured by Conway Morris 1990, figs 28, 29); pl. 2,

fig. 2, UM 6030, assemblage of 2 apparatuses of *Adetognathus* in *Typhloesus*, one retains some primary architecture (oblique posterior collapse with some post mortem disarticulation; refigured by Conway Morris 1990, fig. 18); pl. 2, fig. 7, UM 6100, bituminous mass of broken conodonts (refigured by Conway Morris 1990, fig. 47).

Norby and Rexroad 1985: fig. 4, pl. 1, figs 1, 2, refigured ISGS 62P-701A, *Vogelgnathus campbelli*, (Norby 1976 pl. 19, fig. 1).

Nicoll 1985: Upper Devonian, Western Australia; collection of >200 fused clusters of *Polygnathus xylus* and *Ozarkodina brevis*. Figs 3C-F, CPC25167-CPC25170, partial clusters of 2-3 S and M elements; figs 4AI, 9B, CPC25171-CPC25179, CPC25202, are partial clusters of 2-3 P elements; 3A, CPC25165, S and M array, lateral collapse from side and very slightly above, $x=15^\circ$, $y=21^\circ$, $z=64^\circ$ (cf. figures 18, 19; P and Sb₁ elements not in contact with other elements and therefore not preserved as part of cluster); fig. 3B, CPC25166, oblique lateral collapse from side and above, $x=3^\circ$, $y=23^\circ$, $z=67^\circ$ (cf. figures 18, 19; slightly higher collapse angle); fig. 4J, CPC25180, ?complete apparatus, oblique axial collapse from slightly above, $x=66^\circ$, $y=24^\circ$, $z=1^\circ$; fig. 5A, CPC25181, partial apparatus, S and M elements only, disrupted lateral collapse (dextral M on sinistral side); fig. 5B, CPC25182, partial apparatus, S and M elements only, disrupted lateral; figs 8A, 9C, CPC25199, disrupted ?axial collapse, $x=84^\circ$, $y=4^\circ$, $z=5^\circ$; fig. 8B, 9D, CPC25200, partial apparatus, oblique lateral collapse from posterior, $x=69^\circ$, $y=12^\circ$, $z=17^\circ$; fig. 9A, CPC25201, partial apparatus, no primary architecture. Much of this collection is lost.

Rhodes and Austin 1985: Carboniferous, UK; figured and described 41 bedding plane assemblages, but all are partial, disrupted, faecal or the remains of >1 individual; none preserves significant architectural information. Collection deposited with British Geological Survey has been re-examined, but much material is missing.

Sweet 1985: fig. 1, refigured UI X-1480 (Du Bois 1943, pl. 25, fig. 14)

Swift and Aldridge 1985: pl. 7.1, fig. 12, partial cluster (fused Pa pair), *Neogondolella*.

Aldridge and Briggs 1986: fig. 5, UN 5545/015 new specimen of *Idiognathodus* from Pennsylvanian, Illinois, USA, oblique lateral collapse from side, above and behind, $x=36^\circ$, $y=8^\circ$, $z=53^\circ$ (cf. figures 12, 13; refigured by Aldridge *et al.* 1987, fig. 4.3, Smith 1987, figs 8.1, 8.2, Black 1988, fig. 170, Aldridge *et al.* 1994, fig. 2); fig. 6, IU-IGS 15169 (specimen missing), cluster of *Ozarkodina* from Silurian of Indiana, USA, $x=71^\circ$, $y=4^\circ$, $z=19^\circ$; fig. 8B, refigured IGSE 13822 (Briggs *et al.* 1983, figs 2B, 3B).

Aldridge *et al.* 1986: Lower Carboniferous, Granton Shrimp bed, Edinburgh, UK; figured apparatuses in head of conodont animals: figs 1A, 3, RMS GY 1986.17.1, gen. indet., probable oblique lateral collapse; figs 6, 8, BM X1065, *Chydagnathus windsorensis*, probable oblique lateral collapse.

Barskov and Alekseev 1986: p. 68, reillustrated CGM 1/10499 (Mashkova 1972, fig. 2, pl. 1).

Aldridge 1987: fig. 1.2, refigured UI X-6377 (Du Bois 1943, pl. 25, fig. 21); fig. 1.4, IGSE 13823 (Briggs *et al.* 1983, fig. 6); fig. 1.6, X-1480 (Du Bois 1943, pl. 25, fig. 14); fig. 1.9B, IGSE 13822 (Briggs *et al.* 1983, figs 2B, 3B).

Aldridge *et al.* 1987: figs 4.5, 4.10, ISGS 57P-170 II (from Avcin 1974, thesis collection), oblique collapse from above and behind, $x=47^\circ$, $y=30^\circ$, $z=28^\circ$ (a little more posterior than figures 24, 25). Refigured: fig. 4.2A, UI X-6377 (Du Bois 1943, pl. 25, fig. 21); fig. 4.2B, IGSE 13822 (Briggs *et al.* 1983, figs 2B, 3B); fig. 4.3, UN 5545/015 (although numbered UN 5830/016 in caption) (Aldridge and Briggs 1986, fig. 5); fig. 4.4, ISGS 57P-38 (Avcin 1974, pl. 2, fig. 19); fig. 4.6A, (Schmidt 1934, figs 5a, b and pl. 6, fig. 1); fig. 4.6B, 4.12A, UI X-1480 (Du Bois 1943, pl. 25, fig. 14); fig. 4.8A, ISGS 57P-72(A) (Avcin 1974, pl. 2, fig. 1); fig. 4.9A, ISGS 57P-180, (Avcin 1974, pl. 1, fig. 4).

Clark 1987: fig. 20.A, reillustrated *Lochriea* assemblage (Scott 1942, pl. 37, fig. 4); fig. 20.2B, reillustrated UI X-1480 (Du Bois 1943, pl. 25, fig. 14); fig. 20.5, reillustrated IGSE 13821 and 13822 (Briggs *et al.* 1983, figs. 1B, 2A, B, C, 3A, B).

Nicoll 1987: figured partial clusters (fused Pa pairs) of *Ozarkodina brevis*, *O. eosteinhornensis*, *Icriodus expansus*, *Polygnathus xylus*.

Nicoll and Rexroad 1987: Silurian, northern Indiana, USA; collection of >700 fused clusters of *Ozarkodina*, 14 clusters figured; pl. 3.1, figs 7-9, IU-IGS 16827-16829, clusters of Pa element pairs only; pl. 3.1, fig. 10, IU-IGS 16830, partial cluster, 3 S elements; pl. 3.2, fig. 1, IU-IGS 16831, almost complete apparatus, oblique axial collapse from above and slightly to the right, $x=77^\circ$, $y=12^\circ$, $z=5^\circ$; pl. 3.2, figs 2, 5, IU-IGS 16832, almost complete apparatus, collapse from below and slightly anterior; pl. 3.2, figs 3, 4, IU-IGS 16833, almost complete apparatus, oblique-lateral collapse from the posterior and slightly below, $x=68^\circ$, $y=10^\circ$, $z=20^\circ$; pl. 3.2, figs 6, 7, IU-IGS 16834, partial apparatus, S and M elements only, oblique-lateral collapse from the posterior and slightly below, $x=52^\circ$, $y=4^\circ$, $z=38^\circ$; pl. 3.3, figs 1, 2, IU-IGS 16835, almost complete apparatus, oblique dorso-ventral collapse from above, front and slightly right, $x=56^\circ$, $y=30^\circ$, $z=16^\circ$; pl. 3.3, figs 3, 4, IU-IGS 16836, ?complete apparatus, oblique dorso-ventral collapse from front and below, $x=75^\circ$, $y=15^\circ$, $z=3^\circ$; pl. 3.4, figs 1, 3, 5, IU-IGS 16837, partial apparatus, lateral collapse (cf. figures 4, 5); pl. 3.4, figs 2, 4, IU-IGS 16838, partial apparatus, S and M elements only, oblique-lateral collapse from anterior and slightly below, $x=38^\circ$, $y=9^\circ$, $z=51^\circ$; pl. 3.5, figs 1, 3, IU-IGS 16829, complete apparatus, oblique axial collapse, from below, slightly to right, $x=68^\circ$, $y=18^\circ$, $z=12^\circ$; pl. 3.5, fig. 2, IU-IGS 16840, partial apparatus, no primary architecture.

Norby and Avcin 1987: plate 9.1, figs 1, 2, 3, 4, 7, refigured ISGS 62P-603, 62P-605, 62P604, 62P715, 62P16A (Norby 1976, pl. 10, figs 1, 4, 2, 3, 5); pl. 9.1, fig. 5, ISGS 62P-313, *Lochriea commutata?*, disrupted, ?oblique collapse from behind, below and to one side; pl. 9.1 fig. 6, ISGS 57P-500, *Idiognathodus?*, ?oblique collapse from behind and to one side.

Smith 1987: figs 8.1, 8.2, refigured UN 5545/015 (Aldridge and Briggs 1986, fig. 5).

Black 1988: fig. 170, refigured UN 5545/015 (Aldridge and Briggs 1986, fig. 5).

Sweet 1988: p. 2, refigured UI X-1480 (Du Bois 1943, pl. 25, fig. 14, reversed); ISGS 62P-2A (Norby 1976, pl. 8, fig. 2); fig. 3.1B, C reillustrated IGSE 13821 and 13822 (Briggs *et al.* 1983, figs. 1B, 2A, B, C, 3A, B).

Weddige 1989: refigured: fig. 5, UI X-1480 (Du Bois 1943, pl. 25, fig. 14), CGM 1/10499 (Mashkova 1972, fig. 2, pl. 1); fig. 6, UI X-6377 (Du Bois 1943, pl. 25, fig. 21); fig. 7, *Palmatolepis* cluster (Lange 1968, pl. 1); fig. 9, IGSE 13821 and 13822 (Briggs *et al.* 1983, figs. 1B, 2A, B, C, 3A, B).

Aldridge 1990: fig. 1, refigured UI X-6377 (Du Bois 1943, pl. 25, fig. 21).

Briggs and Crowther 1990: p. 415, refigured IGSE 13822 (Briggs *et al.* 1983, figs. 2B, 3B).

Conway Morris 1989: fig. 1.5 refigured UM 6027 (Conway Morris, 1985, pl. 1, fig. 4), fig. 1.6 refigured UM 6028 (Scott 1973, pl. 3, fig. 2), fig. 4, refigured IGSE 13822 (Briggs *et al.* 1983, figs. 2B, 3B).

Conway Morris 1990: Mississippian, Bear Gulch Limestone Member, Montana, USA; fig. 11, refigured UM 6027 (Conway Morris 1985, pl. 1, fig. 4); figs 16, 18, refigured UM 6030, assemblage of 2 apparatuses of *Adetognathus* in *Typhloesus*, one retains some primary architecture (oblique posterior collapse with some post mortem disarticulation); figs 25, 26, refigured UM 6028 (Scott 1973, pl. 3, fig. 2); figs 28, 29, refigured UM 6029 (Conway Morris 1985, pl. 1, fig. 9); fig. 47, refigured UM 6100 (Conway Morris 1985, pl. 2, fig. 7s) fig. 64, CM 35527, disarticulated elements in *Typhloesus*; fig. 68, CM 6031, scattered *Kladognathus* (prioniodinid) elements in

Typhloesus; fig. 71, UM 5878, *Cavusgnathus* apparatus in coprolite, some post mortem disruption, but may reflect oblique collapse from above and behind, parallel to long axes of S elements.

von Bitter and Merrill 1990: fig. 1A, refigured UI X-1480 (Du Bois 1943, pl. 25, fig. 14); fig. 1B, ISGS 62P-401A (Norby 1976, pl. 4, fig. 2); figs 1C, D, USNM 183567, 183568 (Scott 1973, pl. 1, figs 1 & 2, pl. 2, figs 1 & 2).

Dzik 1991: fig. 1, refigured *Hemilistrana*, Zikmundova specimen (Habetin and Knobloch 1981, figure 72; fig. 3A, reillustrated CGM 1/10499 (Mashkova 1972, fig. 2, pl. 1).

Ritter and Baesemann 1991: Lower Permian, Wolfcamp Shale, Texas, USA; collection of nine bedding plane assemblages; 4, identified as *Sweetognathus*, illustrated. None preserves significant primary architecture.

Dzik 1992: fig. 9.16, refigured CGM 1/10499 (Mashkova 1972, fig. 2, pl. 1)

Lane 1992: fig. 10.18, refigured IGSE 13822 (Briggs *et al.* 1983, figs. 2B, 3B).

Aldridge *et al.* 1993: Lower Carboniferous, Granton Shrimp bed, Edinburgh, UK; figured apparatuses of *Clydagnathus windsorensis* in head of conodont animals: fig. 2, refigured IGSE 13822 (Briggs *et al.* 1983, figs 2B, 3B); figs 4, 6, RMS GY 1992.41.1, incomplete, oblique lateral collapse from side and below, $x=25^\circ$, $y=10^\circ$, $z=63^\circ$ (cf. figures 12, 13, but not as far forward; refigured by Aldridge *et al.* 1994, fig. 4, Long 1995, p. 35); fig. 9, RMS GY 1992.41.2, incomplete, $x=29^\circ$, $y=3^\circ$, $z=61^\circ$ (Pa, Pb, and dextral Sb₁, Sc, Sc), lateral collapse from side and slightly behind (cf. figures 8, 9).

Purnell 1993a: fig. 2, BU 2183, bedding plane assemblage of *Idiognathodus* from Pennsylvanian, Illinois, USA; oblique lateral collapse from side, behind and above (cf. figures 24, 25, but slightly more posterior collapse; refigured by Purnell 1994, fig. 2A).

Purnell 1993b: Mississippian, Bear Gulch Limestone Member, Montana, USA; figs 2, 3, ROM 48915, articulated apparatus of *Kladognathus* (prioniodinid) in guts of *Typhloesus* (specimen also contains small apparatus of *Lochriea*); fig. 4, reillustrated UM 6028 (Scott 1973, pl. 3, fig. 2).

Varker 1994: Namurian, North Yorkshire, UK; collection of >60 fused clusters, figured 11 incomplete apparatus clusters of *Gnathodus bilineatus* and *Lochriea*. Pl. 1, fig. 1, MPK 9774, S elements only, ?faecal, preserves some element juxtaposition; pl. 1, fig. 2, MPK 9775, very incomplete, no primary architecture; pl. 1, fig. 3, MPK 9776, S elements, probably faecal, little or no primary architecture; pl. 1, fig. 4, MPK 9777, S array and Pb element, oblique collapse from behind left, $x=56^\circ$, $y=21^\circ$, $z=25^\circ$ (orientation between figures 2, 3 and figures 24, 25; pl. 1, fig. 5, MPK 9778, S and M elements, no primary architecture; pl. 1, fig. 6, MPK 9779, S and M elements, possibly preserving some primary element juxtaposition; pl. 1, fig. 7, MPK 9780, S and M elements and Pa element, axial collapse from behind, $x=74^\circ$, $y=16^\circ$, $z=3^\circ$ (cf. figures 6, 7, but lower and more posterior); pl. 2, fig. 1, MPK 9781, S elements and Pb, probably faecal, possibly preserving some primary S element juxtaposition; pl. 2, fig. 2, MPK 9782, Pa and S fragments, faecal, no primary architecture; pl. 2, fig. 3, MPK 9783, Pa and Sb₁, no primary architecture; pl. 2, fig. 6, MPK 9786, S elements and Pa, probably faecal, possibly preserving some primary S element juxtaposition;

Aldridge *et al.* 1994: fig. 2, refigured UN 5545/015 (Aldridge and Briggs 1986, fig. 5), RMS GY 1992.41.1 (Aldridge *et al.* 1993, figs 4, 6).

Purnell 1994: fig. 2A, refigured BU 2183 (Purnell 1993, fig. 2); fig. 2B, *Gnathodus bilineatus* (from Norby 1976, thesis collection), some post mortem disruption, oblique lateral collapse from side, above and behind (cf. figures 24, 25).

Stone and Geraghty 1994: Pennsylvanian, Carbondale Formation, Illinois, USA; figs 1, 2. (ISGS 100P-19B) partial apparatus of *Idioprioniodus* (prioniodinid), disarticulated, no primary architecture.

Long 1995: p. 35, refigured RMS GY 1992.41.1 (Aldridge *et al.* 1993, figs 4, 6).

Merrill and von Bitter 1995: described new assemblage of *Neognathodus*, almost complete apparatus, one individual, elements parallel; possibly reflects axial collapse, but disruption of P elements, orientation of M element, and juxtaposition of S elements indicates that faecal origin likely, with little primary architecture preserved (cf. Merrill and von Bitter 1995; photographs kindly provided by G. K. Merrill and P. H. von Bitter).

Nicoll 1995: text-fig. 5, four incomplete fused clusters, P elements only.

Purnell *et al.* 1995: figs 5, 6, refigured IU X-6377 (Du Bois 1943, pl. 25, fig. 21), and IU X-1480 (Du Bois 1943, pl. 25, fig. 14).

Weddige and Hüsken 1995: Lower Devonian, Germany; collection of >250 bedding plane assemblages, ~30 thought by authors to preserve primary architecture, none figured, but collapse patterns probably consistent with our model (personal observation; cf. Weddige and Hüsken).

CHAPTER 2

Growth and Patterning in the Conodont Skeleton

SUMMARY

Recent advances in our understanding of conodont palaeobiology and functional morphology have rendered established hypotheses of element growth untenable. In order to address this problem, I have undertaken an extensive review of hard tissue histology paying particular attention to the relationships during growth of the component hard tissues comprising conodont elements, and ignoring *a priori* assumptions of the homologies of these tissues. Conodont element growth has been further considered in terms of the pattern of formation, of which four distinct types are described which may all be derived from a primitive condition after heterochronic changes in the timing of various developmental stages. It is hoped that this may provide further means of unravelling conodont phylogeny. The manner in which the tissues grew is considered homologous with hard tissues of other vertebrates, and the elements appear to have grown in a way similar to the growing scales and growing dentition of other vertebrates such as acanthodians and lungfish.

1. INTRODUCTION

The affinity of the conodont animal has been the subject of debate ever since its microscopic tooth-like elements were first discovered (Pander 1856; see Aldridge 1987 for a review). This topic remains controversial even after 140 years of research and the discovery of soft tissue remains of the conodont animal itself. More recent discussion has narrowed the debate to the acraniate-craniate level within the chordates, based primarily on characters of soft tissue anatomy (Aldridge *et al.* 1993; Aldridge and Purnell 1996; Aldridge and Donoghue *in press*).

In the years preceding the discovery of preserved soft tissues, the affinity of the tooth-like phosphatic microfossils remained enigmatic. Palaeobiologists had attempted to resolve the affinity conundrum using comparative anatomy of the architecture of the feeding apparatus (e.g. Schmidt 1934, 1950; Schmidt and Müller 1964), element morphology, and histology. Though there are some notable exceptions, histological studies failed to take full advantage of comparative histology, and without any degree of constraint over affinity this proved an unprofitable line of research, resulting in a series of esoteric accounts of hard tissue ultrastructure.

In retrospect, it was never possible to reach an unequivocal conclusion regarding conodont affinity just by analysing element morphology and internal structure. A parallel can be seen in the debate over the affinity of *Hadimopanella*, which is represented in the fossil record almost exclusively by microscopic phosphatic sclerites. The sclerites are two-component hard tissue complexes composed of a microcrystalline base containing tubules, overlain by a hypermineralised glassy cap (Bengtson 1977). The structure and morphology of the sclerites, therefore, made *Hadimopanella* and related taxa convincing micromeric agnathans (Dzik 1986; Märss 1988; van den Boogaard 1988). However, the discovery of exceptionally preserved specimens composed of secondarily phosphatised soft-tissues and articulated sclerites revealed *Hadimopanella* to be a palaeoscolecoid, a poorly known group of Early Palaeozoic worms (Hinz *et al.* 1991; Müller and Hinz 1993).

Now that we have a much clearer perception of conodont affinity, a new era in conodont comparative histology has begun. Dzik (1986), Sansom *et al.* (1992), and to a lesser extent, numerous others, have reviewed element histology in the context of our new phylogenetic understanding. The drawback of these studies is their reliance on direct comparison between specific structures within tissues, without considering other factors such as the interplay between the component hard tissues during growth. Because they failed to consider relative growth, these authors were unable to reconcile their interpretations with existing models of growth in conodont elements,

or knowledge of tissue interaction in modern organisms. These studies have also been criticised because of their failure to consider the full spectrum of chordate hard tissues (Kemp and Nicoll 1995a).

One subject that has been ignored entirely is pattern formation. At present, we have only a broad understanding of how a few conodont elements grew, and then only at the simplest level. The growth of more complex elements can only be resolved by identifying recurrent patterns of growth in the internal structure of the hard tissues. Furthermore, there are a number of recurrent morphological patterns expressed by conodont elements through their fossil record. Do these reflect common ancestry or convergence? The pattern of formation is potentially a useful tool in discriminating homology from analogy. Knowledge of pattern formation would also be useful in comparing the growth of conodont elements with other vertebrate hard tissue complexes, and would enable investigation of the complexity shown during this early craniate experiment with the dermal skeleton.

The present study addresses interpretation of the hard tissues after consideration of growth and patterning, and is organised into two sections. The first entitled 'pattern' is concerned primarily with the description of conodont hard tissues and their patterns of intergrowth. A new model of conodont hard tissue growth is presented, based on these patterns, and patterns of whole element growth are described. The second section entitled 'process' evaluates competing hypotheses of hard tissue homology in the light of results from the first section, and a new interpretation of hard tissue histology is outlined. Patterns of whole element growth are evaluated in the light of these results, and compared with those shown by the hard tissues of taxa outside the Conodonta.

2. A HISTORICAL REVIEW OF STUDIES OF CONODONT HARD TISSUE HISTOLOGY

In the first paper on conodonts, it was Pander (1856) who first addressed the histology of conodont elements. He was the first to note the lamellar nature of crown tissue and the presence of cells or cavities within the albid white matter. However, Pander incorrectly interpreted the direction of growth in the crown as inward, and it was more than 80 years before this was corrected by the work of Furnish (1938) and Hass (1941).

Although intervening years were occupied by various contentions over the affinities of conodonts, 30 years elapsed before Zittel and Rohon's (1886) review of conodont histology and affinities. Zittel and Rohon were the first to attempt to homologise conodont hard tissues with those of another group. They considered lampreys and annelids as possible descendants, and compared the ultrastructure of the toothlets of these two groups with the histology of conodont hard tissues, concluding that conodonts were annelids.

Stauffer and Plummer (1932) provided an excellent review of the conodont controversy to that time. They compared their own observations on element microstructure with ivory (dentine), and also tentatively considered conodont element growth, concluding that the denticles, which were composed of white matter, were inserted into elements after the hyaline crown tissue had been fully formed.

Branson and Mehl (1933) were the first to use histology as a taxonomic character in conodonts, recognising a group of 'fibrous' conodonts, the Neurodontiformes, which they later erected to the rank of suborder, distinct from all other conodonts (Branson and Mehl 1944).

Furnish (1938) briefly considered the growth of conodont elements, clarifying the mode of outer apposition of successive crown tissue layers, and was probably also the first to recognise internal discontinuities in the crown as evidence of *in vivo* damage and repair. This observation is normally attributed to Hass (1941), who recognised the relevance of internal discontinuities as evidence of external and not internal growth. Hass also noted the occurrence of hollow spaces or tubules within white matter and the presence of interlamellar spaces in

lamellar crown tissue. Beckmann (1949) later exhumed Pander's contention of vertebrate affinity, interpreting all component hard tissues as dentine. He was the first to develop a model for conodont element growth, and this is still the only paradigm to have considered the morphogenesis of complex elements (figure 1*a*). Beckmann identified cavities within lamellar crown tissue that he believed to have been interconnected, and to have supplied nutrients from the pulp (basal cavity) to interconnected tubules within white matter. He believed that the nutrients were finally transported to the outer surface of the element which was covered by a temporary mesh-like secreting tissue. The renowned vertebrate histologist Ørvig (1951) considered Beckmann's model "untenable" (p.381), as in his opinion, "the substance of which the cusps are built up is clearly different from all hard tissues met with in vertebrates" (p.381). However, Ørvig's criticisms were only aimed at the final proposed homology of the hard tissues with dentine and did not consider the growth model itself. The presence of the cavities within lamellar crown tissue has subsequently been verified by light microscopy (Müller and Nogami 1971, 1972) and electron microscopy (Barnes *et al.* 1973a, who similarly suggested that their function was to transport nutrients); that they are interconnected has yet to be demonstrated. Interconnections between the white matter cavities that could facilitate transport of fluids from the basal cavity to the external surface of the crown are not present, and Pietzner *et al.* (1968) failed to find any evidence of interconnection whatsoever. Therefore, Beckmann's model is untenable not because the component tissues of conodont elements fail to resemble dentine, but because there is no ultrastructural evidence to support his paradigm.

Gross, another distinguished vertebrate histologist, published a series of considered studies on conodont microstructure (Gross 1954, 1957, 1960), in which he compared conodont hard tissues with those of vertebrates, particularly heterostracan dermal armour. Gross believed that growth increments within the crown did not coincide with the ridges apparent in the basal cavity or on the recessive basal margin (figure 1*b, ci*) which align with the incremental layers in the basal tissue. He conceded that the ridges were parallel with the incremental layers of the crown, but he concluded that incremental layers in the crown and basal body were not secreted synchronously, and invoked an elaborate, *ad hoc* hypothesis whereby special cells partially resorbed each incremental layer of crown tissue shortly after their secretion and prior to secretion of the subsequent layer of basal tissue. In this way, concentric ridges were formed over the base of the crown, parallel to the incremental layers, but not coinciding with them (figure 1*ci*). Hence the incremental layers abut with these ridges, but are not confluent with incremental layers within the crown. However, Gross believed that the earliest phase of growth was restricted to the crown, although his contention was probably based on oblique thin sections, or sections which failed to coincide with the growth centre of the elements. Furthermore, he did not perceive the basal body as a homogeneous structure, and proposed instead that it was composed of a 'Basistrichter' and 'Trichterfüllung' (basal cone and cone-filling). Gross rejected the idea that conodont hard tissues were homologous with dentine and enamel as he erroneously believed that the conodont mode of centrifugal growth was incompatible with such an interpretation. He instead concluded that the elements were composed of exoskeletal bone. Gross's model of conodont element growth was subsequently negated by Müller and Nogami (1971) who clearly demonstrated the confluent passage of growth increments between crown and basal body (figure 1*cii, d*).

Quinet (1962a) provided a detailed account of the histology of *Ancyrodella* and *Polygnathus* Pa elements, confirming much of Hass's work and concluding that conodont elements could not have been teeth, or have performed a tooth function, because of their outer-appositional mode of growth. He also suggested that the ultrastructure of the elements compared well with exoskeletal bone, which is also covered by soft tissue in life. In a later publication, Quinet (1962b) described the histology of *Belodus* sp. with which he favourably compared the

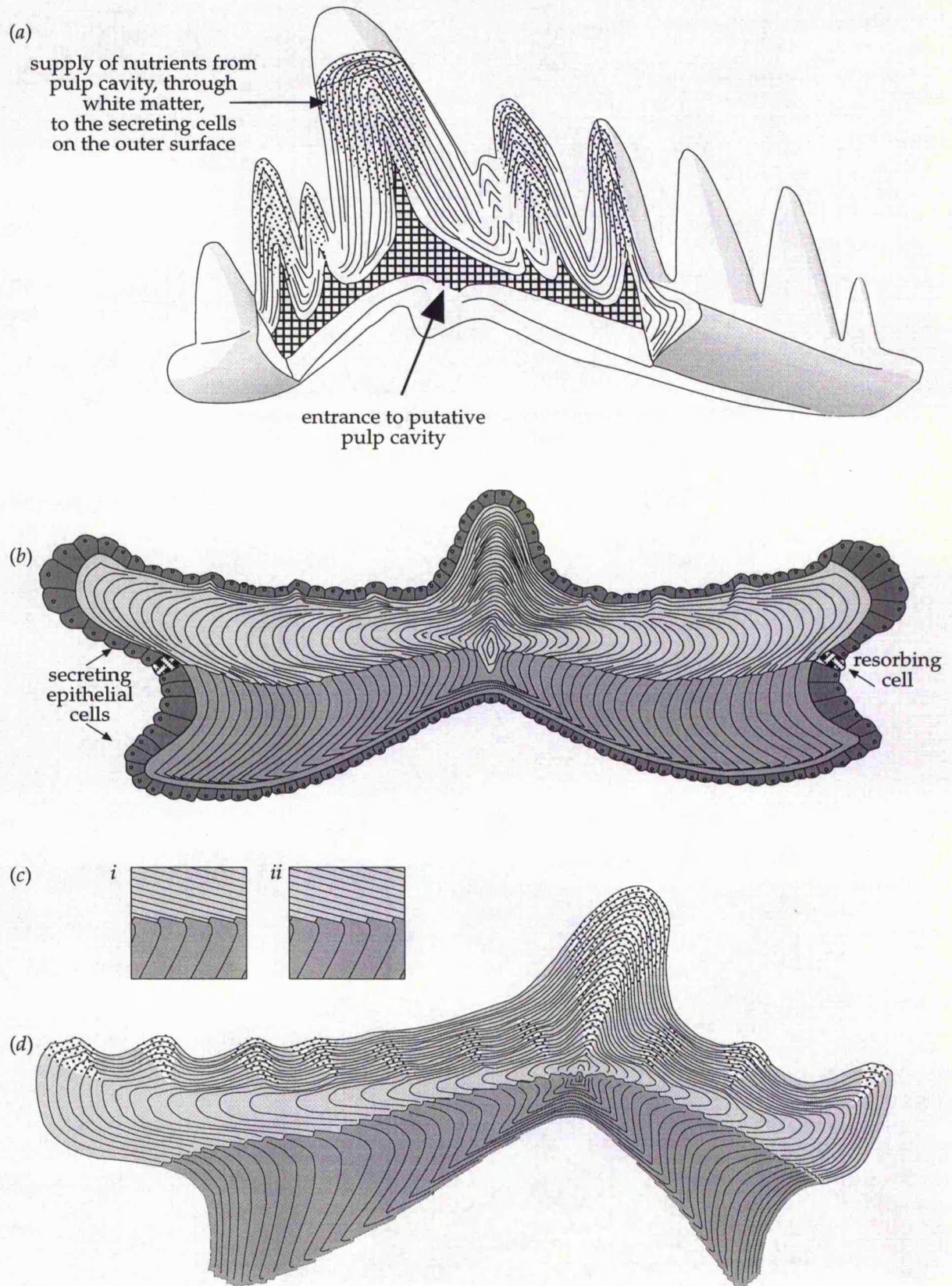


Figure 1. Previous growth hypotheses of Beckmann 1949, Gross 1957, 1960 and Müller and Nogami 1971, 1972. (a) Beckmann's was the only model to account for growth in multidenticulate elements. (b) Gross believed that growth increments within the crown had not been secreted synchronously with those of the basal body. (c) Comparison of (i) Gross' and (ii) Müller and Nogami's hypotheses of growth. (d) Müller and Nogami finally resolved the synchronous growth relationship between the crown and basal body.

feeding elements of the polychaete *Nereis*, concluding that *Belodus* was a polychaete, and that the Conodonts represented a polyphyletic group.

One of the most unconventional interpretations of conodont affinity was proposed by Fahlbusch (1964) who partly justified his hypothesis on histological grounds. Fahlbusch compared the histology of conodont elements to fossil algal material, reinterpreting Gross's model of growth for conodonts to fit his predilections. Fahlbusch's model was poorly received and severely criticised (Beckmann *et al.* 1965).

Lindström (1955) made preliminary observations on the histology of Lower Ordovician conodont elements, describing basal bodies with lamellar and globular internal structures. Later, in his 'state of the art' text Lindström (1964) reviewed all aspects of earlier research and produced an excellent outline of conodont ultrastructure. His conviction that "One may assume *a priori* that the inner structure must have a great systematic significance, greater perhaps than that of the surface morphology" (1964, p.22) was to spark new interest in the histology of conodont elements that was sustained for the following two decades. Amongst many other observations and contentions, he believed that white matter had been formed by a process of resorption of crown tissue resulting in a series of hollows and inclusions within an otherwise lamellar structure (following Gross 1954). He resolved Gross's (1957, 1960) bizarre two-part division of the basal body into a single structure with partially discontinuous growth increments, and cast doubt on the basal resorption hypothesis by demonstrating the clear relationship between lamellar crown increments and the ridges on the aboral surface of elements. Lindström also disagreed with Gross's suggestion that the conodont crown was homologous with exoskeletal bone, but followed Gross's erroneous reasoning in discounting enamel and dentine as component tissues of the conodont skeleton.

Schwab (1965) described lamellar structure in the crowns of neurodontiformes, thereby reinstating them as conodonts. Schwab also distinguished the two structural forms of basal body: a 'cartilage-like' lamellar structure and a 'bone-like' spherular structure, later reinterpreted as atubular dentine (Sansom 1996) and globular calcified cartilage (Sansom *et al.* 1992) respectively. In a later paper (Schwab 1969) Schwab described the histology of *Panderodus denticulatus* as three-layered, including an inner lining surrounding the basal cavity, and inner and outer lamellar layers, the latter containing what he believed to be dentine tubules. His distinction of separate layers is tenuous, and the 'dentine tubules' he described from the outer lamellar layer more probably represent alignment of the long (c) axes of the component crystallites.

Müller and Nogami (1971, 1972) produced the last reviews that were primarily based on light microscope study. These were probably the most influential of all works on conodont histology, describing a wide range of conodont taxa and producing a taxonomic grouping based solely on the internal structures of elements. Although often attributed to Gross, Müller and Nogami were also responsible for resolving the pattern of synchronous growth between the crown and basal body (figure 1*cii,d*). They also elaborated on Staesche's (1964) histological work by distinguishing a number of different types of white matter, which they proposed would be useful in taxonomy.

Three years earlier than Müller and Nogami (1971), the first of a series of studies which heralded a new era in ultrastructural research had been undertaken by Pietzner and colleagues (1968). This work included geochemical, transmission electron microscope (TEM) and scanning electron microscope (SEM) analyses of conodont elements, through which these authors refined knowledge of chemical composition and of the varying organic content of different tissues. They also described the discrete porous nature of white matter, and the structure of the other hard tissues. Structural differences between the crown and the basal body, including different crystal sizes and organic matter content were also noted. Pierce and Langenheim (1969) were the only

other authors to attempt a TEM study, in this case using Pa elements of *Palmatolepis* and *Polygnathus*, but their work failed to reveal any new or useful information.

An SEM study of fractured surfaces led Lindström and Ziegler (1971) to conclude that white matter was secondarily derived from lamellar crown tissue by a process of recrystallisation during the animal's life. In a later paper (Lindström and Ziegler 1972) they documented variation in crystal structure throughout the various tissues, and suggested that the crown and basal body were not secreted synchronously, although each corresponding increment of the two tissues had been secreted in step. They suggested that the basal tissue increment was secreted first, and was subsequently matched by an increment of crown tissue. However, they presented no evidence in support of this paradigm. They went on to review advances of conodont histology published since Lindström's 1964 monograph, paying particular attention to alternative interpretations of the growth of protuberances on the surfaces of Pa elements of *Pseudopolygnathus* (Ziegler and Lindström 1975).

During the early 1970s Barnes and his co-workers published a series of studies on conodont histology with the aim of constructing a suprageneric classification scheme based on ultrastructure (Barnes *et al.* 1970, 1973a, b, 1975). This work revealed a number of characters which appear unique to specific groups, thereby at least partially fulfilling their objective. Most notably, a new internal microtexture was described from neurodontiform hyaline elements - elongate crystallites containing microspheres 0.5µm in diameter. Later, Wright (1989, 1990) interpreted these structures as microspherules expelled by golgi apparatuses during mineralisation. The Barnes team advocated a secondary origin for white matter from lamellar crown tissue, supporting the earlier contention of Lindström (Lindström 1964; Lindström and Ziegler 1971; Lindström *et al.* 1972).

Bengtson (1976, 1983) described and compared the histology of proto-, para-, and eu-conodonts, proposing that they represented an evolutionary series. Szaniawski (1982, 1983, 1987) compared the most primitive group, protoconodonts, with the histology of modern chaetognath spines, concluding that protoconodonts were indeed the spines of fossil chaetognaths. Hence, if the proto-, para-, eu-conodont evolutionary series were correct, this would indicate that the affinity of true conodonts lay with the chaetognaths. By 1993 protoconodonts were considered a distinct group of animals, although the evolutionary relationship between para- and eu-conodonts was reaffirmed (Szaniawski and Bengtson 1993).

The advances made in conodont hard tissue histology during the late 1960s and the 1970s led to the possibility of using histology to distinguish conodonts from the sclerites of other organisms. Clark *et al.* (1981) even went so far as to include the histological complexity of conodont elements as a character in his diagnosis of the Conodontia. Chauff and Price (1980) used histological characters to justify the conodont affinity of their new Devonian genus *Mitrelltaxis*, which they briefly compared microstructurally with fish scales from the same deposits. Wang (*in* Wang and Klapper 1987; Wang 1989) similarly used internal structure as a means of justifying the affinity of *Fungulodus*. The presence of white matter, apparent in thin sections, was taken as unequivocal support for a conodont affinity, offering a contrast with the histology of thelodont dermal denticles. However, this interpretation remains equivocal (Wang and Turner 1985; Wang 1993). Adding further confusion, Wang (*in* Wang and Klapper 1987) disputed the conodont affinity of *Mitrelltaxis* (Chauff and Price 1980) on histological grounds, concluding a vertebrate affinity. Histology was also used by Klapper and Bergström (1984) to assess the affinity of *Archeognathus*. They described *Archeognathus* as bearing a 'fibrous' crown and a lamellar basal body entirely lacking tubules or cell spaces. Klapper and Bergström thus concluded that dentine and bone were not present and that the fossils represented the remains of a conodont, and not a vertebrate.

In contrast, Barskov *et al.* (1982) described spongy and lamellar forms of basal body in *Neocoleodus* and *Coleodus*, compared spherical structures in the spongy form with osteocyte lacunae, and homologised the tissue with bone, concluding a vertebrate affinity for conodonts.

von Bitter and Merrill (1983) described the histology of *Ellisonia* using naturally fractured specimens. The fibrous nature of the crown tissue led them to suggest that ellisoniids were neurodonts, a group of conodonts conventionally deemed restricted to the Ordovician. Their observations suggested, however, that the neurodonts were present at least as late as the Late Carboniferous (Pennsylvanian).

Before 1983, conodont histologists were evidently in a state of confusion; some authors recognised vertebrate hard tissues amongst conodont elements, and used this as evidence of vertebrate affinity for conodonts. Conversely, other authors recognised a distinct histology which they used to discriminate conodonts from vertebrate microremains. This all changed with the discovery of the conodont animal (Briggs *et al.* 1983; Aldridge *et al.* 1986; Aldridge and Briggs 1986); conodont histologists finally had a context in which to evaluate the histology of the feeding elements (Dzik 1986). Dzik was the first to take advantage of this, and began by homologising conodont basal tissue with dentine, and comparing conodont crown tissue with enamel. Similarly, when Andres (1988) described the histology of a number of Cambrian and early Ordovician conodonts representative of para- and euconodonts, he homologised basal tissue with dentine and crown tissue with enamel. Again, following Dzik, Andres concluded that paraconodonts were the ancestors of both euconodonts and vertebrates. Later, Burnett and Hall (1992) compared lamellar crown tissue with protoprismatic enamel.

Krejsa *et al.* (1990a, b) introduced a neontological perspective to conodont palaeobiology, comparing and homologising the tissues of conodont elements with those of myxinoïd keratinous toothlets (figure 2). They suggested that the basal body was a developing replacement tooth for the overlying functional crown, enabling the conodont animals periodically to shed and replace their 'teeth'. They also interpreted spaces within white matter to be homologous with the goblet-shaped pokal cells that underlie the keratinous toothlet covering in hagfish, apparently confirming the myxinoïd affinities of conodonts. However Krejsa *et al.*'s paradigm ignores conodont histological features which render their model untenable, such as the confluence of growth between the crown and basal body indicating that the two structures grew synchronously, not as separate generations. Furthermore, the histogenesis of hagfish toothlets is poorly understood, and attempts to draw homology between them and conodont elements should be reserved until the histogenesis of hagfish toothlets has been properly documented.

In a series of papers, Sansom and his colleagues reviewed element histology in the light of the chordate affinity of conodonts (Sansom *et al.* 1992, 1994; Sansom 1996). Many of the observations of their 1992 paper had been made earlier by other authors (Barnes *et al.* 1975; Dzik 1986; Jeppsson 1980; Smith *et al.* 1987, Smith 1990), but Sansom *et al.* (1994) were the first to describe unequivocal dentine from conodonts, most notably in *Neocoleodus*. Sansom (1996) also described protoprismatic enamel from the Ordovician-Devonian conodont lineage *Pseudooneotodus* and placed the model of conodont element growth established by Müller and Nogami (1971, 1972; figure 1*cii,d*) into a biological and developmental perspective. Smith *et al.* (1996) extended the number of conodont taxa covered, and reviewed the relevance of the affinity and relative antiquity of conodonts to understanding the early evolution of the vertebrate skeleton.

The interpretations of conodont hard tissues by Sansom *et al.* (1992, 1994) remain controversial even though many accept conodonts as vertebrates (=craniates). Forey and Janvier (1993) aimed their criticisms primarily at the proposed homology between lamellar crown tissue and enamel. The extreme variation in the orientation of crystallites in lamellar crown tissue, ranging from parallel, to a highly angular relationship with the

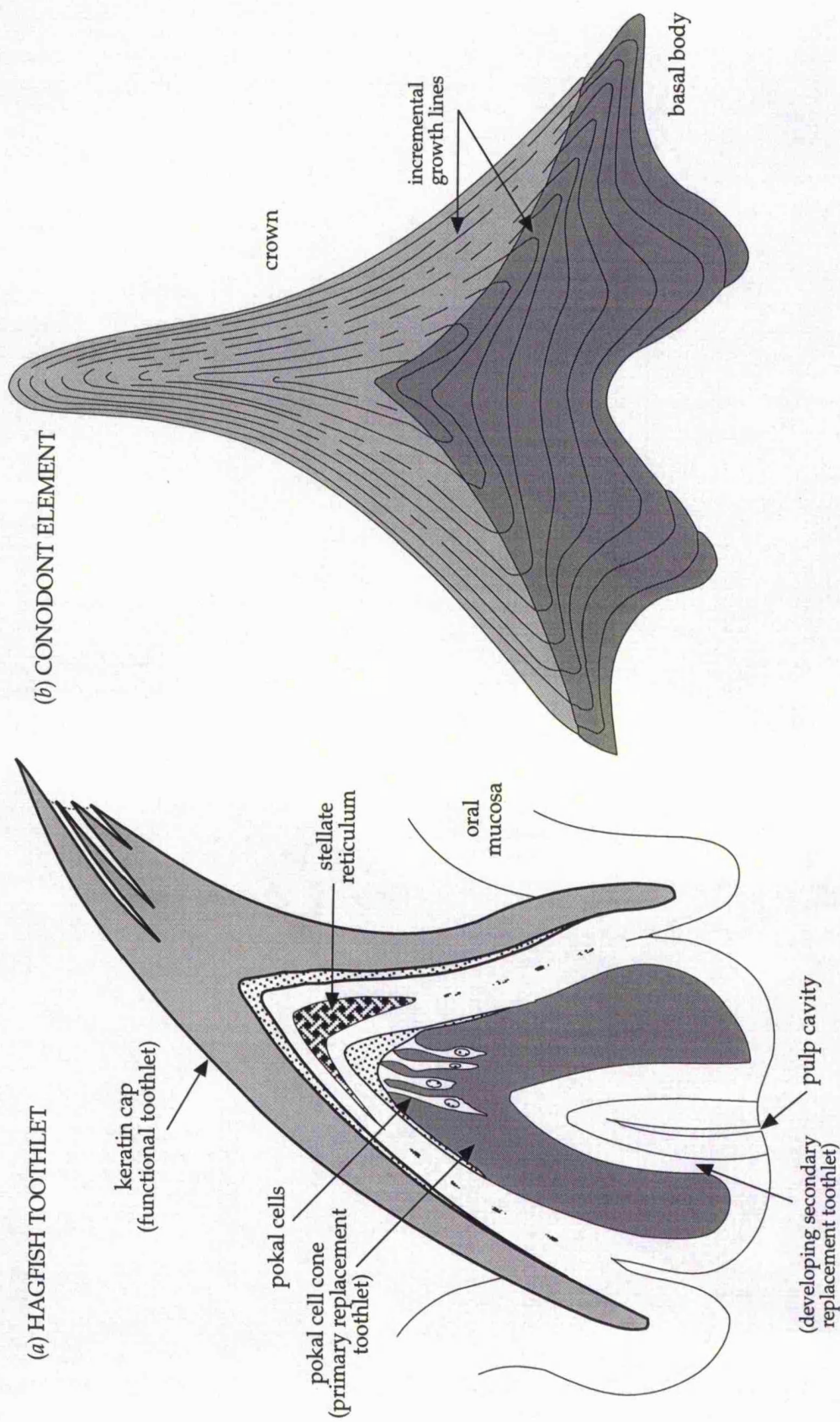


Figure 2. (a) Lingual tooth of *Myxine* in longitudinal section, after Dawson (1963). (b) Pa element of *Ozarkodina* in transverse section, after Müller and Nogami (1971). The functional keratin cap and replacement toothlet (pokal cell cone) of the myxinoïd grow as distinct structures, whereas the crown and basal body (putative replacement crown of Kresja 1990a, b) grew in intimate association.

surface (particularly evident in taxa figured in Sansom *et al.* 1992; figure 3i), was thought to be incompatible with enamel, neither orientation corresponding precisely. The description of prismatic structure in the lamellar crown of *Pseudooneotodus* (Sansom 1996) has demonstrated that lamellar crown can mirror the structure of some enamels; however, Sansom and his colleagues have still failed to reconcile the wide variation in conodont crown structure with the range of known enamels. Further, although Sansom (1996) has been able to reconcile his interpretations of hard tissue histology with both Müller and Nogami's (1971) model of conodont growth, and modern developmental systems, he has achieved this reconciliation without *a priori* considering how the tissues grew. Janvier (1995, 1996a, b) has further criticised the suggested homology of white matter with cellular dermal bone, suggesting a mesodentine affinity to be more likely. Schultze (1996) also disagreed with Sansom and his colleagues over their interpretations of conodont hard tissue histology. Most of these criticisms have been made earlier, but other points of contention result from Schultze's assumption that the work of Gross (1954, 1957, 1960) is correct, and he concludes "that the placement of conodonts in the animal kingdom will be solved as soon as a recent relative has been found".

Histological study of conodont elements has not been restricted to the mineralised hard tissues. Fähræus and Fähræus-Van Ree (1987) undertook a histochemical study (using haemalum and eosin) of preserved soft tissue remnants from the organic components of the mineralised tissues, finding them to be histochemically reactive after 415 Ma! Much of the tissue is very similar to modern collagen and also appears to preserve cell spaces; however, many of the structures remain enigmatic, and Fähræus and Fähræus-Van Ree (1987, p.109) preferred to wait 'until stained tissue sections of early Palaeozoic vertebrate tissue (e.g. ostracoderms) have been produced' before firm conclusions were reached. However, although this work had already been undertaken over twenty years earlier (Tarlo and Tarlo 1961; Halstead Tarlo and Mercer 1966) the fidelity of preservation is too poor to be useful in comparison.

Kemp and Nicoll (1995a, b, 1996) also attempted to identify organic molecules within the mineralised matrix by staining them *in situ*, applying histochemical tests for collagen (picosirius red), DNA (DAPI), keratin (Gram's stain), cartilage (Alcian blue), and protein (toluidine blue). These tests used a series of positive and negative controls (Kemp and Nicoll 1993, 1995a, b, 1996). Lamellar crown stained positive for collagen, so Kemp and Nicoll rejected the hypothesis that lamellar crown tissue is homologous with enamel, which is a purely epidermal product and contains no collagen. White matter and basal tissue failed to stain for collagen, but bone, cartilage and dentine are derived from ectomesenchymal and epidermal interaction, and therefore contain collagen in life. Kemp and Nicoll (1995a) concluded that conodont hard tissues are not comparable with those of vertebrates. Attempts to repeat the results, even with modern vertebrate material and unequivocal fossil vertebrates, have failed (M.M. Smith personal communication 1996). Kemp and Nicoll have also failed to demonstrate the effectiveness of this test on uncontested fossil vertebrate material. Towe (1980) has shown that, although tissues like collagen may be preserved physically with high fidelity, biochemical preservation is negligible. Furthermore, the instability of collagen is such that it can only be expected to survive biochemically intact for up to 1Ma (Aldridge and Purnell 1996). Therefore, although Fähræus and Fähræus-Van Ree (1987, 1993) may well have been correct in interpreting their isolated organic residues as containing collagen, it is unlikely that Kemp and Nicoll's results are meaningful.

Many questions regarding conodont hard tissue histology remain unanswered: the primary or secondary nature of white matter has yet to be conclusively determined; no clear model has been published to show how

conodont elements grew, other than at the very simplest of levels (Müller and Nogami 1971, 1972); and we need to address the problem of how more complex elements were grown.

3. MATERIAL AND METHODS

(a) Material

The present study was based primarily on material from the reference collection of the micropalaeontology unit, Leicester University Geology Department. The majority of specimens figured in the illustrations remain at present in my personal collections (PCJD), although specimen numbers with a BU prefix have been figured by me elsewhere and are repositated at the Lapworth Museum, University of Birmingham, and those with a C prefix are repositated at the Geological Survey of South Africa, Pretoria.

(b) Methods

Conodont element ultrastructure has been examined using a variety of methods including thin sectioning, the examination of naturally and artificially fractured specimens, and the use of scanning electron, incident light, transmitted light and laser confocal microscopy.

Thin sections were made by embedding elements in cold-curing polyester resin, set in nitrile Beam capsules, the elements oriented according to the required section. The polyester cylinders were then ground to the appropriate level and polished on a rotating felt lap with 0.05µm alumina powder. The polished surface was bonded to a frosted glass slide using cold-curing epoxy resin (Buelers' Epothin). The opposing side of the polyester cylinder was removed using a diamond-tipped annular saw, and the excess resin ground away using 600 and 1000 grade carborundum powder until the desired level within the conodont element was reached. The exposed surface was polished as before, either by hand, or using an automated attachment to the rotating felt lap.

Thin sections were studied using transmitted light and laser-confocal microscopy. For scanning electron microscope study, the thin sections were etched using 0.5% orthophosphoric acid for varying periods, always less than 10 minutes. The sections were either permanently coated with gold, or temporarily coated with carbon (following Repetski and Brown 1982) or silver (following Mills 1988).

Of the naturally and artificially fractured specimens studied, natural fractures were found to be less revealing due to diagenetic alteration of element ultrastructure. Artificial fractures were produced using an entomological needle mounted in a pin vice; inverted conodonts elements were fractured by applying pressure to the pin, which was seated in the basal cavity of the element. Immersion of the specimen in a small droplet of water was found to prevent loss during this procedure. Specimens were subsequently etched using 0.5% orthophosphoric acid for 6-8 minutes and coated for SEM study.

The simplest and most rapid method of studying microstructure is by immersion of elements in oil of a refractive index close to that of apatite (1.68). It is also important for the oil to have a relatively high viscosity, thus preventing flow away from the specimen. In this way, tens of elements can be studied at once using traditional light and laser confocal microscopy. For laser confocal microscopy the specimen was first bonded to the slide using a small amount of gum tragacanth. In contrast with other techniques, this method is non-destructive and the oil can readily be removed by washing the specimens in ethanol.

Light micrographs were taken using a Leitz Aristoplan fitted with differential interference contrast. Scanning electron micrographs were taken on a Hitachi S-520.

PATTERN

4. THE CONODONT ELEMENT

Conodont elements are characteristically constructed from two basic units, the crown and underlying basal body (figure 3*a,b,c*). The crown is composed either entirely of hyaline lamellar crown tissue (figure 4*e,f,g,h,i,j*), or of a combination of lamellar crown and white matter (figure 3*a,b,c*). The basal body is a single component structure composed from a hard tissue herein termed basal tissue.

*(a) The Component Tissues**(i) Lamellar Crown Tissue*

This is the most coarsely crystalline of all conodont hard tissues and usually comprises the major component of conodont elements. The length of individual crystallites is extremely variable, ranging from less than 1 μm to in excess of 30 μm , but they are usually no more than a few microns long. The crystallites are bounded at either end by the punctuating growth lines which define the lamellae that are so characteristic of the tissue (e.g. figure 3*d,e*). The orientation of the crystallites relative to the growth increments, and thus the surface at the time of growth, is inconsistent (e.g. figure 3*i*) and has in the past been attributed to “the direction in which the main ontogenetic growth occurred at the place in the lamella where the crystal is located” (Hass and Lindberg 1946, p.501). In simple coniform elements the crystallites are arranged with their long (c) axes parallel or sub-parallel to the long axis of the element, such that the entire crown is composed of a single homogeneous prism of crystallites in a fan-like arrangement. In ‘complex’ conodont elements, the prismatic structure of the element is broken up into a number of individual prisms, each comprising a denticle (figure 3*h*). Because the crown of a multidenticulate element is structurally more differentiated than the crown of a coniform element, the main ontogenetic vector of growth is not so extreme. As a result, the more extreme variations of crystallite arrangement, such as sub-parallel to the growth lines, are less prevalent than in coniform elements. In areas of complex elements that were simply being enlarged by successive increments of lamellar crown tissue, without development of new morphological features (e.g. growth around the main body of blade-like or platform elements), the crystallites are usually oriented perpendicular to the outer surface (e.g. the variation in figure 3*i,k*). Crystallites adjacent to the basal cavity are inclined upwards and outwards relative to the junction of the crown with the basal body (figure 3*j*).

(ii) White Matter

White matter is a term derived from the appearance of this tissue in reflected light. White matter contrasts sharply with lamellar crown tissue because of its more finely crystalline composition (figure 4*a,b,c,d*), its markedly greater resistance to standard dental acid etchants (e.g. Stauffer and Plummer 1932; figure 4*b*), its lower organic content (Pietzner *et al.* 1968) and the lack of punctuating growth increments. White matter occurs exclusively in denticles as cores (figure 5*i*) and has sharply defined lateral margins. The cores appear dark in transmitted light (figures 3*a*, 5*i,j*) because of the cavities enclosed within the fine grained groundmass (figure 4*a,c,d*). These cavities vary considerably in their size, shape, and orientation. Most common are tubular cavities (figure 4*d*), which occur in two size distributions both of which are predominantly oriented with their long axes parallel to the long axis of the denticle: longer tubules, typically 20-30 μm in length, and shorter tubules (figure 4*c*), usually only a few microns in length. The calibre of the tubules is usually in the order of 0.25 to 1 μm , but they sometimes expand into a large (3-7 μm diameter), sometimes irregular, cell-shaped cavity, from which other tubules may splay (figures 4*c*, 5*l*). These

Figure 3. (a) Longitudinal section through an Sc element of *Coyssognathus dubius* composed of a basal body (to left) and crown (to right); the crown includes an opaque core of white matter; PCJD 346, frame width 547µm. (b) light micrograph, and (c, f) scanning electron micrographs of a transverse section through a Pa element of *Ozarkodina confluens*; note the relationship between the white matter in (b) and (c), and the variation in crystallite orientation at the crown-basal body junction in (f); PCJD 190, frame widths (b, c) 458µm, (f) 158µm. (d) Perpendicular arrangement of crystallites in a Pa element of *Ozarkodina confluens*; PCJD 173, frame width 27µm. (e) Pre-prismatic arrangement of crystallites in a Pa element of *Scaliognathus anchoralis*; BU 2613, frame width 55µm. (f) Proto-prismatic arrangement of crystallites in a Pa element of *Idiognathodus* sp.; PCJD 265, frame width 114µm. (g) Transverse section through the cusp of a Pa element of *Ozarkodina onfluens*, note the oblique orientation of crystallites relative to the bounding incremental growth lines; PCJD 114, frame width 22.5µm. (h) Arrangement of crystallites into distinct prisms which form the denticles in the free blade of a Pa element of *Mestognathus beckmanni*; PCJD 185, frame width 284µm. (i, k) Variation in crystallite arrangement in a horizontal section through a Pa element of *Ozarkodina confluens*, (i) changing from perpendicular at the margin of the element, and oblique at the core of the element; PCJD 177, frame width 76µm; (k) subvertical arrangement of crystallites adjacent to the core of white matter; PCJD 177, frame width 118µm.

Figure 3

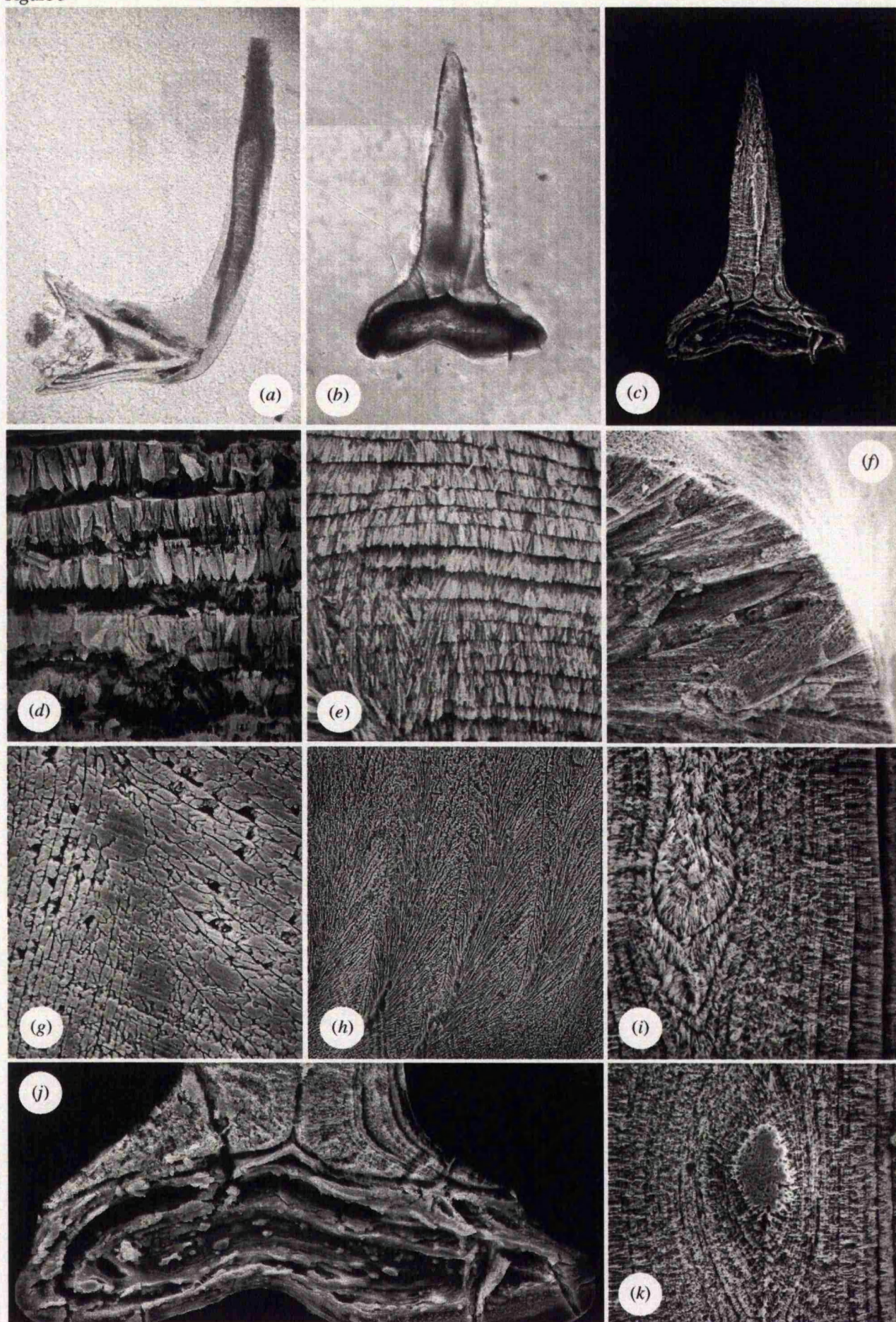
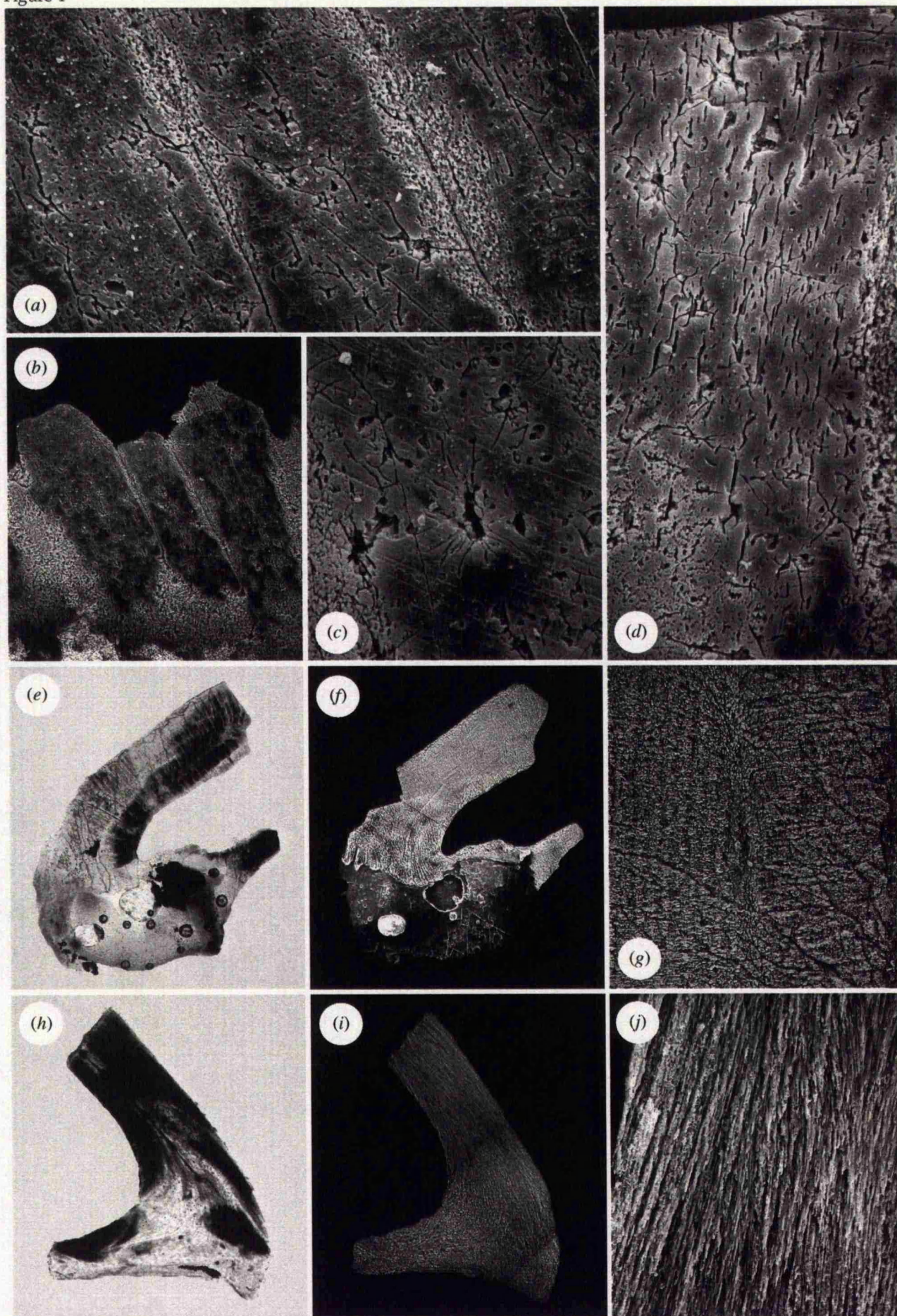


Figure 4. (a, b) Longitudinal section through an Sc element of *Ozarkodina confluens*, the white matter cores are bound by a thin sheath of lamellar crown tissue which expands orally; PCJD 339, frame width (a) 121µm, (b) 233µm. (c) Cell-shaped space incorporated within the fine-grained groundmass of white matter from a Pa element of *Ozarkodina confluens*; BU 2615, frame width 26.7µm. (d) White matter core of an Sc element of *Ozarkodina confluens*, the tissue is dominated by vertically-orientated tubules many of which branch in the plane of the section; PCJD 335, frame width 50µm. (e, f, g) Longitudinal section through an element of *Cordylodus* sp., note the relationship between the opaque areas in (e) and the scanning electron micrograph in (f) which indicates a complete absence of true white matter; the opaque areas probably result from optical effects produced by the prism boundaries in (g); PCJD 171, frame widths (e, f) 1541µm, (g) 200µm. (h, i, j) Longitudinal section through an element of *Ligonodina* sp., as in (e, f, g), despite the presence of opaque areas in (h), (i) reveals an absence of true white matter resulting from interfering crystallite arrangement in (j); PCJD 172, frame widths (h, i) 805µm, (j) 90µm.

Figure 4



larger cavities are rare but ubiquitous, and usually occur at the oral end of connected tubules (figure 5l). It is likely that the tubules and cavities represent the sites of mineral-secreting cells.

Although white matter and lamellar crown tissue are extremely distinctive tissues, the junction between the two is imperceptible in transmitted light (figure 5j,k). This is the main reason why conodont histologists in the 1970s generally interpreted white matter as secondarily derived from lamellar crown tissue. However, when these tissues are studied in etched sections, their mutual boundary is extremely sharp. (compare figure 3a and b)

The transitional zone apparent to Barnes *et al.* (1973a) between the two tissues does not appear to be lamellar, coarsely crystalline, or cancellate in transmitted light, so it is difficult to resolve whether it is lamellar crown, white matter, or a third previously unrecognised tissue. However, in properly etched sections, no transitional tissue is evident, and the boundary between white matter and lamellar crown is extremely sharp. The apparent transitional zone is in fact white matter that lacks cavities.

The problem of distinguishing white matter from lamellar crown is further complicated because not all the tissues which appear albid in reflected light are true white matter; when they are examined in fracture or thin-section they can be seen to be forms of lamellar crown tissue (figure 4e,f,g,h,i,j). In most cases, the albid area occupies a site where crystallites in successive increments of lamellar crown are not aligned. An albid effect can also result from hypocalcification (figure 13f), and may additionally occur at sites of radiating prismatic structure. Such 'pseudo white matter' includes Müller's (Müller, 1981) white matter categories 3a-d and can usually be distinguished by transmitted light examination under immersion oil. True white matter is cancellated in appearance and can only be identified unequivocally by thin sectioning and examination of etched surfaces with an SEM.

(iii) Basal tissue

Basal tissue comprises the entire basal body and is often clearly punctuated by growth striae (figure 3a). The tissue is so finely crystalline that individual crystallites cannot be discerned under light microscopy. In complete specimens, successive increments extend over the lower surface of the basal body, thereby encapsulating all previous increments (figure 3j). However, basal tissue is the most variable of all conodont hard tissues, both between taxa and within a single taxon. For instance, the structure of the *Cordylodus* basal body is known to vary from coarse spheroids (Müller and Nogami 1971; Sansom *et al.* 1992; figure 5a,b,c) to laminated (Kemp and Nicoll 1995a); *Pseudooneotodus* exhibits both spheroidal structure (figure 5d,e) and lamellar form with microspherules (Sansom 1996). Some specimens of *Chirognathus* possess a basal body with lamellar structure and perpendicular fine calibre tubules (Sansom *et al.* 1994; Müller and Nogami, 1971, 1972), but other specimens apparently have a clearly atubular laminated structure (Kemp and Nicoll, 1995a). Müller and Nogami figured a single specimen of *Neocoleodus* with a lamellar basal body, while Sansom *et al.* (1994) have recorded a non-lamellar basal body which includes branching tubules. Some basal tissue is neither laminated, spheroidal, nor tubular.

The fine calibre tubules described from the basal body of *Chirognathus* and *Neocoleodus* have only rarely been recorded in conodont elements, whereas coarser tubules have been recorded in many more taxa, including all those claimed to possess dentine tubules prior to the work of Sansom *et al.* (1994) (e.g. Andres 1988; Dzik 1986). The coarser tubules are typically 50µm diameter (too coarse to be dentine processes) and meander throughout the basal body.

The majority of basal bodies are atubular, particularly those of the order Ozarkodinida (*sensu* Sweet 1988), and they usually occur within concentric growth increments equivalent to growth striae in the crown (figure 5f,g). The basal tissue lamellae are rarely perfectly concentric and are discontinuous or disrupted, usually

because of incorporated micro-calcospheres which often occupy much of the area just below the crown-basal body junction, and frequently occupy the core of the structure (figures 3j, 5e,f). Integradation between all forms can occur within a single taxon, and sometimes within a single specimen (figures 3j, 5c), indicating that all the structures are features of a common tissue possibly affected by the time scale of growth. The presence of the microspherules in a homogeneous, unstructured matrix therefore indicates rapid growth, and the well organised, lamellar, and tubular structures represent slower, ordered growth.

Reduced mineralisation of the basal body is a consistent feature of early to late Palaeozoic conodont elements, and many lineages have no record of basal body. Pathological features of crown morphology in elements of some taxa (e.g. *Polygnathus xylus xylus* in Nicoll 1985, text-fig.1H, V) indicate the presence of an inflexible structure, and so a basal body was certainly present *in vivo*; the reason for lack of preservation of the structure is unknown, although the most likely reason is that it was not completely mineralised.

By the Carboniferous, very few taxa have any record of the presence of a mineralised basal body. This is evident in the Carboniferous conodont animals with soft tissue preservation (Aldridge *et al.* 1993), and the exceptionally preserved 'bedding plane assemblages' which represent the undisturbed but collapsed remains of the feeding apparatus (Chapter 1). Not one of the many hundreds of articulated skeletal remains of ozarkodinids possesses even the remnants of a basal body. Interestingly, although gondolellid elements (order Prioniodinida) have been recovered with intact basal bodies from sediments of the Carboniferous and later (e.g. Müller and Nogami 1971, pl. 15, fig. 4), the many bedding plane assemblages of *Neogondolella* and *Gondolella* (Rieber 1980; Orchard and Reiber 1996; Merrill and von Bitter 1977) possess no basal tissue. This is also true of all recorded fused clusters. However, this bias may be taphonomic as collections from the Devonian of Western Australia contain polygnathid clusters with no basal tissue, whereas isolated elements from the same sample have fully preserved basal bodies (Nicoll 1985 and personal observation).

(b) Interrelationships of the tissues during growth

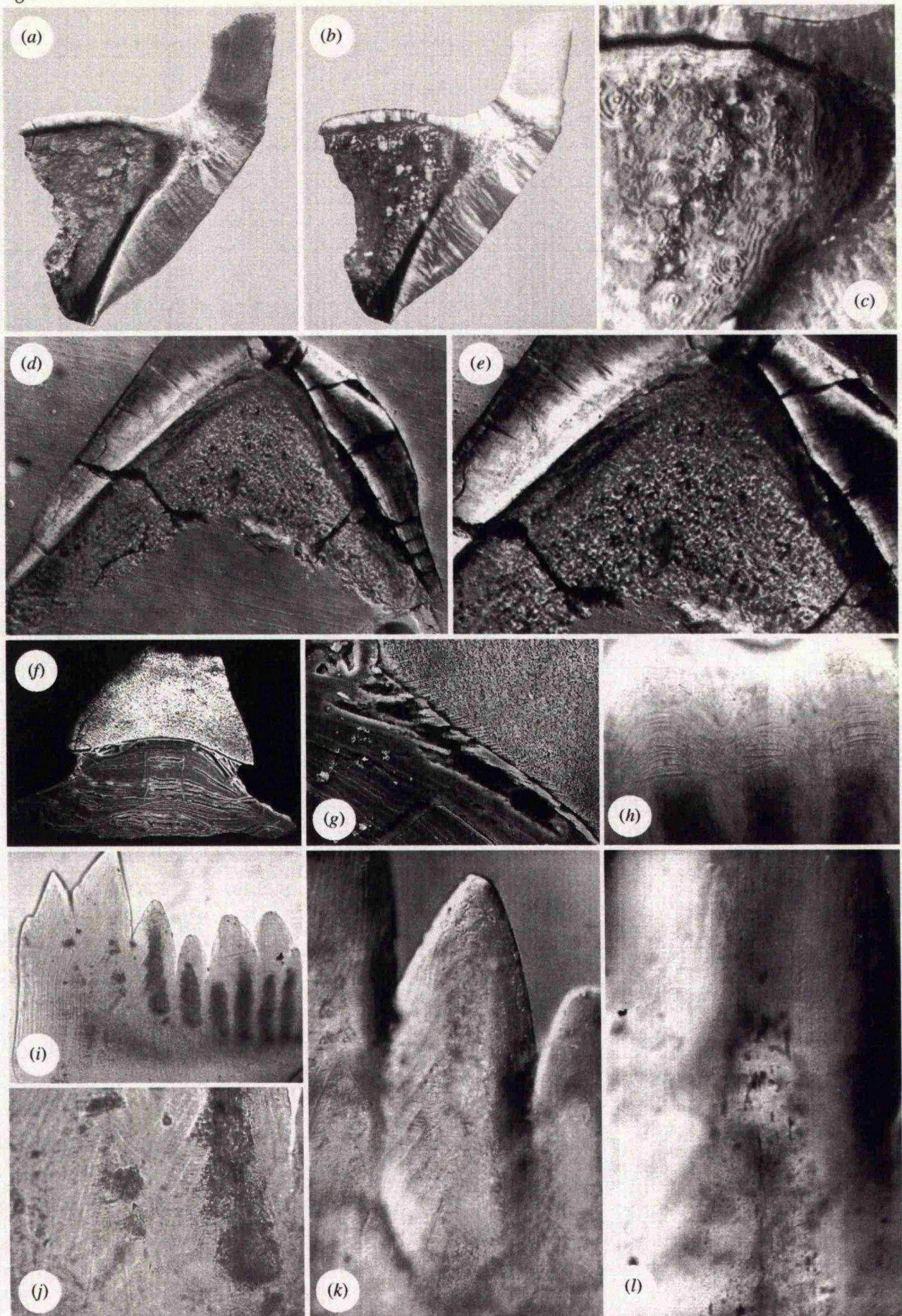
The crown is known to have grown by outer apposition because many elements display evidence of episodes of damage and subsequent repair (Furnish 1938; Hass 1941; figure 5h). The confluent passage of incremental growth striae between the crown and basal body indicates that the two structures were grown synchronously (*contra* Gross 1957, 1960; Krejsa 1990a, b), and by inference, that the basal body also grew by outer apposition. The innermost core of each element therefore represents the earliest growth stage, and the outermost layer the latest.

It is possible to determine the growth relationship between the lamellar crown tissue and the junction with the underlying basal body. At the base of the crown, crystallite orientation indicates growth up and away from the junction with the basal body (figure 3j). Unfortunately, the crystallites that compose the basal tissue are too small to determine orientation, and growth direction can only be resolved by inference. However, the nature of the growth relationship between the crown and the underlying basal body indicates a mirroring of the pattern of growth apparent in the crown.

The two basic units which compose a typical conodont element therefore grew in opposing directions relative to the crown-basal body junction (figure 1ci, d; c.f. Sansom 1996, although his conclusions are based on *a priori* interpretations of the component tissues). This pattern alone is evident in coniform conodont elements that lack white matter, but elements with an albid component are far more complex structurally, and their growth is

Figure 5. (a, b, c) Longitudinal section through an Sc element of *Cordylodus* sp.; the basal body is dominated by spherulitic structure, each spherule indicated by an extinction cross in cross-polarised light (b); BU 2614, frame widths (a, b) 644µm, (c) 204µm. (d, e) Transverse section through an element of *Pseudooneotodus* sp. in plane-polarised light (d) and cross-polarised light (e); the basal tissue of this specimen also exhibits a spherulitic structure; PCJD 341, frame widths (d) 531µm, and (e) 337µm. (f, g) Longitudinal section through a Pa element of *Ozarkodina confluens* with a basal body exhibiting lamellar structure; note the confluence of growth increments between the basal tissue and lamellar crown tissue in (g); PCJD 31, frame widths (f) 380µm, and (g) 72µm. (h) Pa element of *Ozarkodina gulletensis* photomicrographed under oil; this element exhibits a conspicuous internal discontinuity with evidence of subsequent repair; specimen lost, frame width 225µm. (i, j, k, l) Pa element of *Ozarkodina confluens* photomicrographed under oil. (i) Ventral portion of the element viewed in plane polarised light, the denticle in the centre of the frame exhibits a staggered ventral margin where the increments of white matter and lamellar crown tissue are clearly confluent; PCJD 345, frame width 453µm. (j, k) Denticle in (i) at higher magnification; PCJD 345, frame widths 88µm. (l) tubules and cell-shaped cavities within the white matter; PCJD 345, frame width 35µm.

Figure 5



much less well understood. Given their antiquity and importance in our understanding of the early evolution of vertebrates and their skeletons, this is an important area of investigation.

Although the flanks of white matter cores are usually planar (figure 4a,b), more rarely they are stepped (figure 5i,j,k), each step coinciding and confluent with incremental layers in the surrounding crown tissue, thereby providing an insight into the relationship between these two tissues during growth. This arrangement appears to indicate that the two tissues grew synchronous and at the same rate. Examples where increments of the lamellar crown pass conformably into white matter have been figured many times (e.g. Barnes *et al.* 1973a, fig. 6.6; Sansom *et al.* 1992, fig. 3e), but in figure (5i,j,k) the white matter is bounded by the growth increments. The length of the long tubules within the white matter core greatly exceeds the thickness of individual increments of the adjacent crown tissue (figures 4a, 5l). This indicates that growth of white matter was more continuous than the punctuated growth of lamellar crown, and that the control over the secretion of the two tissues was distinct. Because of the outer appositional mode of growth of the surrounding tissue, it is likely that white matter also grew in this way. The polarised nature of the cell-shaped cavities within white matter therefore suggests that the secreting cells retreated orally, usually ahead of the mineralising front, and hence only the cell processes (the tubules) were commonly incorporated into the mineralised matrix. Furthermore, the polarisation of the shorter, perpendicular tubules and attached cavities indicates that they grew away from their junction with the lamellar crown tissue. This contrasts strongly with the direction of growth of the lamellar crown tissue, which from the orientation of the crystallites was usually perpendicular (figure 5j,k) or sub-perpendicular (figure 3g) to the flanks of the white matter cores and long axes of the denticles.

White matter was therefore secreted as a continuous core of mineralised tissue, partially controlled at the margins by the secretion of lamellar crown. White matter, therefore, forms a series of upwardly-tapering collars around, and merging with, the core (figure 6). Although secretion of the two tissues was independently controlled, the lack of a plane of weakness, such as at the junction of the crown and basal body (figure 5g), suggests that the mineralisation of the two tissues simultaneous rather than staggered.

5. GROWING THE CONODONT SKELETON

Although I have outlined the morphogenetic pattern of intergrowth between the two structural units and three component tissues comprising most conodont elements, this goes little further than explaining the morphogenesis of the conventional perception of a simple coniform element, or a single denticle in a complex element. Most conodont elements are far more complex and their morphogenesis can only be explained by studying recurrent patterns of growth. This study has revealed a restricted number of morphogenetic patterns expressed by complex elements; these are described primarily with reference to conodonts of the order Ozarkodinida, but some evidence from members of the orders Prioniodinida, Prioniodontida, and Proconodontida is included.

Different groups of conodonts have followed different morphogenetic pathways in the construction of their feeding elements, and as a result, there is a great diversity of element morphology. However, a number of element morphologies have been converged upon by different morphogenetic paths, these can only be discriminated by considering pattern formation in reconstructing conodont phylogeny.

(a) Ramiform Element Morphogenesis**(i) Type I**

This first group includes taxa bearing elements composed of numerous isolated denticles. The best source of evidence is from *Promissum pulchrum*, a balognathid with a nineteen element apparatus from the late Ordovician Soom Shale of South Africa which is found almost exclusively in bedding plane assemblages (Theron *et al.* 1990; Aldridge *et al.* 1995; figure 7a,b,c,d). The ramiform elements of *Promissum pulchrum* consist of denticles which are united by a single underlying structure which appears to be neither part of the crown nor the basal body (figure 7a). The denticles themselves are variable, those on the (conventional) posterior processes, structurally differentiated into tri-denticulate units (figure 7a,b); denticles on other processes are structurally distinct (figure 7a,c,d; Theron *et al.* 1990). In both cases, each denticle possesses a distinct crown and basal body (figure 7b,d), indicating that they grew independently of adjacent denticles (figure 8a). In ontogenetically older specimens, the cusp and adjacent denticles exhibit a tendency to fuse at the margins of their crowns and their basal bodies. Each denticle therefore appears to be homologous with a simple coniform element, although it represents only part of a complex element. It is likely that each denticle would have been regarded as a single element if found only in a discrete element collection. Thus, Nicoll (1982) appears to have been correct in interpreting fused clusters of hundreds of simple cones in association with P elements of *Icriodus* as component denticles comprising multidenticulate elements. van den Boogaard (1990) and Miller and Aldridge (1993) reached a similar conclusion in their interpretations of the ramiform elements of *Coryssognathus*.

(ii) Type II

Carniodus is an Silurian conodont genus of unclear affinity (family 6 order unknown of Aldridge and Smith 1993). Like the ramiform elements of type I, *Carniodus* grew many of its denticles as morphogenetically distinct units (figure 8b), but unlike type I, the denticles on *Carniodus* ramiform processes are compound structures (figure 7e). Each of the denticle units is defined by an rostral and/or caudal border with adjacent units which is conspicuous only in transmitted light (figure 7f,h,j). Each of the units has its own basal cavity, and is composed from a distinct crown and basal body (figure 7f,h,j), indicating that each of the units grew independently. Unlike type I elements, the crowns of type II elements were entirely fused prior to growth of the subsequent unit. New units began to grow separately from the rest of the element, usually some distance caudally (figure 8b). The unit began to grow equally in rostral and caudal directions until eventually it reached the caudal edge of the preceding unit. Later increments would then envelop both the new unit and the entire pre-existing element, leaving the join between successive units imperceptible on the surface of the crown or basal body.

Carniodus possesses a very characteristic, repetitive denticulation which relates directly to the underlying morphogenetic units (figure 7e,f). The basal cavity does not appear to be directly linked with any specific denticle within the repeated unit, although the conspicuously large denticle may be considered the cusp of each unit. The basal cavities instead relate to the growth of each morphogenetic unit as a whole. Each of the denticles in a *Carniodus* element cannot, therefore, be considered equivalent to the denticles of elements conforming to type I growth, which are instead homologous with each unit of type II growth. Denticle formation and addition within these units follows a pattern typical of type III elements (figure 8b; see below). This same pattern of growth is also found in the ramiform elements of taxa including *Amorphognathus* and *Prioniodus*.

Microzarkodina also exhibits the type II morphogenetic pattern in all but its M elements. In this genus, the successive units consist simply of a large proximal and small distal denticle. The smaller denticle is subsequently

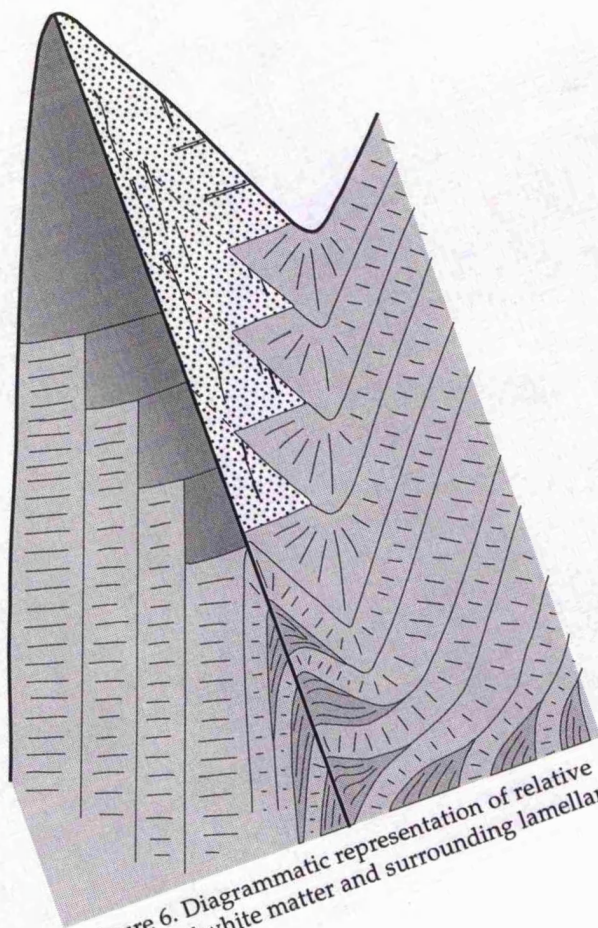
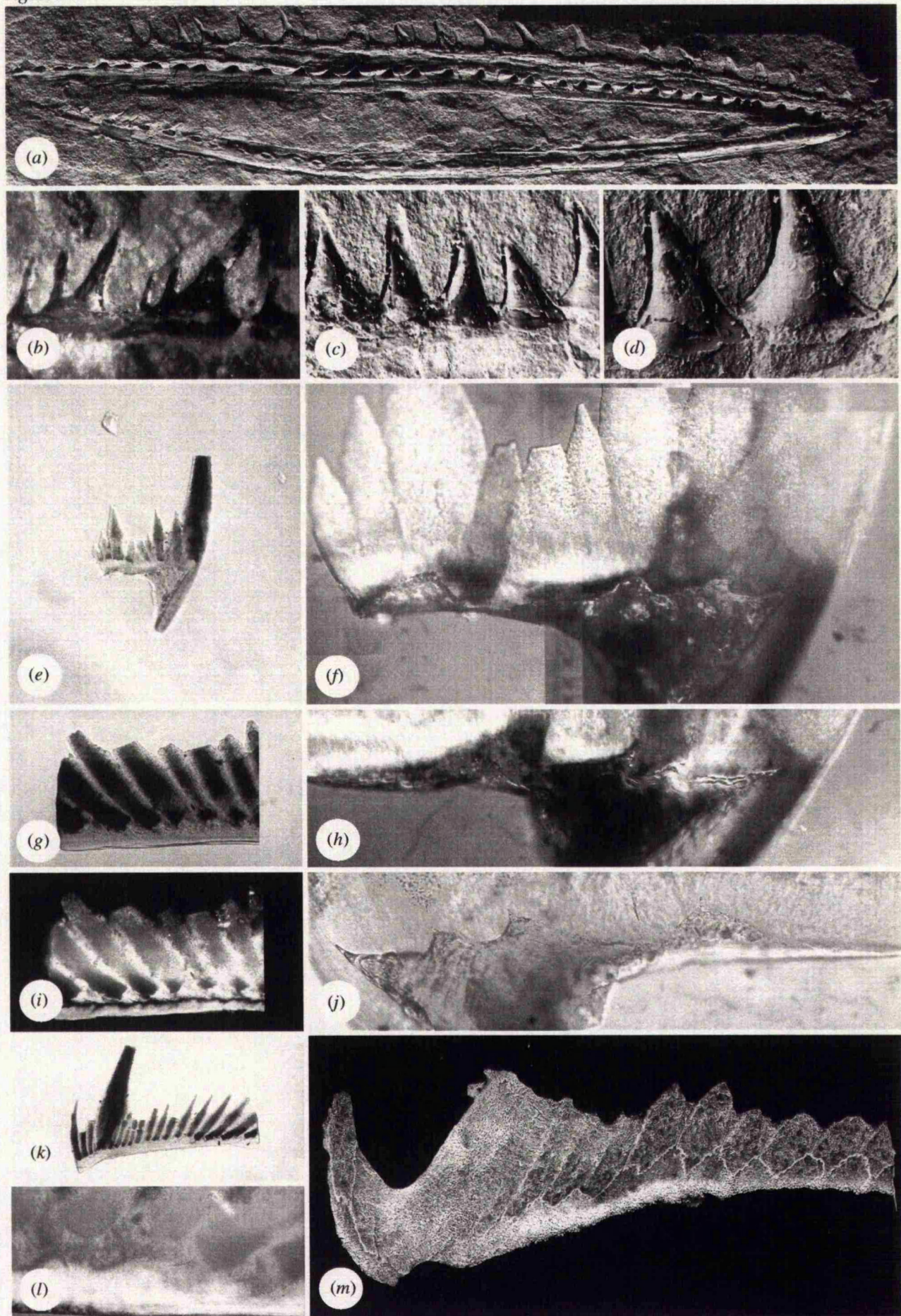


Figure 6. Diagrammatic representation of relative growth of white matter and surrounding lamellar crown tissue.

Figure 7. (a, b, c, d) Details of elements of *Promissum pulchrum*. (a) Sc element with a posterior process composed from individual multidenticulate units (b), and lateral processes composed from individual denticles (c, d); frame widths (a) C424 21234µm, (b) C424 2037µm, (c) C679 836µm, and (d) C679 495µm. (e, f, h, j) Sc elements of *Carniodus* sp., note the optical distinction between the multidenticulate units comprising these elements, each unit includes a distinct basal cavity; frame widths (e) PCJD 349, 1375µm, (f) PCJD 349, 438µm; (h) PCJD 350, 288µm, and (j) PCJD 351, 294µm. (g, i, k, l, m) Sc elements of *Ozarkodina confluens*. (g, i) Plane-polarised light and cross-polarised light respectively; PCJD 305, frame widths 562µm. (k, l) Growth cavities along the ventral margin of the element; PCJD 343, frame widths (k) 1406µm, (l) 225µm. (m) Scanning electron micrograph of an etched ground section exhibiting distinct white matter cores within the lamellar crown tissue; PCJD 318, frame width 1098µm.

Figure 7



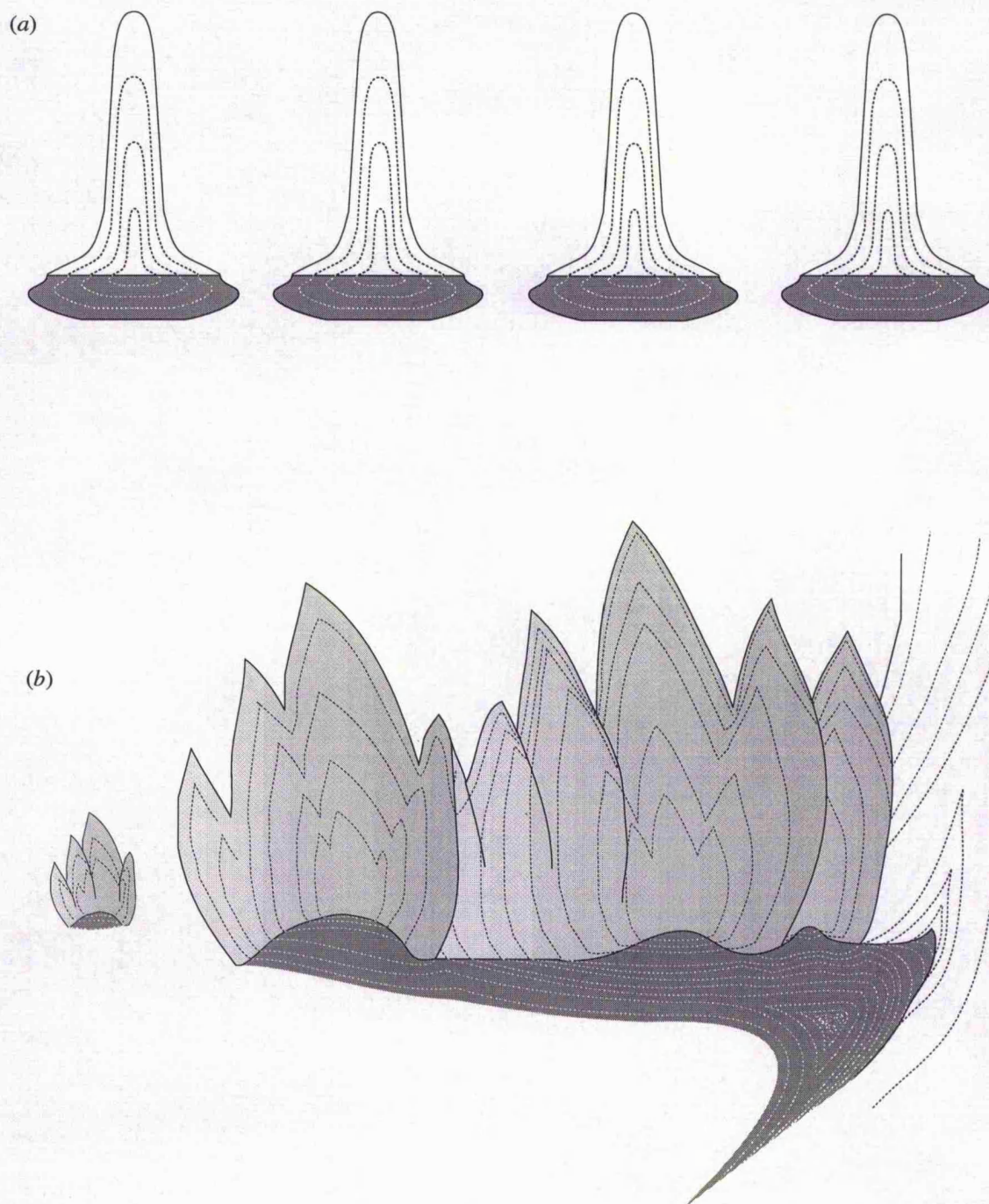


Figure 8. (a) Growth type I typified by *Promissum pulchrum* ramiform elements where individual denticles grew synchronously. (b) Growth type II typified by *Carniodus* ramiform elements where the repetitive sets of denticles gradually became incorporated into the rest of the element as it continued to grow.

encapsulated during growth of the next morphogenetic unit, resulting in an external pattern of denticulation more akin to *Ozarkodina* and type III growth. Alternatively, in early representatives of *Cordylodus*, the crown of each unit remains undifferentiated, each denticle composed of a distinct crown and basal body (e.g. Nicoll 1991).

(iii) Type III

The ramiform elements of *Ozarkodina confluens* bear an undifferentiated denticulation pattern, with each denticle almost entirely composed of white matter and surrounded marginally and aborally by a small amount of lamellar crown tissue (figure 9*a*). Growth increments are clearly apparent within the crown tissue but are only rarely traceable through the blocks of white matter (figures 7*g,i,k,l,m*, 10*a,b*). Unlike the growth patterns outlined above in types I and II, the type III growth pattern produces a compound structure which extends processes by marginal accretion of individual denticles (figure 9*a*). The first stage of growth of an individual denticle is marked by an evagination of an incremental layer of crown tissue at the distal extremity of the process. The evagination encloses a hollow cone-shaped, distally-tapering cavity with step-shaped margins representing the abutment of surrounding micro-lamellae, and crowned by an all-enveloping final layer (figures 7*l*, 10*a,b*). This is succeeded by a series of thick growth increments encapsulating similar cone-shaped cavities. The successive cone-shaped cavities or 'growth cavities' are stacked one upon another, but aligned in an arcuate, distally-convex pattern (figures 9*a*, 10*a,b*). The growth of an individual denticle finishes with a final phase of white matter secretion. The first point of denticle formation, enclosing the first cavity, is close to the first point of white matter secretion because growth is concentrated in an oral, and not distal, direction (as in type IV; figure 10*a,b*). No specimens have yet been discovered where the growth cavities contain any mineralised tissue. This category also includes elements of '*Plectodina*', the putative ancestor of all ozarkodinids (Sweet 1988).

Type III growth also occurs in taxa at one time placed within the now defunct order Neurodontiformes. Although the elements appear to have grown by marginal accretion, such taxa remain histologically distinguishable from other euconodonts, and their separate classification may well be biologically valid. In addition to the more obvious Ordovician forms, many Middle and Late Palaeozoic forms retain this unique histology, particularly taxa which are assigned to the order Prioniodinida (*sensu* Sweet 1988) e.g., *Idioprioniodus*, *Cryptotaxis*, *Ellisonia* (c.f. von Bitter and Merrill 1983). The structure of the crown differs from most conodonts in its 'fibrous' nature; growth increments are present but very faint (figure 4*h,i,j*). The tissue is dominated by elongate fibre-like crystals which can reach 20–30 µm in length, and their arrangement is more complex than that seen in any other group of conodonts. Early growth, and growth along the axes of individual denticles, exhibits a divergent arrangement of crystal fibres; subsequent growth records a reversal in arrangement of the fibres so that they converge distally (note the subtle change in crystal fibre orientation to the left of figure 4*j*). It is this arrangement of crystallites which produces Müller and Nogami's (1971; Müller 1981) 'M'-shaped type 3d white matter. Clearly it is not true white matter.

(iv) Type IV

This group includes gnathodids, *Cavusgnathus*, *Vogelgnathus*, *Lochriea*, polygnathids, some palmatolepids and at least some cyrtoniodontids (e.g. *Phragmodus*). Most of these families and genera are derived from *Ozarkodina* (Sweet 1988) but display a more complicated morphogenetic pattern of growth (figure 9*b*). The ramiform elements are generally much more elongate than those of their ancestor and possess a differentiated pattern of denticulation, similar to that of *Carniodus* but apparently achieved *via* a different pattern of formation. The elements are

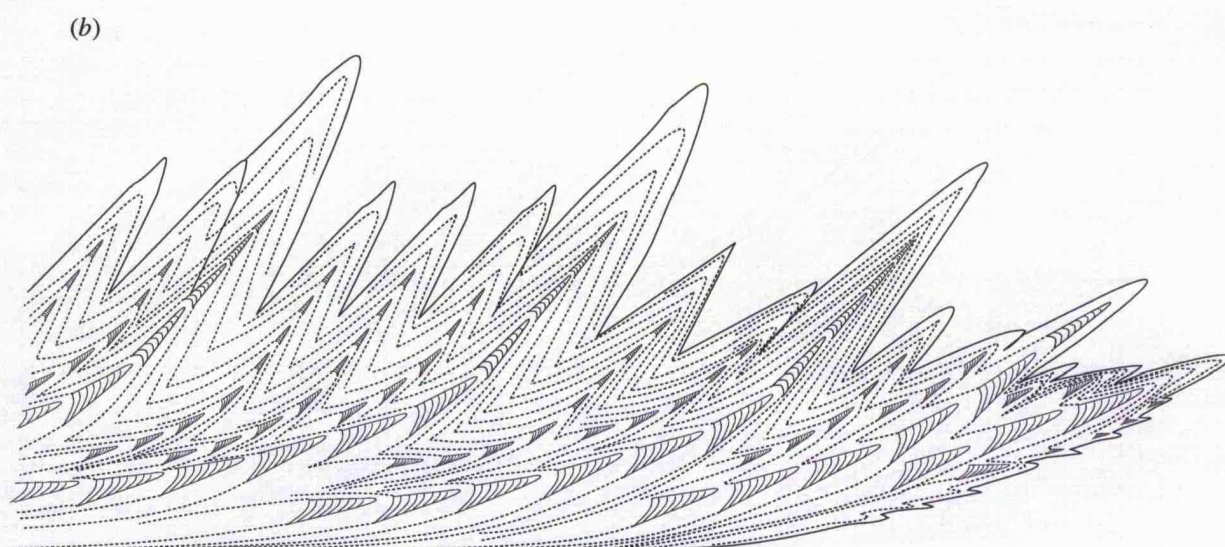
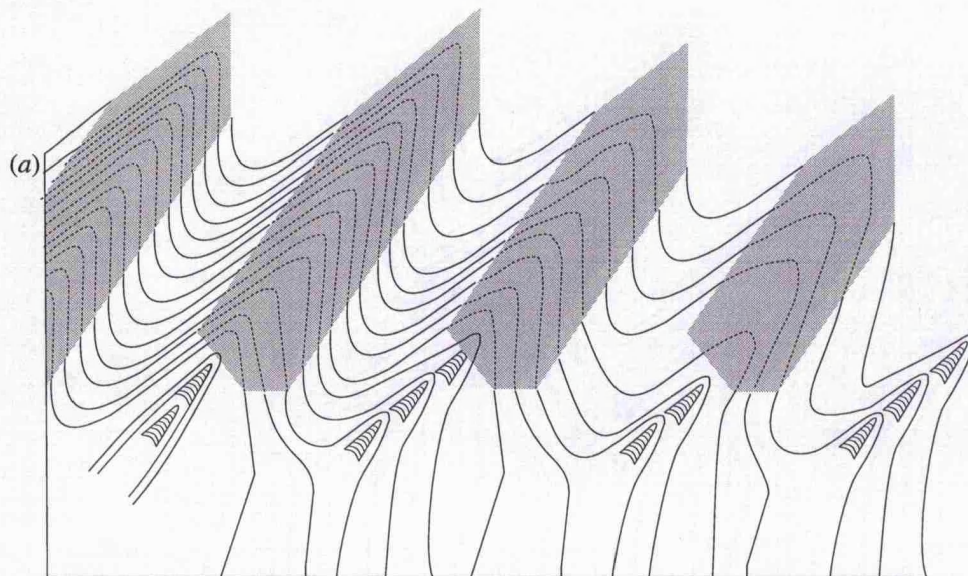
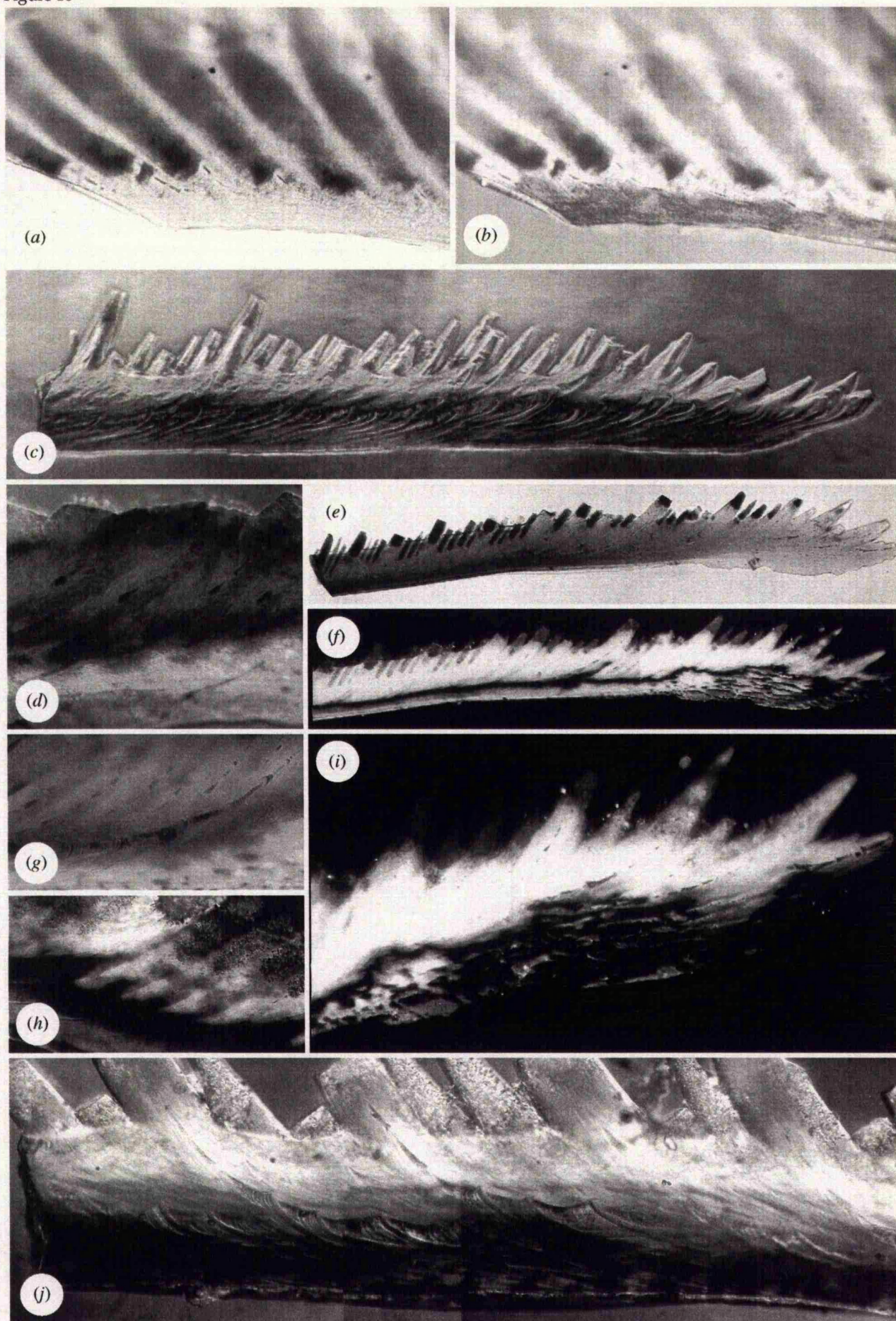


Figure 9. (a) Type III growth typified by *Ozarkodina* ramiform elements where new denticles were added periodically during marginal secretion of lamellar crown tissue. Denticle genesis was first instigated by evagination of normal lamellar growth and incorporation of a 'growth cavity'. (b) Type IV growth typified by gnathodid ramiform elements where denticles were added continually during marginal accretion of crown tissue. The repetitive denticulation results from differentiation of the denticles.

Figure 10. (a, b) *Ozarkodina confluens* Sc element (a) viewed in plane-polarised light, and (b) in differential interference contrast; note the conspicuous growth cavities along the ventral margin of the element; PCJD 344, frame widths 562µm. (c) S element of *Idiognathodus* photomicrographed under oil and in differential interference contrast, note the conspicuous growth cavities within the main body of the element, each set of growth cavities relate to the overlying sets of alternating denticulation; PCJD 354, frame width 1894µm. (d, e, f, g, h, i) S element of *Mestognathus beckmanni*. (e, f) Photomicrographed in plane-polarised light and cross-polarised light respectively, note the extinction pattern exhibited by the prisms which represent the gradual development of denticles; PCJD 353, frame widths (e) 1894µm (f) 1660µm. (i) Detail of the caudal portion of the element in cross-polarised light; PCJD 353, frame width 625µm. (d, g, h) Detail of denticle structure; PCJD 353, frame widths (d) 225µm, (g) 225µm, and (h) 225µm. (j) S element of *Idiognathodus* photomicrographed in plane-polarised light and differential interference contrast, note the relationship between the sets of growth cavities and overlying alternating denticulation; PCJD 352, frame width 425µm.

Figure 10



dominantly composed of lamellar crown tissue, and white matter generally becomes sparser from Middle to Late Palaeozoic. The denticles of palmatolepids and polygnathids are almost entirely composed of white matter extending deeply into the elements, whereas the denticles of gnathodids usually only include white matter in the portion of the denticle emerging from the main body of an element, and even then only during late ontogeny (figure 10c).

Transmitted light clearly reveals the complex growth history of type IV elements (figure 10c,d,e,f,g,h,i,j). Cone-shaped growth structures of the type seen in *Ozarkodina* are present, but in this case occurring in sets relating directly to the overlying denticulation (figure 10c,j). The first evagination is palm-shaped (figure 11a,b), each digit relating to, and ultimately resulting in, a single and specific denticle (figures 10j, 11g). The denticles within each unit are distinct optical units, traceable as discrete prisms through ontogeny (figure 10f,i). During the ontogeny of each denticle set, the angle of inclination of each denticle increases progressively from nearly parallel with the long axis of the element to the erect position more typical of 'mature' denticulation (figure 10j). This is expressed in surface morphology by a transition from suberect to erect denticulation proximally (figure 10c,e). Elements conforming to type IV growth were constantly morphological change by addition of new denticles. This condition is different from type III growth where elements underwent enlargement between episodes of denticle addition. The long axis of a process in a type IV element was the main axis of growth from which the developing denticle sets diverged. The progressive development of the individual denticles within each unit can be traced by the presence of the cone-shaped cavities (figure 10j). After the axis of growth of the large denticle diverged from the main axis of growth of the process, the growth axes of the smaller denticles diverged in turn from the growth axis of the larger denticle (figure 10e,f,g,i,j). The growth axes then translated their orientation into a progressively higher angle relative to the process. As in *Ozarkodina*, the proximal margins of the growth structures are aligned in a convex-distal arrangement. The last cone-shaped cavity occurs exactly at the point at which white matter secretion first occurred (figures 10g,j, 14e,g). The large denticle represents the distal extremity of each unit.

Early growth distally occurs synchronously with late growth proximally. Because of the pattern of growth exhibited by type IV taxa, each unit of denticulation is considered equivalent to each unit in taxa with type II growth, and to an individual denticle in taxa with types I and III growth.

(b) Morphogenesis of elements in P positions

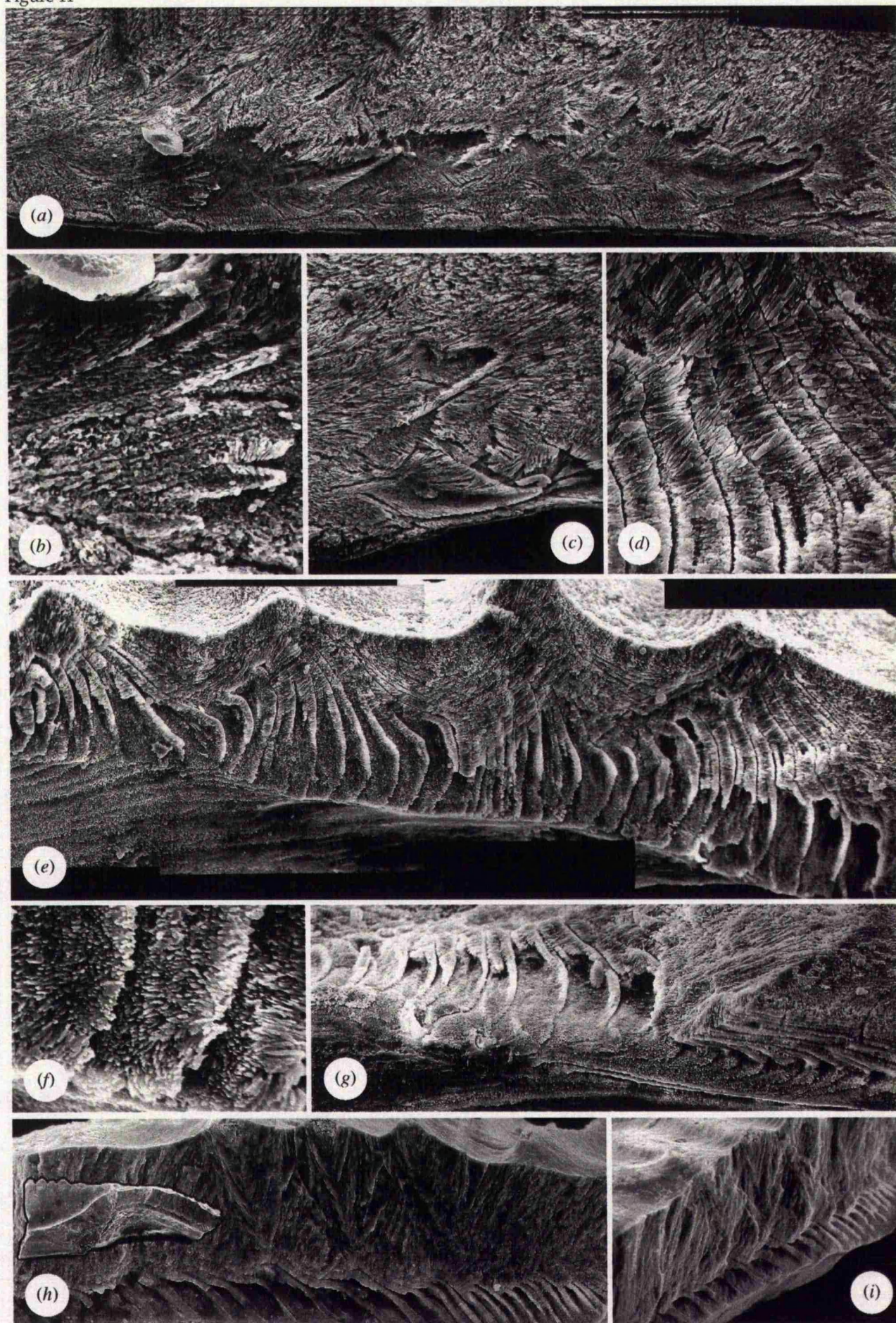
Elements filling P positions within the apparatuses of complex conodonts can be broadly divided into blade-like and platform-bearing morphologies, and more rarely, ramiform morphologies (prioniodinids -see earlier). Most, if not all platform-bearing P elements are essentially modified type III ramiforms, and therefore, exhibit similar growth patterns. However, some attempts at platform construction are merely elaborations of type III pattern of element formation. Instead of arranging denticles linearly, P elements of this type are composed of three-dimensionally arranged denticles; in *Promissum*, for example, these remain structurally distinct, but in *Coryssognathus* they are gradually fused together during ontogeny (c.f. van den Boogaard 1990). Despite the more variable morphology exhibited by elements filling Pa positions, the morphogenetic patterns are much more conservative than those exhibited by elements in S and M positions.

(i) Blade morphogenesis

The morphogenesis of blade-like elements and the blade portion of platform-bearing elements is very similar to type III ramiform growth, and is typified by the P elements of *Ozarkodina*. Initial growth of the crown

Figure 11. (a, b, c) Etched ground-section of an S element of *Mestognathus beckmanni*, the growth cavities along the axis of the element can clearly be seen, and individual denticles can be traced throughout growth as distinct prisms from inception; PCJD 327, frame width of (a) 410µm. (b) Palm-shaped growth cavity representing one of the first growth stages of a forming set of denticles, each digit representing a distinct prism and denticle; PCJD 327, frame width 32.5µm. (c) Growth cavity representing the inception of a new set of denticles at the caudo-ventral margin of the element; PCJD 327, frame width 93µm. (d, e, f, g) Etched artificially-fractured specimen of a Pa element of *Icriodella inconstans*. (e) Growth cavities in sets along the dorso-ventral axis of the element, each set relates to the overlying denticulation; PCJD 270, frame width 388µm. (d) Crystallite arrangement adjacent to the growth cavities; PCJD 270, frame width 47µm. (f) Perpendicularly-oriented crystallites forming the walls of the growth cavities; PCJD 270, frame width 27µm. (g) Oblique view of the basal margin showing that the growth cavities are open to the basal body (not preserved); PCJD 270, frame width 185µm. (h, i) Etched artificially-fractured section of the platform component of a Pa element of *Idiognathodus* sp. (inset) exhibiting sets of growth cavities relating to the overlying denticulation and intervening preprismatic structure. (h) PCJD 247, frame width 267µm, width of inset 736µm. (i) PCJD 247, frame width 153µm.

Figure 11



involved only lamellar crown tissue and very soon afterwards white matter secretion began. Denticles formed as distinct optical units as in ramiform elements. Maximum growth was in dorsal and ventral directions and new denticles are added marginally by localised evagination of a layer of lamellar crown tissue. White matter forms the core of all denticles in juvenile elements, but later growth, which modifies the shape of an element, is generally restricted to the ventral portion of the element and is devoid of white matter. During late-stage growth, white matter deposition is halted, and the cores are enveloped by layers of lamellar crown tissue. The tips of denticles forming dorsal or mid-oral surfaces are generally devoid of crown tissue, but this condition may be due to attrition resulting from function, rather than reflecting a pattern of growth.

The blade portions of platform elements were constructed by a pattern of growth identical to that of wholly blade-shaped elements (figure 9a). All the following patterns are derived from this.

(ii) Type A platforms

This first category of platform morphogenesis represents a modification of the standard blade pattern (figure 12a). In taxa such as *Idiognathodus* (*sensu* Baesemann 1973; Grayson *et al.* 1991), *Gnathodus* and *Icriodella* the platform is restricted to the dorsal portion of the element, and the internal construction of its crown incorporates a series of cavities within the lamellae, along the main growth axis of the element (figure 11d,e,f,g,h,i). The cavities mimic the arrangement of cone-shaped cavities present in ramiform and blade-shaped elements, where the proximal margins of the cavities are aligned in ascending fashion, with the structure ultimately produced (denticle or ridge; figure 11e,h). However, these cavities are not wholly encapsulated by the crown, and extend down to the base of the crown where they open into the basal cavity through a restricted opening which can often be observed in SEM (figure 11e,g). The upper margins of the cavities are aligned in an undulating arrangement, directly reflecting the overlying ridge morphology (figure 11e,h).

In almost all platform elements which bear transverse ridges, the ridges occur in pairs on either side of a central trough which directly overlies the axial cavities, and varies in its development from a large dividing depression, to a narrow slit. The ridges have a structure similar to denticles, being formed as discrete and homogeneous prisms which are centred about the apices of each set of 'growth cavities' (figure 11h,i). The symmetry or asymmetry of each prism is a direct reflection of the shape of the overlying structure; whether or not the prisms merge at their margins is dependent on whether the ridges are of low relief (e.g., gnathodids; figure 11h), or whether the ridges are more peg-like (e.g., *Icriodella*; figure 11e).

Paired platform ridges occur in a number of different taxa, particularly among Middle and Upper Carboniferous ozarkodinids. The significance of this is borne out by examination of the juvenile component of the internal growth record. For instance, the early growth stage of a *Cavusgnathus* platform reveals an original blade-like morphology (figure 13a,b,c; and see Purnell (1992) for the ontogeny of *Taphrognathus*, a closely related taxon). Prismatic structure and maximum growth coincide with the axis of the blade (figure 13b; in transverse view). However, after relatively few increments, the axis of primary growth bifurcates into two distinct growth axes, oblique to the original axis (figure 13c). The crystallites in subsequent layers of crown tissue are organised in two prisms, disposed about the new primary growth axes, and with an intervening area which is aprismatic, where all crystallites are organised approximately parallel to each other, perpendicular to the outer surface. Ontogenetic bifurcation of denticles appears to be the main method of platform formation within type A platform bearing taxa, and may have implications for deducing their evolutionary origin.

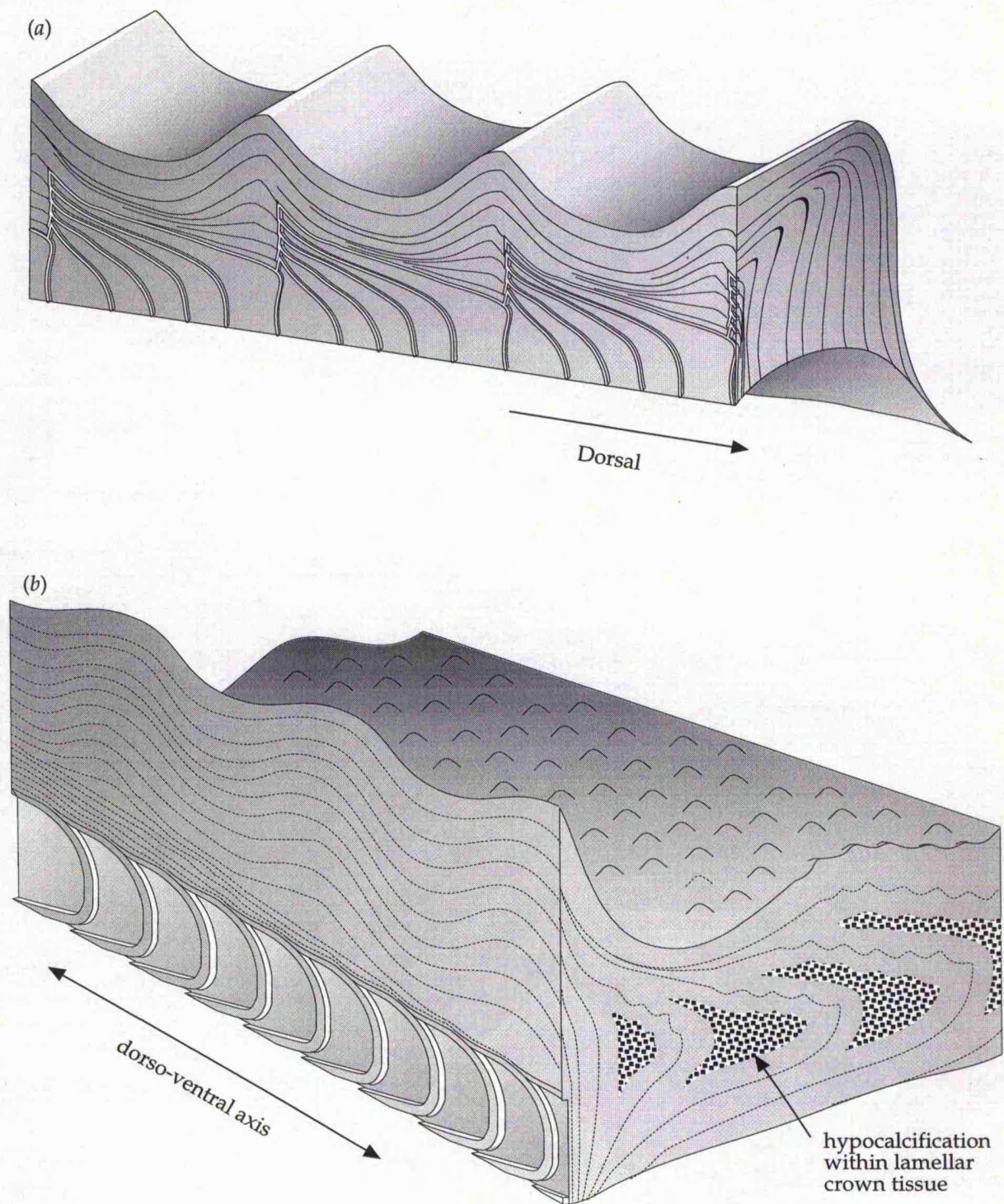


Figure 12. (a) Growth type A typified by the platforms of gnathodid Pa elements. The junction between the crown and the (unpreserved) basal body is irregular, the basal body invading the crown between successive increments of lamellar crown tissue. The paired ridges are often derived from differentiation of individual denticles in juvenile stages. (b) Growth type B typified by the platforms of *Palmatolepis* Pa elements. The crown-basal body junction is similarly irregular, but the crown is formed by exaggerated lateral growth, often resulting in hypocalcification within the enamel.

Additional nodes may be incorporated into the platform. Like the ridges, their internal structure is optically distinct from the surrounding crown tissue. Cross-crystallographic arrangement of the prisms of crystallites within the platform results in an albid appearance in reflected light. True white matter is usually absent from the platform but may occur in the blade (if one is present).

(iii) Type B platforms

This category includes such taxa as gondollelids, palmatolepids, polygnathids, *Siphonodella*, and most platform bearing prionodontids (figure 12b). They differ from type A in that their platforms are formed by lateral expansion of the incremental layers of lamellar crown tissue (figure 13e,g). The axes of growth are dorso-ventral in most of these elements (and a third lateral process in some taxa e.g. palmatolepids), contain growth cavities strongly resembling those along the growth axis of type A platforms (figure 13d). These cavities are generally larger than their type A counterparts and are overlain by fewer layers of crown tissue.

Away from the main axes of growth, successive increments include patches of poor mineralisation and often enclose large cavities, particularly in areas of maximum growth on the outer margins of elements (figure 13e,f). As a result, prominent growth increments vary in thickness from a few microns to thirty or forty microns. The outer surfaces of each of the increments in the areas of maximum growth parallel surface morphology.

The internal structure of surface morphological structures such as ridges and nodes also differ from those of type A elements which bear prismatic structure. Comparable surface morphological features in type B taxa show that they were produced by alternating and precisely located swellings and pinches in incremental thickness (figure 13e).

Like type A platforms, type B platforms also lack true white matter within the platform although they exhibit areas of albid appearance in reflected light. White matter is present in the free blade and carina.

The most conspicuous difference between surface morphology of type A and B platforms is the absence and presence of a carina respectively. The platform in type A platforms often lack a carina because the denticles which composed the dorsal blade in juvenile (and ancestral?) forms were split ontogenetically to form the paired ridges common to this element type. Type B elements retain a prominent carina throughout ontogeny because the denticles perform no role in formation of the platform. However, some forms appear to combine both morphogenetic patterns e.g. *Gnathodus bilineatus*. Some species of *Cavusgnathus*, a typical type A platform, also exhibit evidence of a combination of the two growth types where a small carina at the dorsal-most tip of the Pa element is developed in specimens representing late ontogeny. All work so far suggests that beside minor elaborations, such as platform development, pattern formation is the same in all elements in a given apparatus.

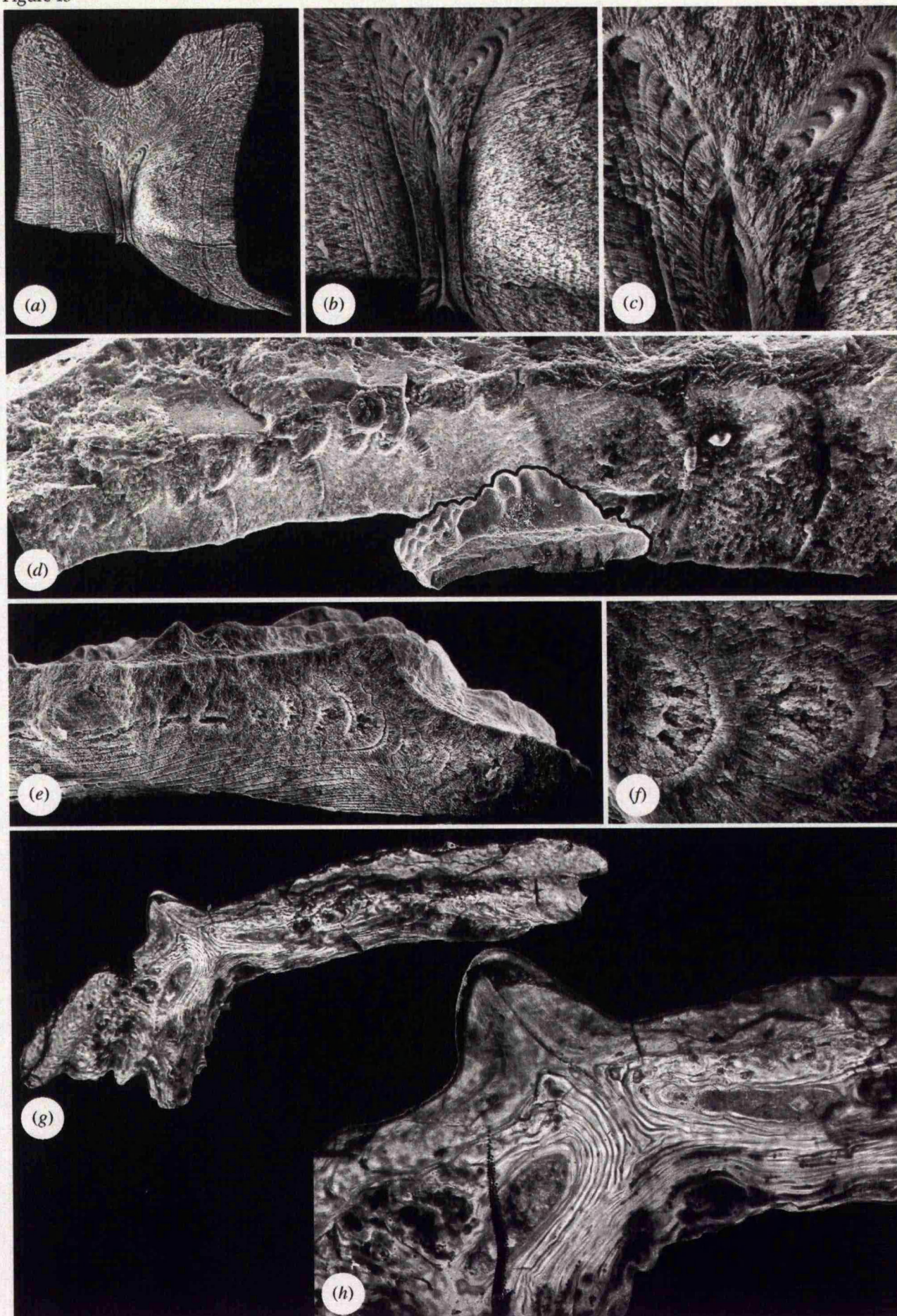
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6. INTERPRETATION OF THE HARD TISSUES

Considering the widely diverging views of conodont affinity expressed over the past 140 years, there have been surprisingly few competing hypotheses to explain element histology. Most authors have contended that the hard tissues represent forms homologous to those of vertebrates and except for a few off-beat interpretations (Zittel and Rohon 1886; Quinet 1962b; Fahlbusch 1964; Bischoff 1973) all other considerations of conodont hard tissue histology are refutations of the vertebrate hypothesis (Kemp and Nicoll 1995a, b, 1996; Schultze 1996).

Figure 13. (a, b, c) Etched transverse section through a Pa element of *Cavusgnathus alta* in progressively higher magnification, note the change from blade to paired-ridge morphology during ontogeny; PCJD 182, (a) frame width 436µm. (b) frame width 150µm. (c) frame width 76µm. (d) Etched artificially-fractured section through a Pa element of *Palmatolepis* sp. (inset); PCJD 272, frame with 472µm, inset width 967µm. (e, f) Etched artificially-fractured section through a Pa element of *Palmatolepis* sp.. (e) relationship between structure and morphology; PCJD 273, frame width 285µm. (f) hypocalcification within lamellar crown tissue; PCJD 273, frame width 42µm. (g, h) Transverse section through a Pa element of *Palmatolepis* sp. photomicrographed in plane-polarised light with differential interference contrast. (g) Entire element; PCJD 347, width 1523µm. (h) Detail of the basal body exhibiting large internal cavities which indicate that the basal tissue was secreted both from the inside and outside; PCJD 347, frame width 562µm.

Figure 13



Conodonts are now widely regarded as craniates probably most closely related to the extant agnathans (Aldridge *et al.* 1993; Forey and Janvier 1994; Gabbott *et al.* 1995; Janvier 1995, 1996a, b), although some authors believe that conodonts represent a more primitive condition akin to amphioxus (Kemp and Nicoll 1995a, b, 1996; Nicoll 1995). However, there is currently consensus over the chordate affinity of conodonts, and it is in this context that the following interpretation of conodont hard tissues has been considered.

(a) Lamellar crown tissue

Biom mineralisation among protochordates has recently been reviewed (Lambert *et al.* 1990) and it appears that only the ascidiacean and soberacean tunicates are able to secrete biomineralised tissues. Amongst these two groups, phosphatic biomineralisation is largely restricted to amorphous deposits and in some cases dahllite. However, even this one record of mineralised phosphate may be questionable because of the inherent instability of amorphous calcium phosphate (e.g. Lowenstam and Weiner 1985). In either case, lamellar crown tissue is clearly not composed from dahllite (Pietzner *et al.* 1968).

Although myxinoids are capable of secreting non-skeletal calcium phosphate in the form of statoliths and statoconia (Carlström 1963), this system is also unlikely to be responsible for conodont hard tissues. Agnathan statoliths are composed from an amorphous (polyhydroxyl) calcium phosphate which is highly unstable, dissolving in a solution of pH 8 or less (R. W. Gauldie personal communication 1995). Lamprey biomineralisation is similarly restricted to the formation of statoliths, although under the right conditions (*in vivo* or *in vitro*) lampreys are capable of skeletal biomineralisation, in particular, calcification of cartilage (Langille 1987; Langille and Hall 1993; Bardack and Zangerl 1971).

Considering the range of chordate hard tissues, the only possible homologues of lamellar crown tissue are enameloid and enamel. Both enamel and enameloid are hypermineralised, but enameloid crystallites are generally much larger than those of enamel, the crystalline structure of which is punctuated by incremental growth lines. Enamel crystallites are aligned in a preferred orientation which is usually perpendicular to the growing surface, although this alignment can vary considerably. Enameloid crystallites, which more usually resemble long fibres, are not always aligned preferentially and can range from a completely random arrangement (e.g. tangled fibre enameloid (Preuschoft *et al.* 1974, pl. 8, fig. d) to highly ordered woven and interwoven sheets (e.g. parallel fibre enameloid (Preuschoft *et al.* 1974, pl. 8, fig. e). Lamellar crown tissue most closely resembles enamel, and I believe them to be homologous. This conclusion has been reached by several authors in the past (e.g. Dzik 1986; Burnett and Hall 1992; Sansom *et al.* 1992), but heavily criticised (e.g. Blieck 1992; Kemp and Nicoll 1993, 1995a, b, 1996; Schultze 1996; Forey and Janvier 1993; Janvier 1995, 1996a, b).

Although Forey and Janvier (1993) felt that the apparent "extreme variation" of crystallite orientation in conodont lamellar crown tissue was irreconcilable with enamel, it is not without parallel in known enamels (e.g. Smith 1989), although the sub-parallel arrangement of crystallites is unusual. The dearth of comparable microstructures in other vertebrates probably results from their lack of enamel-bearing structures of comparably intricate morphology. Although other vertebrates may produce dental and other structures which are as intricate, such elements invariably lack enamel and are instead largely composed from the various types of enameloid.

The presence of prismatic structure and elaborate surface ornament in some conodont taxa indicates that the enamel organ responsible for secretion of the tissue was relatively sophisticated, capable of controlling mineral secretion and mineral alignment in any one site, producing textures comparable with the surface ornamentation of the tooth enamel of gnathostomous fish (c.f. Smith 1989, text-fig. 5 *Laccognathus biporcatus*).

(b) Basal body

Interpretations of basal tissue have varied more than for any of the other tissues of conodont elements. They range from bone (Barskov *et al.* 1982), to globular calcified cartilage (Sansom *et al.* 1992), and various dentines (Dzik 1986; Sansom *et al.* 1994; Sansom 1996), to 'a mineralised extracellular matrix, organised like connective tissue or the inner core of embryonic or chordate notochord' (Kemp and Nicoll 1995a, p.238).

The last interpretation warrants separate discussion because it is so conspicuously different from the other competing hypotheses. Kemp and Nicoll (1993, 1995a, b; 1996) have followed earlier work (Fähræus and Fähræus-Van Ree 1987, 1993) concerned with organic remnants retrieved after acid dissolution of conodont elements. The organic matrices retrieved from the basal tissue of *Prioniodus amadeus* and *Cordylodus* sp. form the basis of this interpretation and are figured in fig. 3a-e of Kemp and Nicoll (1996) and pl. 1, figs. 4, 7, 8, pl. 2, figs. 9-12 of Kemp and Nicoll (1995a). It is remarkable that organic remnants or replacements of original soft tissues could be preserved, but the least remarkable factor is the low fidelity of preservation. Indeed the preservation is such that the organic remnant cannot be compared with any specific modern tissue with any confidence because of the lack of distinguishing characters. The organic remnant does, however, compare well with connective tissue, which led to Kemp and Nicoll's interpretation of conodont basal tissue as their hypothetical 'extracellular mineralised matrix' tissue; they proffer no homologous tissue from any animal extant or extinct.

The divergent growth relationship between the basal tissue and the enamel supports interpretations of basal tissue as bone, mineralised cartilage or dentine. All three tissues are involved in odontogenesis in extant and extinct vertebrates, are neural crest derived, and can often occur together with enamel/enameloid as a result of epithelial-ectomesenchymal interaction. Enamel overlying dentine is a pattern characteristic of the vertebrate dermal skeleton, and contrary to Kemp and Nicoll (1995a), and Schultze (1996), enamel overlying bone is not unparalleled among the vertebrates (Smith 1979; Sire 1994). Although hypothetically possible, I know of no instances where enamel can be observed directly overlying cartilage.

Sansom *et al.* (1994) contended that during the Ordovician acme of vertebrate evolution (Halstead 1987) the conodonts, like all the other armoured agnathan groups, were experimenting with different tissue combinations. However, the other vertebrate groups were expressing this experimental episode in the production of variably structured dermal armour. Based on the evidence presented here and elsewhere, Sansom's scenario suggests that conodonts were directly substituting different tissues in a homologous site of an otherwise entirely unchanged mineralised skeleton, sometimes within individual species.

The case for the interpretation of conodont basal tissue as bone, as made by Barskov *et al.* (1982), was based on the presence of concentric hollow spheres and tubules within a lamellar matrix, respectively suggested to be osteocyte lacunae and vascular canals. However, the putative cell lacunae bear little resemblance to structures in bone; the spheres are infilled, bear no processes, and are better interpreted as components of dentine. Evidence for the presence of vascular tubules is also very poor, although structures similar to these have been described in other conodont taxa (e.g. *Prolematocoenites* in Andres 1988 and *Semiacontiodus* in Dzik 1986).

The case for the interpretation of basal tissue as mineralised globular cartilage is considerably stronger. Smith *et al.* (1987), Smith (1990) and Sansom *et al.* (1992) have all compared the basal tissue of *Cordylodus* (figure 5a,b,c) to the globular calcified cartilage found in the Harding Sandstone vertebrate *Eriptychius* (Denison 1967). However, Smith and Hall (1990) have postulated that cranial exoskeletal cartilage is always associated with bone, which, as we shall see below, was evidently lacking in conodonts. Furthermore, as Sansom *et al.* (1992) admitted, 'it is possible that other mineralisation processes could produce spherulitic structures such as these'.

The strongest case is for an interpretation of conodont basal tissue as dentine. Dentine exhibits a great variation in structure, including forms which do or do not include cells i.e., mesodentine, semidentine, orthodentine (see Ørvig 1967a, and Smith and Hall 1990, for reviews). Variations also occur within these categories due to factors such as environmental and physiological stress (e.g. Appleton 1994). Although the claims of dentine in conodont elements by Dzik (1986) and Andres (1988) are equivocal, the identification of mesodentine in *Neocoleodus* (Sansom *et al.* 1994) is unequivocal. The assertion by Kemp and Nicoll (1995a) that the structure of the *Chirognathus* basal tissue is a preservational artefact is unfounded, unless the histological integrity of the whole Harding Sandstone vertebrate fauna is called into question.

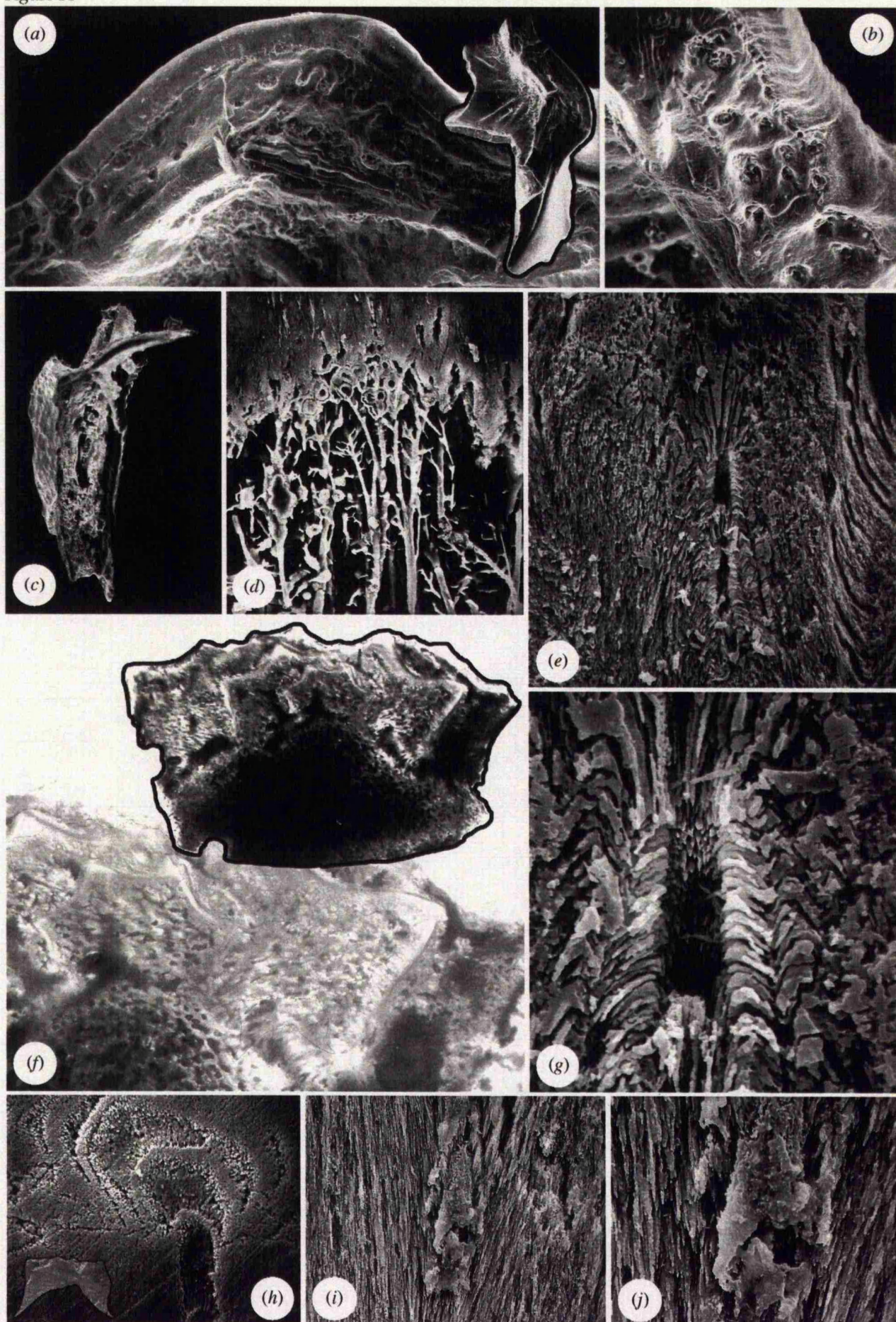
Thus, at least some basal bodies are demonstrably composed of dentine, and other structures which apparently support alternative interpretations are also sometimes displayed by dentine. The spheroidal structure compares favourably in morphology and scale with dentine calcospherites which commonly occur within dentine (figure 14d) and result from poor mineralisation (Halstead 1974), rapid growth, or other factors such as disease (Appleton 1994). Atubular dentine has been described from the basal body of *Pseudooneotodus* (Sansom 1996), but other material of *Pseudooneotodus* (figure 5d,e) reveals a spherulitic structure directly comparable with the basal body of *Cordylodus*, also described by Sansom and his colleagues (1992), but as globular calcified cartilage. Most basal bodies are lamellar and lack evidence of tubules, but even these fit within the range of known dentines, specifically (atubular) lamellar dentine (e.g. Karatajute-Talimaa *et al.* 1990; Karatajute-Talimaa and Novitskaya 1992). In most dentines these structures can occur together, so that lamellar dentine contains calcospheres, as do most tubular dentines. This is also observed in conodont basal tissues. Interpretation of all conodont basal tissue as dentine is therefore supported by the structural variation and integradation seen in a range of conodont taxa. In the light of this, the coarse structures previously interpreted as dentine tubules (Dzik 1986; Andres 1988) can be homologised with pulp canals.

The pattern of growth displayed by the basal tissue is extremely variable. The basal body of *Pseudooneotodus* is dominantly lamellar but is spheritic at the crown junction, the site of the terminal dentine network (Sansom 1996). The basal body of *Ozarkodina* is usually lamellar, except for the flanks of the structure below the contact with the crown which may be either disruption of the mineralising dentine by vascular supply from the pulp, or the site of attachment fibres.

The basal body of *Palmatolepis* also has a variable structure, though this may result from processes of preservation. In optimally preserved specimens, the flanks of the squat plate-like structure incorporate coarse calibre canal-like structures which are infilled from the outside inwards (figure 13g,h). Thin sectioned elements reveal a hollow internal structure which indicates that as the element grew rapidly laterally, the successive growth increments of basal tissue incorporated large spaces into the structure (mirroring hypocalcification in the crown). The specimens examined exhibit evidence of gradual enlargement without morphological modification, punctuated by periodic lateral expansion of the structure, again, by incorporation of a large space. The spaces did not remain hollow, but were gradually infilled by successive lamellae, the secreting tissue probably maintained *via* the canals in the flanks of the basal body (figure 14a,b,c). The rapid growth has resulted in the incorporation of pulp tissue within the mineralised structure. The lateral walls of the basal body occupied by vascular canals are poorly or weakly mineralised; this may explain the less completely mineralised state of most *Palmatolepis* basal bodies, where only the portion above the vascular region is present. In these specimens, the growth increments do not exhibit closure around the lower surface of the basal body. Either the lower half fell away *post mortem* or it was never mineralised. Most often the basal body is not preserved at all.

Figure 14. (a, b) Detail of Pa element of *Palmatolepis* sp. (inset) exhibiting the position of infilled pulp canals. (a) Caudal margin; PCJD 238, frame width μm , length of element in inset μm . (b) Rostro-ventral margin of element, note the section of a concentrically-infilled tubule at upper left; PCJD 238, frame width μm . (c) Ventral view of a Pa element of *Palmatolepis* sp. with a hollow basal body which opens to the venter; PCJD 246, frame width $488\mu\text{m}$. (d) Ground section through a crushing tooth of *Lissodus minimus*, a Rhaetian elasmobranch; the scanning electron micrograph details mantle dentine with remnants of the associated dentine tubules; PCJD 260, frame width $153\mu\text{m}$. (e, g) Etched ground section through an S element of *Polygnathus* sp. exhibiting the recurrent relationship between growth cavities, the bounding crystallites, and white matter. (e) White matter secretion appears to have been initiated immediately after a growth cavity; PCJD 328, frame width $93\mu\text{m}$. (f) Typical arrangement of crystallites adjacent to growth cavity; PCJD 328, frame width $23\mu\text{m}$. (f) Thin section through the dermal scale of *Gomphonus* sp., an acanthodian (inset); PCJD 348, frame width $357\mu\text{m}$, inset width $586\mu\text{m}$. (h) Ground section through a Pa element of *Idiognathodus* sp. (inset) exhibiting growth cavities infilled by a tissue similar to white matter; PCJD 116, frame width $37\mu\text{m}$, inset width $578\mu\text{m}$. (i, j) Thin section through an S element of *Idioprioniodus* exhibiting growth cavities infilled by a tissue similar to calcospheric dentine; PCJD 170, frame widths (i) $55\mu\text{m}$, and (j) $23\mu\text{m}$.

Figure 14



The temporal trend towards unmineralised basal bodies is potentially a serious weakness in the interpretation of basal tissue as dentine, as this homology relies partly on evidence from relative growth between the component tissues of elements. Within the vertebrate dermal skeleton, the signal for enamel secretion is believed to be the presence of a mineralised surface, typically mineralised dentine (Smith 1992). Reduced mineralisation in conodont basal bodies poses no developmental problem as long as dentine adjacent to the enamel-dentine junction was mineralised. This could explain why many Devonian conodont taxa retain a thin remnant of basal tissue which would otherwise have performed no useful purpose (e.g. see Smith *et al.* 1987).

Enameloid displays a different relationship with dentine to that between enamel and dentine. In enameloid, the enamel-secreting cells, ameloblasts, begin secretion before mineralisation of the dentine instead of after. As a result, the extracellular matrices of the two tissues intermix and the resulting tissue mineralises from the outer surface inwards, the opposite of how enamel grows. The difference between enameloid and enamel, therefore, has been proposed to be the result of a heterochronic shift in the timing of secretion by the ameloblasts, from post to pre-mineralisation of dentine (Smith 1992, 1995). In conodonts, all histological data point toward interpretation of crown tissue as enamel, but the lack of a basal body could not be explained away even if the crown were enameloid because the growth increments of the crown are still sharply truncated by the basal cavity.

To explain the then apparent absence of dentine in conodont elements (only the basal body of *Cordylodus* had by then been described), Smith and Hall (1993) suggested a shift in timing of ameloblast differentiation to an even earlier phase, prior to odontoblast differentiation. In such a scenario, epithelial-ectomesenchymal interaction would have taken place to produce ameloblast and chondroblast precursors, ultimately resulting in the secretion of enamel and mineralised cartilage. Sansom *et al.*'s (1992) interpretation of the *Cordylodus* basal body has just been discussed and rejected, and so this scenario is no longer necessary or appropriate. However, could such a heterochronic shift in timing be invoked to explain the absence of dentine in Middle and Upper Palaeozoic conodonts? The mechanism is not unparalleled (Smith 1992, 1995; Moya Smith personal communication 1996), and it is certainly plausible, but it would indicate that the signal for enamel secretion is not the presence of a mineralised surface. Smith *et al.* (1996) have attempted to homologise conodont elements with odontodes, basic units of the vertebrate dermal skeleton, which are viewed as "single, modifiable morphogenetic system[s]" (Schaeffer 1977). Odontodes are theoretically (and often in practice) perceived as flexible enough to allow any of their component tissues (enamel, dentine, and bone) to have evolved before the others, or be present independently of the others, by uncoupling or independently regulating odontoblast and ameloblast differentiation (Smith and Hall 1993). If conodont elements are homologous to odontodes, the lack of preserved mineralised dentine in many conodont elements could quite easily be explained.

(c) White matter

White matter is perhaps the most problematic of all conodont hard tissues. The most recent interpretation of white matter contends that the tissue is cellular dermal bone (Sansom *et al.* 1992; reiterated in Sansom *et al.* 1994, Sansom 1996, and Smith *et al.* 1996). The polarised arrangement of the putative cell processes and cell spaces within white matter, however, argue against an interpretation of white matter as dermal bone.

Although the arrangement of cell spaces and processes within white matter adjacent to lamellar crown is like a dentine, the inclusion of cell-shaped spaces within the groundmass appears atypical. Most modern dentines are highly organised in structure and include only spaces left by cell processes. Cells themselves are not included within the matrix because they retreat ahead of the mineralising front. However, the fossil record of dentine

reveals an evolutionary series of dentine-types from a poorly organised cell-including primitive condition, through increasingly more organised arrangements of cells and cell-processes, to a rigidly organised acellular advanced condition (Ørvig 1967a). White matter resembles the disorganised structure of mesodentine (e.g. figure 14f), the most primitive in this evolutionary lineage. However, the match is not exact because white matter lacks associated pulp canals which often occur in mesodentine. The organisation of white matter indicates, however, that the tissue grew orally, so the lack of associated pulp structures may not be so surprising. The implication is that white matter was dead once the sustaining vascularisation had been removed to facilitate element function.

The tissue lacks punctuating growth striae which (except for the most primitive types) commonly occur in most dentines. The tissue also reacts differently from the dentine of basal bodies when etched with acid. One possible alternative interpretation is that white matter is a form of enameloid, which commonly includes spaces left by the processes of odontoblasts, close to the dentine-enameloid junction. However, the microcrystalline groundmass of white matter is inconsistent with this hypothesis, as most forms of enameloid are composed of elongate fibre-like crystals.

At present, the most likely interpretation, on the basis of growth pattern and structure, is that white matter is a dentine-related tissue comparable with mesodentine, but exclusive to conodonts. Similarity to primitive enameloids may be shown in the future, e.g. tubercles of *Astraspis* possess a 'glassy cap', although the lack of large crystal fibre bundles suggests that this tissue is not identical with the enameloids of higher vertebrates (Smith *et al.* 1995) and is more similar to white matter. The interpretation of white matter as enameloid appears flawed because white matter is usually completely enveloped by enamel, and is never in contact with the dentine basal tissue. However, there is a direct relationship between the occurrence of growth cavities in the enamel crown, and the initiation of white matter secretion (figure 14e). The few examples in which in such cavities are infilled, reveal a mineralised tissue resembling white matter (in *Idiognathodus*, figure 14g) or calcospheritic dentine (in *Idioprioniodus*, figure 14i,j). Furthermore, the step-sided margins of the cavities, resulting from the abutment of surrounding enamel increments, could represent appositional growth of enamel and dentine (figure 14g). These cavities could, therefore, represent a source of odontoblastic cells which combined with ameloblasts of the forming enamel to produce an enameloid (bitypic enamel of Smith 1989). Such a scenario may be analogous to the formation of acrodin blisters on the dermal denticles of some fossil actinopterygians (e.g. Ørvig 1978a, b, c).

Refutation of the presence of cellular dermal bone in conodont elements negates the conclusions of Smith and Hall (1990) and Smith *et al.* (1996) with regard to the primacy of cellular over acellular bone, and both tissues retain their previously established (coeval) antiquity (Smith 1991).

White matter is not ubiquitous amongst conodonts and is absent from many taxa. The tissue was not essential to the formation of denticles as elements of almost all taxa contain denticles without white matter. The presence of white matter was, however, certainly beneficial in terms of structural integrity. Conodont element crowns are composed almost entirely from enamel, which is the hardest wearing of all vertebrate biominerals but is extremely brittle. Simple enamels which lack the strengthening effect of prismatic structure are particularly weak. The incorporation of a second tissue, such as white matter, which has different rheological properties, helps to strengthen the element and aids in the decussation of propagating cracks. Through the Upper Palaeozoic, many conodont lineages, particularly ozarkodinids, record a pattern of reduced white matter in P elements in favour of increased complexity in enamel microstructure.

White matter appears to be unique to conodonts, but because it is not present in the earliest of conodont elements it cannot be considered a synapomorphy of the group.

(d) Discussion

Examination of patterns of growth recorded by conodont hard tissues has facilitated testing of recent hypotheses of homology with tissues of other organisms. Patterns of growth displayed by individual tissues and by combinations of tissues are consistent with homologies with specific vertebrate dermal hard tissues. This supports the main conclusions of Sansom and colleagues (Sansom *et al.* 1992, 1994; Sansom 1996) although some reinterpretation of their results is necessary. The complexity in patterns of growth previously unrecognised in multidenticulate elements highlights the difficulty in identifying homology between the conodont skeleton and other vertebrate hard tissue systems. This study implies, however, that conodonts must have mineralised their skeleton through the evolution of a suite of hard tissues indistinguishable from those of vertebrates. To even the most ardent opponents of parsimony analysis, an entirely independent origin must appear unlikely. Nevertheless, whatever the outcome of the debate over affinities, the patterns of growth of conodont hard tissues and of element morphogenesis established in this paper will remain intact.

7. UNDERSTANDING CONODONT GROWTH*(a) Homology within the growing skeleton*

The full interpretation of conodont hard tissues now available allows reassessment of the morphogenetic patterns described earlier, taking into consideration patterns of growth of comparable tissues in extant and well documented extinct vertebrates. The descriptions of the morphogenetic growth patterns included some attempt to draw homology between the different categories. It is clear that individual denticles of type I elements represent the basic unit of the conodont skeleton. It is also apparent that these undifferentiated units are homologous with the individual multidenticulate units which collectively comprise type II elements. It is also the case that these units are homologous with multidenticulate elements of more derived taxa such as the ozarkodinids, representative of types III and IV. This last stage of homology is, however, misleading as both type III and IV elements exhibit evidence of repair. These repair events have recently been reinterpreted as episodes of post-functional growth (Chapter 3) indicating that these elements, like type II elements underwent post-eruptive growth, by envelopment by subsequent odontodes. Whereas juvenile multidenticulate elements of type III and IV taxa are homologous to individual units of type I taxa, gerontic specimens are composed of several such units. Elements of type III and IV are homologous at coeval stages in ontogeny, but the differentiated denticle units of type IV are homologous to individual denticles of type III elements.

The basic structural component of the conodont skeleton can now be seen as a denticle consisting of an enamel lamellar crown cap and a dentine base. Incremental lines within both the enamel crown and dentine basal body meet at the enamel-dentine junction (basal cavity), indicating that the two tissues grew in opposing directions, beginning at the enamel-dentine junction with a layer of dentine, followed by a layer of enamel. This pattern is widely recognised amongst vertebrate dermal units and is known as appositional growth. In the vertebrate dermal skeleton, the incremental lines within the two tissues usually share an angular relationship. This is dependent on the shape of the pulp cavity, which is rarely as evaginated in conodont elements. In conodonts, an acute angular relationship is restricted to coniform elements with deep pulp (basal) cavities.

Discrete dermal units within the vertebrate skeleton consisting of enamel and dentine are known as odontodes (Ørvig 1967a) and are the basic building blocks of the dermal skeleton. Odontodes usually include a third component, bone, which acts as a tissue of attachment. However, bone is not ubiquitous within odontodes

and is absent from the scales of thelodonts, a group of extinct jawless fish, and the scales and teeth of chondrichthyans. On this basis Smith *et al.* (1996) have argued for a homology between conodont elements and odontodes, but in the light of morphogenetic patterns described here, their contention is clearly a gross oversimplification. Type I elements are composed of up to tens of individual odontodes, but they remained structurally as well as histogenically distinct from each other, united only by an underlying supporting structure. Although the individual odontodes of type II elements were histogenically distinct, their lack of structural identity makes the resulting element an odontocomplex (*sensu* Ørvig 1977; Reif 1982). Odontocomplexes vary in their mode of formation such that successive odontodes may be added to one side, from above or circumferentially. Type III and IV elements are also odontocomplexes and exhibit circumferential addition of successive odontodes. The establishment of the new dental papilla for each odontode, at the boundary between the pre-existing crown and basal body, makes distinguishing the successive odontodes difficult.

(b) Discussion

If the growth patterns described here are to be considered in terms of current hypotheses of conodont phylogeny their arrangement from primitive to advanced would be II-(I)-III-IV; the simplest form, type I, is an evolutionary offshoot, apparently restricted to forms such as *Promissum*, *Coryssognathus* and *Icriodus*. The differences between the four categories are most easily rationalised as resulting from heterochronic changes in the timing of various developmental stages. Type II is found in *Cordylodus*, the earliest taxon bearing multidenticulate elements. It has been interpreted as either an evolutionary dead-end (Sweet 1988), or as the root of all conodonts (Dzik 1991). *Cordylodus* elements exhibit a pattern of morphogenesis typical of type II, suggesting that either the slightly later forms exhibiting the same pattern are convergent (after Sweet 1988) or else *Cordylodus* is ancestral to all subsequent multidenticulate element-bearing taxa (or possibly they have a common ancestor and *Cordylodus* is divergent). This pattern was elaborated upon in later forms and perhaps within *Cordylodus* itself, where the growth units differentiated morphologically producing multidenticulate units, as in *Carniodus*. Type I appears to be secondarily simple, derived from type II stock and representing a condition where preceeding units continued growth after subsequent units were added. This change may have been facilitated by an extension of the early ontogenetic stage of odontode growth in a type two ancestor. Type III probably represents a change in the timing of development in a type II ancestor such that the adult stage is delayed and the primary unit allowed to extend its growth. As there are no spatial restrictions on growth, the element may continue extending along its growth axes. At first it appears as though both III and IV have abandoned the ancestral condition of adding odontodes after primary growth. However, the pattern of periodic repair and enlargement exhibited by these taxa is a vestige of the ancestral growth strategy (Chapter 3). The subsequent growth stages are adapted from marginal accretion, to completely surround the existing structure, homologous with the growth of acanthodian scales (see below).

The timing of white matter secretion is potentially another important character when comparing the different growth categories, particularly as it consistently represents the latest stage of growth in individual denticles. Whereas denticles in type III elements are dominated by white matter, denticles of type IV elements contain less, and through the Devonian and Carboniferous white matter is further reduced, until by the Carboniferous, many taxa bore elements where only in late stage growth and only the portion of denticles emergent from the main body of the element, contain white matter. As a result, type IV elements resemble the juvenile stage of denticle growth in type III elements, suggesting a heterochronic shift in the timing of secretion of the different tissues.

The complexity of denticle genesis, described here, clearly contradicts Szaniawski and Bengtson's (1993) hypothesis on the origin and genesis of denticulation in euconodonts. Their model proposed that denticles originated in early euconodonts by the accretion of layers of lamellar crown tissue onto a worn, jagged region of primitive coniform elements. If early euconodonts do indeed exhibit this pattern of growth, it is more likely that the denticles formed by repair, having replaced pre-existing, but worn denticles. The pattern of denticle genesis proposed by Szaniawski and Bengtson is certainly not present in any of the ozarkodinids, prioniodinids, prioniodontids, panderoodontids, belodellids, or proconodontids observed by this author.

8. COMPARISON OF THE MORPHOGENESIS OF CONODONT ELEMENTS AND OTHER VERTEBRATE HARD TISSUES

The pattern of periodic re-growth in conodont elements which facilitates repair and enlargement is unusual in the vertebrate dental record, particularly as the elements include, and are indeed dominated by enamel. In most systems which include enamel, the enamel organ is destroyed during the process of eruption and even in those where the enamel organ survives eruption, enamel secretion is spatially restricted (e.g., rodent teeth), and it cannot facilitate repair to the functional surface. There are very few dental systems which facilitate repair, mainly because most craniates have adopted a strategy of shedding and replacement. However, 'growing' scales are much more common than 'growing teeth' in the vertebrate record and include a facility for post-eruptive repair (if the scale does indeed erupt) for example, some acanthodian (e.g. figure 14f) and actinopterygian scales. After some period of time, an erupted scale sinks within the dermis and is enlarged by the growth of another odontode around, above, or to one side of the pre-existing structure. As a result, scales are enlarged and can thus be repaired by successive layers of ganoine (a homologue of enamel, Sire *et al.* 1987; Sire 1994) over the outer surface, occurring in step with successive layers of dentine around the lower surface. Such scales must have spent much time enclosed within soft tissue, in contrast with conodont elements, which, although not teeth in the strictest sense, functioned as such. Conodont elements must periodically have sunk within the dermis, or else the dermis must have grown over the surface of the element, to facilitate growth and repair. As many elements, particularly types I and II, exhibit marginal growth independent of the remainder of the structure, it is possible that at least some elements were partially enclosed within soft tissue throughout life.

The pattern of denticulation in type II and IV is paralleled in a great number of gnathostome dentitions, particularly amongst teleosts. In most cases each denticle is a structurally distinct odontode [tooth] which is situated in a jaw and individually shed and replaced. Conodont elements were not situated within a jaw apparatus and were permanent, not shed and replaced (Chapter 3). Some acanthodian dentitions were also permanent and bear a remarkable similarity to conodonts in 'tooth' arrangement and pattern of growth. Ischnacanthid acanthodians bore dentigerous jaw bones in which the teeth were incorporated, and remained undifferentiable from the jaw proper (figure 15a); it is largely for this reason that these groups were believed to have possessed permanent dentition. Like type II and IV conodont elements, the jaw bone grew by marginal accretion and dental units comprising alternating dentition were added sequentially (figure 15ai, aii, aiii, aiv). The sequential units are not divisible into distinct teeth and are considered multidenticulate teeth (Ørvig 1973). The dentigerous jaw bones grew rostrally in contrast to the caudal direction of marginal accretion in type I-IV conodont ramiform elements. Acanthodian tooth spirals also exhibit the same pattern of marginal accretion, although the dentigerous units are unidentifiable and grew by accretion on the caudal margin of the spiral. The tooth spirals differ from those of elasmobranchs because the successive teeth are fused together in a single structural unit (figure 15c), and so, as

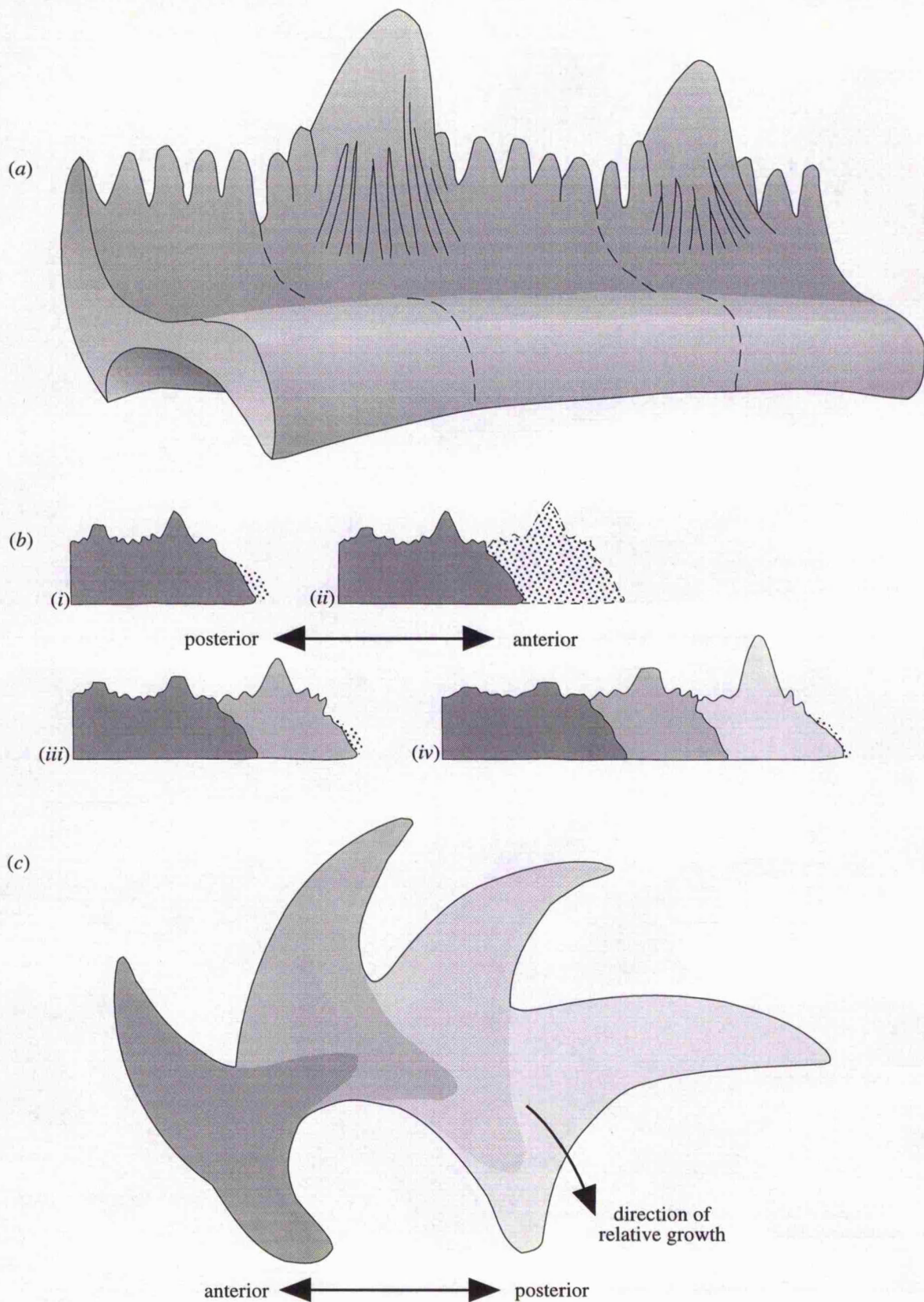


Figure 15. (a) Part of a dentigerous jaw bone in *Xylancanthus grandis* Ørvig, after Ørvig (1967b, 1973) with omission of the supporting jaw cartilage. Dashed lines delineate units of growth. (b, i, ii, iii, iv) Illustration of growth of acanthodian dentigerous jaw bone by marginal accretion at the anterior end of the jaw; illustration also includes successive wearing-down of the teeth, after Ørvig (1973). (c) Illustration of growth of acanthodian tooth whorl, based on *Nostolepis*, shading delineates units of growth which were added to the posterior of the whorl, after Ørvig (1973).

each tooth was replaced by its successor, it was not immediately shed but retained and shed with the whole spiral when the last tooth was no longer functional (Ørvig 1973). Although growth of acanthodian dentigerous jaw bones has been poorly documented, there appears to be no evidence of repair to existing dentition during the addition of new dental units, a significant difference from conodont elements. Also, acanthodian jaws are entirely composed of dentine and bone in the upper and lower portions respectively, they completely lack enamel, and there is no evidence for enameloid, again, differing considerably from the condition of conodont elements.

The pattern of growth displayed by the toothplates of modern lungfish represents another possible analogue to the pattern of formation of some conodont elements. The lungfish toothplate is a permanent tooth which grows by accretion of odontodes onto the growing margin (labial in this case). The new odontodes are aligned with ridges of the toothplate which represent fusion of previously formed odontodes; each ridge is thereby interpreted as homologous with a tooth family (Kemp 1977). Lungfish toothplates are also capable of some degree of repair, but this is achieved by hypermineralising the dentine, infilling the spaces left by the cell-processes which were responsible for the secretion of the original tissue (Smith 1979). The pattern of odontode addition is directly comparable with the addition of denticles in type II conodont ramiform elements and the bifurcation of toothplate toothfamilies comparable with the addition of secondary and tertiary processes in conodont elements such as ramiform elements.

Young *et al.* (1996) challenged the primacy of the odontode as the plesiomorphic patterning component of the vertebrate dermal skeleton. Their new model of the primitive dermal skeleton is based upon fragments of putative dermal armour from the Late Cambrian of Australia, slightly younger than the first records of *Anatolepis*, another putative vertebrate (Bockelie and Fortey 1976; Repetski 1978; Smith *et al.* 95, 96), and the first true conodonts. These broken plates are composed of a tripartite tissue complex including a laminated basal layer, calcospheritic middle layer, and continuous hypermineralised capping layer. The middle layer is composed of a series of polygonal fields, radially arranged about vertical canals which traverse the capping layer and open onto the surface through tubercles. The capping tissue is considered homologous to enamel, and although Young *et al.* refrain from attempting to draw homology between the middle and basal layers, and the tissues of other vertebrates, they consider dentine absent. The lack of dentine or bone of attachment in this material is taken as evidence that they are not primitive for the dermal skeleton of vertebrates, and thus an unreliable indicator of vertebrate affinity. In the light of this, one wonders on what basis the new Cambrian material is ascribed to the vertebrates? The identification is based largely on comparative morphology of surface ornament, and the tripartite tissue combination form which the sclerites are composed. Comparative morphology has, in the past, been recognised as an unreliable indicator of affinity (e.g. Schallreuter 1983, Schallreuter *in* Blieck 1991). Furthermore, the tripartite tissue combination is typical of vertebrate dermal armour because odontodes are three-layered, and yet Young *et al.* (1996) conclude that odontodes are not plesiomorphic in the vertebrate exoskeleton. Yet on this basis, Young *et al.* go on to reinterpret the hard tissue histology of *Anatolepis* and conodonts, concluding that the two groups “represent divergent specialisation’s with the early diversification of vertebrate hard tissues” and that conodont hard tissues are unique. Even if the new Cambrian material were vertebrate, there is no evidence, stratigraphic or otherwise, that it is any less derived than *Anatolepis* or the hard tissues of conodonts. It could as easily have been derived from *Anatolepis*. The evidence from *Anatolepis* and from conodonts suggest that odontodes are plesiomorphic patterning units of the vertebrate dermal skeleton.

9. DISCUSSION

The apparent complexity inherent within the structure of conodont elements is remarkable. Conodonts were capable of producing elements of diverse shape and structure, from unidenticulate coniform elements to multidenticulate ramiform elements, through addition of any number of odontodes. However the basic architectural plan of the feeding apparatus remained conservative throughout the conodont record. The architecture of the feeding apparatus of ozarkodinids is known to have remained stable in element number and position throughout much of its record (Silurian-Carboniferous from a record extending latest Ordovician to Permian; Chapter 1). Given the variety of morphogenetic patterns exhibited by different conodont taxa, architectural stability is even more remarkable.

Prioniodinids also bore a standard fifteen element apparatus (Purnell and von Bitter 1996), and although *Promissum* possessed a nineteen element apparatus, other evidence suggests that this apparatus is representative of balognathids alone and not the prioniodontid order as a whole (Stewart 1995). Taxa representative of ancestral stocks, such as *Panderodus*, may have had up to seventeen elements (Sansom *et al.* 1994), but the evidence for this is poor (Chapter 1).

There must have been a controlling factor in the growth of the conodont apparatus which prevented deviation from the standard fifteen element PMS division through much of the conodont record. The elements as unitary structures are not directly comparable with teeth or dermal teeth, but with aggregations of them, so it is convenient to consider each element position to be analogous to a gnathostome tooth family, where growth is restricted to within the 'tooth position'. Growth between such positions in conodont elements, as in tooth families may have been prevented by a 'zone of inhibition'. However, unlike most tooth families, functional teeth were not replaced in successive generations, but added to by new teeth, as in the dentigerous jaw tooth families of ischnacanthid acanthodians.

The difference between teeth and other odontodes is the locus of formation, teeth are formed only within a dental lamina, which probably did not evolve until after the mandibular arch (Reif 1982). However, if conodont elements are homologous to vertebrate teeth (e.g. Gaengler and Metzler 1992), they must have formed within a dental lamina. Such a dental lamina would have to have been permanent, but instead of facilitating growth of replacement teeth, it would have been responsible for periodic growth and repair of damaged elements. If such a scenario is realistic, it is likely that the dental lamina was discontinuous, and the proposed plesiomorphic fifteen element plan of the conodont feeding apparatus was a result of segregated dental laminae of the same number.

10. THE REST OF THE CONODONT SKELETON

The feeding elements are the only part of the conodont skeleton to have been consistently mineralised, but is there any other evidence of skeletal biomineralisation? Phosphatic spheres found associated with conodont elements have been attributed to the conodont animal and have been coined 'conodont pearls' (Glenister *et al.* 1976, 1978). Glenister *et al.* further proposed that the structures represented the animal's response to irritation, whether by detritus or parasitic invasion. The animal alleviated the irritation by secretion, around the stimulus, the mineral normally used to grow the feeding elements. The pearls have since been demonstrated as belonging to an extinct group of bryozoans (Donoghue 1996).

The only other mineralised structure associated with conodonts is a small phosphatic object found adjacent to the feeding apparatus in one of the Scottish conodont animals. This sphaeroid strongly resembles lamprey statoliths which are also phosphatic, and appears in a position within the head consistent with the otic

capsules (Aldridge and Donoghue *in press*), organic remnants of which may also be preserved in another of the Scottish specimens (Briggs *et al.* 1983; Aldridge *et al.* 1993). However, otoliths, statoliths and statoconia are non-skeletal (Maisey 1987).

The conodont animal must also have possessed some form of internal skeleton, if for no other reason than to have provided support and articulation for manipulation of the feeding apparatus (Chapter 1). Despite preservation of soft tissues (Briggs *et al.* 1983; Aldridge *et al.* 1986, 1993; Aldridge and Theron 1993), sometimes in exquisite detail (Gabbott *et al.* 1995), there is still no record of such an internal skeleton, mineralised or otherwise. It is likely that the animal possessed a cartilaginous endoskeleton much like that of the extant agnathans, hagfish and lampreys. Fossil representatives of these groups (Bardack and Zangerl 1968, 1971; Bardack and Richardson 1977; Bardack 1991), also lack preserved evidence of their cartilaginous endoskeleton.

11. CONCLUSIONS

Description of growth patterns in conodont elements has provided a means of testing competing hypotheses of hard tissue histology which were originally based simply on isolated morphological characters. The results of the study have vindicated the suggestion that there is homology between conodont and vertebrate hard tissues. Conodont elements are more complex structures than previously recognised. They are not homologous with 'odontodes' (*contra* Smith *et al.* 1996), but each element appears to comprise one or a number of odontodes, analogous (or homologous) to a tooth family. The different patterns of formation are believed to reflect heterochronic shifts in the timing of developmental stages. However, most complexity is apparent only in primitive conodonts and is not plesiomorphic for the group. This implies that the growth patterns in conodonts were evolved entirely independently from similar patterns in more advanced vertebrates. The formation patterns do exhibit similarities with the vertebrate skeletogenic patterns, having more in common with the dermal skeleton than with oral odontodes.

CHAPTER 3

Were conodont elements permanent or deciduous?

Abstract

Currently, our entire perception of the conodont fossil record relies upon the assumption that the feeding elements were retained throughout the life of the animal. However, the alternative hypothesis, that conodonts periodically shed and replaced their elements, has also been advocated in the recent literature. The two hypotheses are mutually exclusive, yet resolution of the debate has been resisted by the lack of independent criteria on which they can be tested. Here, I interpret internal discontinuities in the growth record of conodont lamellar crown tissue as the result of wear during normal function. The cyclical development of internal discontinuities in crown tissue indicates that periodically the conodont animal underwent a phase of fasting or dormancy during which the elements were enlarged and repaired. Growth was facilitated in ozarkodinids by circumferential envelopment of odontodes around existing elements. This strategy is unique amongst vertebrate dental structures, but may be homologous with the growing scales of elasmobranchs and acanthodians. *Conodont palaeobiology, functional morphology, deciduous dentition, permanent dentition, growth, repair, wear, odontode.*

Introduction

Conodonts are an extinct group of wholly marine animals that are almost exclusively represented in the fossil record by their phosphatic, tooth-like elements. Their affinity has remained controversial since they were first discovered in the Ordovician greensands of Estonia by Pander (1856). The recovery of soft tissue remains of the conodont animal has led to a gradual increase in our knowledge of its anatomy (Briggs *et al.* 1983; Aldridge *et al.* 1986; Mikulic *et al.* 1985a, b; Aldridge *et al.* 1993; Gabbott *et al.* 1995) to a stage where conodonts are now widely accepted as chordates, and debate continues to resolve their acraniate (Kemp & Nicoll 1995a, b, 1996) or craniate affinity (Aldridge *et al.* 1993). However, many regard this once elusive creature as a vertebrate, comparable with the modern agnathans (e.g. Janvier 1995, 1996a; see Aldridge 1987, and Aldridge & Purnell 1996, for a review).

Although debate over the affinity of the animal has occupied centre stage of the conodont arena in the past decades, there is no aspect of conodont palaeobiology that is uncontroversial. The question of element function has been wrestled with since conodonts were first discovered, and two opposing hypotheses have emerged. One contends that the elements represent the filter supports of a microphage, while the other contends that the elements represent the functional 'teeth' of a macrophage; both are beset with their own special difficulties. The filter-support hypothesis (Nicoll 1977, 1985, 1995) fails because conodont elements fail to show the significant positive allometry in growth that would be expected if the animal had been a filter feeder (Purnell 1993a, 1994). On the other hand, the 'tooth' hypothesis has also appeared to be flawed; despite decades of study attempting to demonstrate the wear on the surface of the elements that would be expected if they had functioned as teeth, none was found (e.g. Hass 1941; Rhodes 1953; Pierce & Langenheim 1970; Jeppsson 1979; Nicoll 1987). The impasse was recently breached by the description of patterns of microwear on the surfaces of elements, thereby providing unequivocal support for the tooth hypothesis (Purnell 1995).

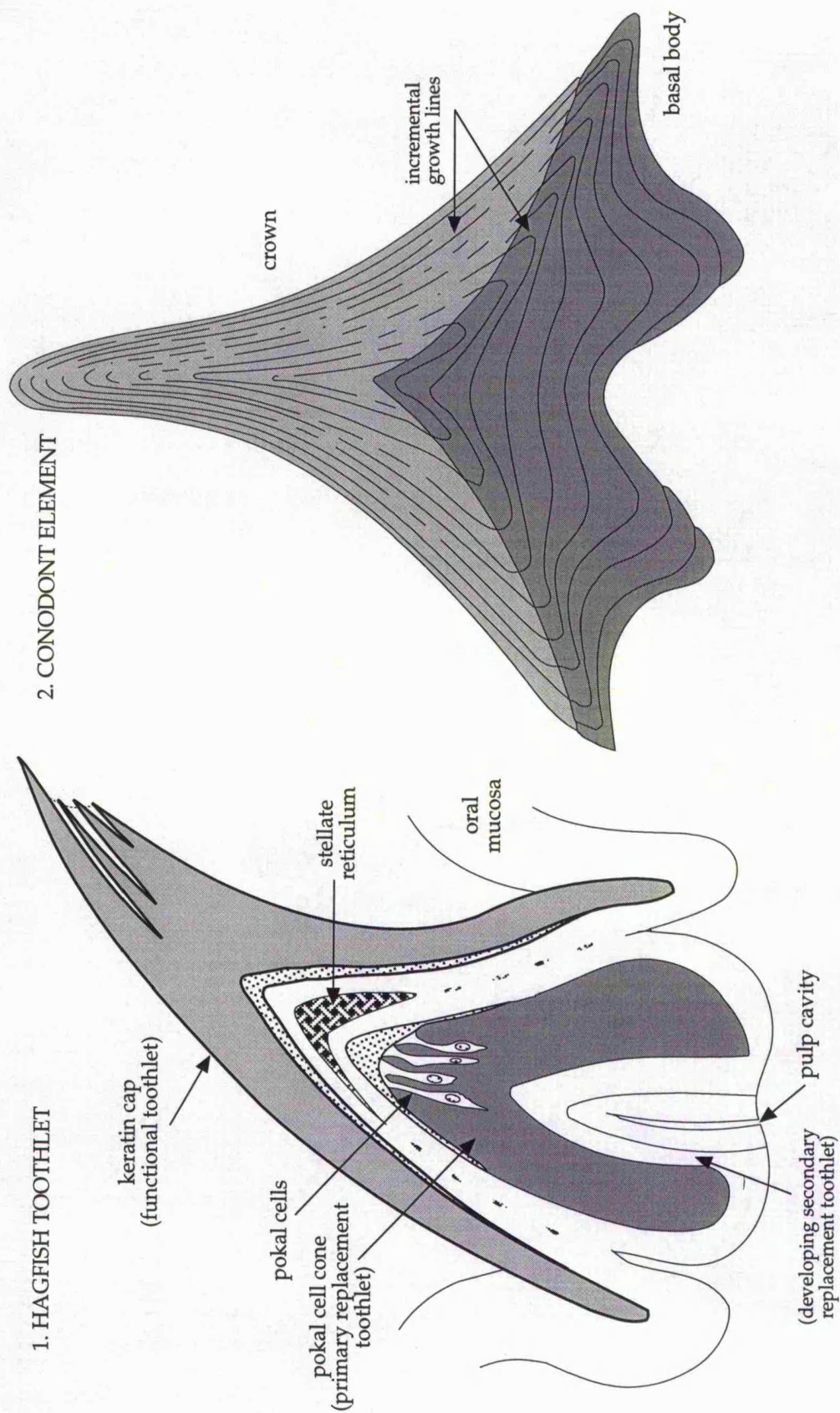
An issue which the tooth-function hypothesis must address is whether conodont elements were deciduous, that is, shed and replaced, or whether they were permanent, retained throughout life by the animal; this issue is currently unresolved. However, if conodont elements were permanent, we must reconcile this with the hypothesis that the elements were continually grown throughout life, yet remained functionally viable. This problem was

considered by Bengtson (1976) and Jeppsson (1979). The resolution of the deciduous versus permanent nature of conodont dentition is important not only in terms of conodont biology, but it relates also to our understanding of the conodont fossil record.

Hass (1941) formalised the view that conodont elements were permanent and that each fossil element represents "the last stage of the ontogeny that was reached before the death of the conodont-bearing animal" (Hass 1941, p. 80). However, Gross (1954) appears to have been the first to doubt this, suggesting that the animal might have repeatedly formed new elements of increasing size during ontogeny. Gross's doubt remained unaddressed for many years, although most authors have simply assumed *a priori* that the elements were permanent. Carls (1977) resurrected the deciduous hypothesis, basing his contention on the imbalance between the ratio of elements in Mashkova's (1972) bedding plane assemblage of *Ozarkodina steinhornensis*, and the ratio of elements in discrete collections. However, more recent studies of the hydrodynamics of conodont elements have shown that Carls' reasons for discounting biostratigraphic effects were unfounded (Broadhead *et al.* 1990; McGoff 1991). The imbalance in the ratios between element types in bedding plane assemblages and elements in discrete collections is almost certainly the result of the differing hydrodynamic properties of the elements within a given apparatus, and not the result of *in vivo* biological effects.

The question of whether conodont elements were permanent or deciduous has most recently been raised in connection with attempts to draw homologies with the keratinous toothlets of extant myxinioids (Krejsa *et al.* 1990a, b; Krejsa & Leaffer 1993; but see Slavkin & Diekwisch 1996). These authors proposed that the conodont crown is homologous to the functional keratin cap of myxinioids, and the basal body homologous to the developing replacement tooth/teeth situated beneath the keratin cap (Fig. 1). Krejsa *et al.* also believed the cancellate tissue known as white matter in conodonts to be comparable to the concentration of moribund pokal cells incorporated within the keratinised functional cap of myxinioids. They further suggested that conodonts are ancestral myxinioids that stopped mineralising their keratinous toothlets during their transition to modern forms. A detailed histological comparison between hagfish toothlet and conodont element hard tissues was not provided, but the suggestion of homology was based primarily on the common bipartite structure. However, it follows from this that as hagfish toothlets are deciduous, conodont elements were too (Krejsa & Leaffer 1993).

There are many problems with the hypothesis that conodont elements are homologous with hagfish toothlets. From soft tissue evidence, it is unlikely that conodonts and hagfish are as closely related as Krejsa *et al.* contend (Aldridge & Donoghue *in press* tackle this specific point). Furthermore, unlike successive generations of toothlets in the hagfish, there is rarely any relationship between the external morphology of the crown and the upper surface of the basal body of conodont elements (Fig. 1), and one cannot simply replace the other (Smith *et al.* 1996). More fundamentally, the mode of growth of the component parts of a conodont element are incompatible with how hagfish toothlets grow (although the histogenesis of hagfish toothlets is also poorly understood). The functional toothlet and subsequent generations of replacements grow completely independently in the hagfish, whereas the crown and basal body of a conodont element grew synchronously, growth increments passing confluent between the two structures (Fig. 1; Müller & Nogami 1971, 1972; Sansom 1996; Chapter 2). The conodont crown and basal body cannot be subsequent generations of teeth. There is also no real evidence supporting a switch from a keratinous system to an apatitic system, or *vice versa* (Smith *et al.* 1996), and the structure and patterns of growth displayed by conodont elements and their component hard tissues are more comparable with hard tissues such as dentine and enamel, than with keratin (Sansom 1996; Chapter 2).



TEXT FIG. 1. 1. Lingual tooth of *Myxine* in longitudinal section, after Dawson (1963). 2. Pa element of *Ozarkodina* in transverse section, after Müller and Nogami (1971). The functional keratin cap and replacement toothlet (pokal cell cone) of the myxinoïd grow as distinct structures, whereas the crown and basal body (putative replacement crown of Kresja 1990a, b) grew in intimate association.

Conodont elements are not homologous to the toothlets of myxinioids, but this in itself does not prove that they were permanent. If they were permanent, however, some evidence might be expected in natural assemblages. If conodonts had replacement elements which developed before shedding of their functional counterparts, they should be recognisable in at least some natural assemblages. No such assemblages have been recorded, although some are found with less than a full set of fifteen elements (Avčin & Norby 1973; Chapter 1, fig. 6). There is also no evidence for differential growth in bedding plane assemblages (Purnell 1993a, 1994). Nevertheless, it is possible that the conodont animal shed its entire apparatus before beginning to grow replacement elements. In this case, testing hypotheses of permanent versus deciduous elements becomes difficult; it may not be possible to find evidence directly indicating that conodont elements were not shed, but if there is any evidence suggesting that the elements were retained, shedding is unlikely also to have occurred.

The significance of growth discontinuities

It is conventionally accepted that conodonts grew their 'teeth' in a manner distinct from other craniates (Gross 1954; Lindström 1964). The model for their supposedly unique mode of growth is based on the occurrence of internal discontinuities within the crown tissue of the elements (Figs. 2-5), where denticles and platforms have been damaged during early ontogeny and subsequently repaired. Many authors have taken this as evidence of growth interrupted by episodes of function (e.g. Jeppsson 1979; Weddige 1990; Purnell 1995; and many others), but internal discontinuities have also been interpreted the result of accidental damage (Furnish 1938; Hass 1941; Lindström 1964), episodes of resorption (Müller & Nogami 1971, 1972; Müller 1981; Merrill & Powell 1980), or abnormal deformation during growth (Rhodes 1954).

Rhodes' (1954) hypothesis can be dismissed immediately. If the elements had been damaged during growth it is likely that the mineral-secreting organ, too, would have been damaged, and we would expect to find evidence of trauma in the crown tissue. However, other than the internal discontinuities, there is no obvious pathology.

On what criteria could we test the three remaining hypotheses? If the discontinuities represent episodes of resorption, we would expect to find irregular pitted surfaces, characteristic of resorption. The best comparable evidence comes from vertebrate dental hard tissues (Boyde & Jones 1987), where pits ranging in size from approximately ten microns in diameter to over one hundred microns occur (based on *in vitro* study by Jones *et al.* 1986), well within the range of conventional optical microscopy. Furthermore, we would not expect the discontinuities to occur consistently in the same topographic area of the element; the distribution of areas of resorption should occur randomly or affect the whole surface of the element. The polygonal micro-ornament on the surface of the crown tissue of some conodont elements is not the product of resorption, and has been linked with secretion (von Bitter & Norby 1994).

If the internal discontinuities represent true pathologies resulting from accidental damage, we would not expect recurrent patterns of distribution, consistent between specimens. Accidental damage could be distinguished from resorption by the presence of clean breaks instead of pitted, irregular truncation surfaces.

Alternatively, if the discontinuities result from wear due to normal function, we would expect their distribution to be consistent, occurring in areas where opposing elements came repeatedly into contact, independent evidence for which can be derived from studies of microwear (Purnell 1995) and integrated functional morphology (Chapter 4). Microwear was first discovered when it was recognised that certain parts of an element came into repeated contact during function (Chapter 1). The same considerations should enable testing of the hypothesis that the internal discontinuities represent episodes of function during the growth of conodont elements. If the

topographic distribution of the discontinuities coincides with sites that came into repeated contact during function, it is likely that the discontinuities result from *in vivo* wear. Growth subsequent to function would indicate that elements were probably permanent, as it is unlikely that conodonts would have adopted the dual strategy of repair, plus shedding and replacement.

Testing the Hypotheses

The discontinuities in ozarkodinid Pa elements figured by Hass (1941), Müller and Nogami (1971, 1972), and Müller (1981) are restricted to the oral surfaces of the elements. Accidental damage cannot be ruled out for most of Hass's (1941) examples. Müller & Nogami (1971), however, figured thin-sections of polygnathids (pl. 9, fig. 5; pl. 19, fig. 2; pl. 22, fig. 4), all of which exhibit a series of truncations of growth increments of the oral face of the element only. Furthermore, the discontinuities are restricted to those parts of the face which would be predicted as occlusal (Nicol 1985, 1987; Chapter 4), such as the margins of the trough adjacent to the carina which would have occluded with the carina of the opposing element. The growth increments overlying the truncations can be traced throughout the elements and are conformable with the underlying incremental layers in areas that would have been non-occlusal, such as the rostral, caudal, and dorsal margins of the elements. The consistency of the correlation between truncation surfaces in the *Polygnathus* elements figured by Müller & Nogami (1971), and the occlusal surfaces identified by Nicol (1987; reappraised in Chapter 4) argue strongly against both accidental damage and resorption, and indicate that the discontinuities are most likely to have resulted from wear.

The function of *Idiognathodus* has recently been considered in great detail (Purnell 1995; Chapter 4). Opposing Pa elements of this genus exhibit very accurate occlusion which resulted in considerable surface wear during function, particularly along the crest of the denticles at the junction between the blade and the platform (Fig. 2A). If these elements had undergone an earlier phase of function, followed by subsequent growth, they should exhibit evidence of denudation and subsequent compensatory growth in this area. Figure 2B, as one example of many, shows just this with the extent of the repair directly comparable with the wear facet in figure 2A. The consistent correlation between the distribution of surface damage caused by function and the position of internal discontinuities argues strongly against accidental damage as a cause of the latter. Together with the lack of evidence of pitting along the plane of the discontinuity, this distribution also indicates that resorption is an unlikely cause of the truncation.

A microwear study of the blade-shaped Pa elements of *Ozarkodina* (Purnell 1995) has shown that these elements performed a shearing function. To facilitate this, all blade-shaped elements and blade-portions of Pa elements, exhibit a developmental asymmetry between their (conventionally) inner and outer faces, such that when viewed in cross-section, one face (usually the 'left' in conventional terms; Chapter 4) is flatter than the other. This allowed opposing elements to slice past each other in a manner analogous to scissor blades (Purnell & von Bitter 1992; Purnell 1995). Many elements show smooth polishing on these surfaces caused by repeated enamel-enamel contact or by processing of soft prey (Purnell 1995; sometimes there is evidence of brittle failure of the enamel crown tissue. Smooth polishing is impossible to detect in the internal structure of elements because the amount of hard tissue removed is negligible, just enough to remove the fine surface micro-ornament. Evidence of more considerable wear and brittle failure is much easier to detect as the discontinuities produced are much larger. Figure 3 is an etched dorso-ventral thin section cut parallel to the aboral margin of a Pa element of *Ozarkodina confluens*. The developmental asymmetry of the blade is highlighted by the incremental layers of enamel crown tissue from which the denticles are constructed; the flat, occlusal side is to the left. This side is also marked by a

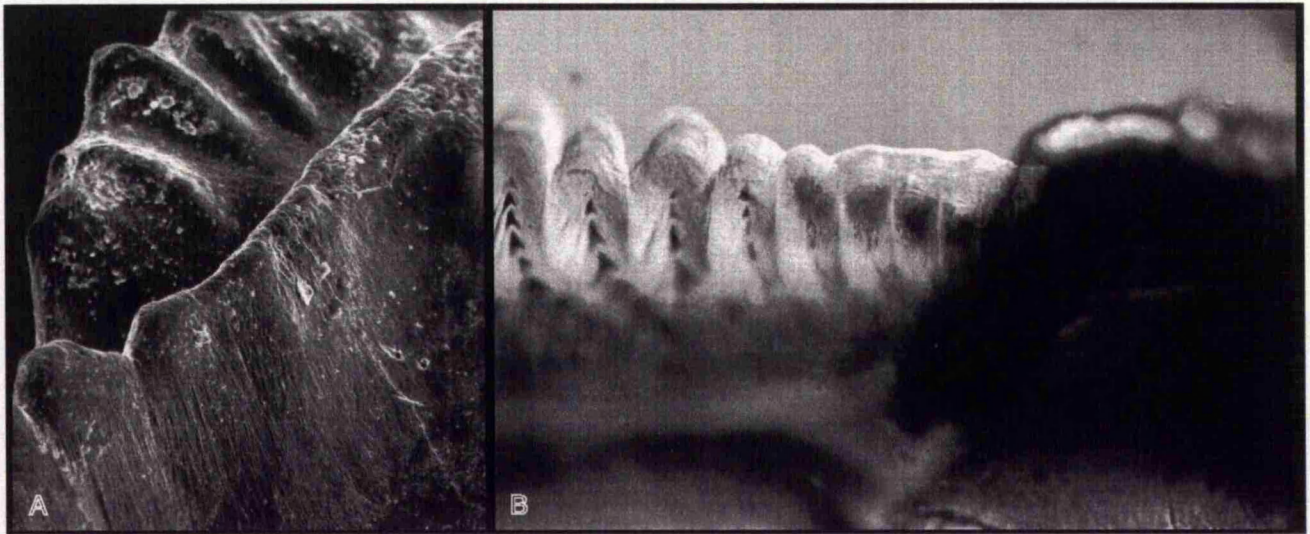


Fig. 2. Surface wear and internal discontinuities in Pa elements of *Idiognathodus*. A. PCJD 145d. Specimen exhibiting a platform-blade junction that is worn to the extent that the individual denticles comprising this structure are no longer discernable. x330. B. PCJD 342. Another specimen exhibiting fused denticles at the platform-blade junction. Because the specimen has been photographed in transmitted light, individual denticles can be distinguished, each of which bears a conspicuous truncation above which are horizontal layers of lamellar crown tissue. x192.

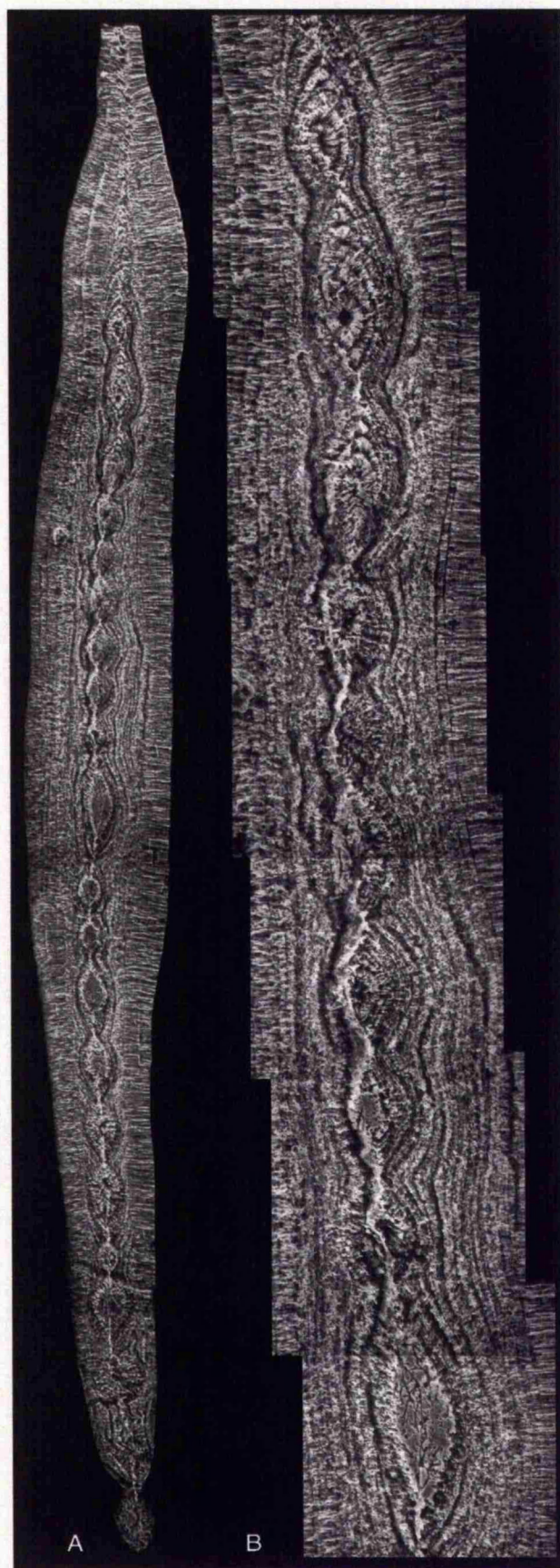


Fig. 3. A-B. PCJD 175, etched thin section through a Pa element of *Ozarkodina confluens*. A. Overview of the entire section, dorsal is top. x143. B. Detail of dorsal surface of the element in A; note the conspicuous truncation along the left margin of the denticles. x396. The section has been cut parallel to the long axis of the element, and perpendicular to the long axis of the denticles. The Element is viewed from below.

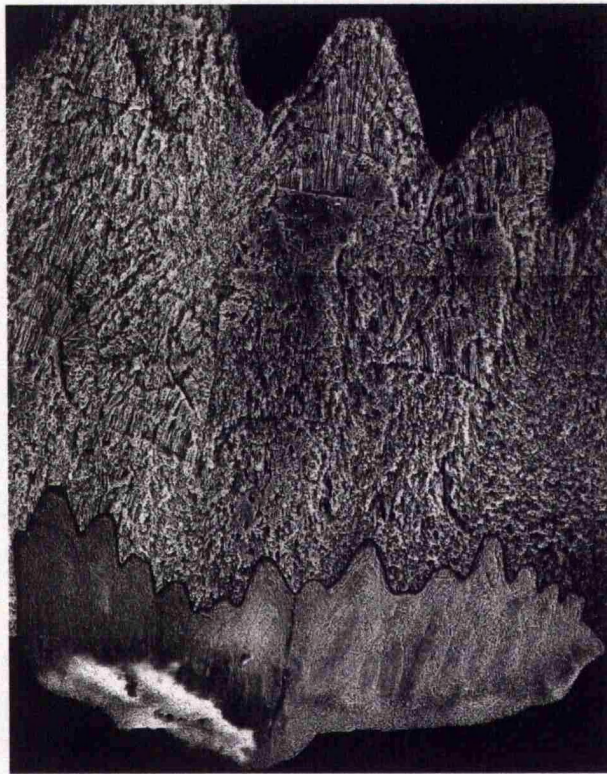


Fig. 4. PCJD 176, etched thin section through a Pa element of *Ozarkodina confluens*. Inset, overview of the whole element. x59. Main image, detail of the dorsal surface which includes more than one generation of conspicuous truncations. x332. The section is cut parallel to the long axes of the element and denticles.

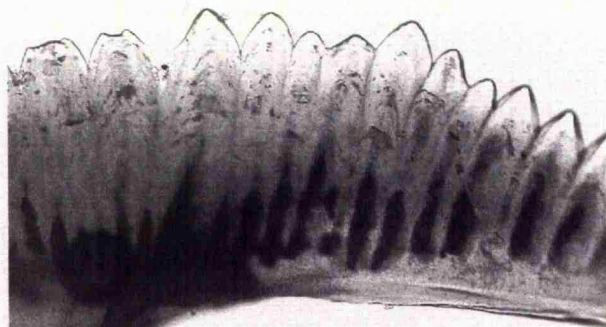


Fig. 5. PCJD 343. Pa element of *Ozarkodina confluens* exhibiting two sets of internal discontinuities, both corresponding to the distribution of worn and fractured denticles on the surface of the element. The two sets of internal discontinuities delimit three phases of growth. x71.

line which truncates the incremental layers, the layers to the left of this are not continuations of those to the right and so the element was clearly worn or broken. The dorsal limitation of the truncation further corroborates the likelihood of this facet representing damage due to function (Chapter 4).

Similarly, figure 4 is a thin section of *O. confluens* Pa element in which a series of conspicuous discontinuities are present, restricted to the functional dorsal portion of the element, which appear to represent successive events interrupted by periodic repair.

Growth and Function

The discontinuities long apparent within conodont elements, evidently testify to phases of function prior to the ontogenetic stage represented by the final morphology of any given element. This has implications for how we perceive conodont element growth, function, and the ontogeny and life cycle of the animal. Firstly, the discontinuities do not occur through the whole growth record of conodont elements, but are restricted to specific levels, indicating episodes of function. The intervening growth record often exhibits no evidence of function, indicating that during genesis, growth was punctuated by phases of function. Although it is impossible to ascertain the length of time that the elements were in use between episodes of growth, the low number of growth increments which constitute the phases of growth are likely to represent no more than a few weeks if analogy can be drawn with the time scale represented by incremental growth lines in vertebrate hard tissues (see Zhang *et al. in press* and references therein).

Alternate phases of growth and function were implicit in Bengtson's (1976, 1983a) model for growth of conodont elements, which reconciled the need for tissue cover to perpetuate appositional growth with the then equivocal tooth function for conodont elements. Bengtson proposed that between phases of function the elements grew within epithelial pockets, to be everted from the surrounding soft tissue when required and subsequently retracted; the whole mechanism is reminiscent of cat claws (Bengtson 1976). However, as the functional episodes were probably a good deal longer than the intervening phases of growth, there is very little likelihood that conodonts possessed a specialised set of retractor muscles to return the elements to the dermis. It is more likely that the elements periodically sank within or were enveloped by the dermis in a manner analogous or possibly homologous to the growing scales of living and fossil vertebrates. Indeed, Smith *et al.* (1996) have suggested that conodont elements are homologous to odontodes, the basic building block of the vertebrate dermal skeleton (= a tooth or non-growing scale; see Ørvig 1967a, and Reif 1982). Donoghue (Chapter 2) has further evaluated the histology and disparity of morphogenesis amongst conodont elements and found that multidenticulate elements are grown by marginal accretion and/or envelopment by successive odontodes.

If Smith *et al.* (1996) and Donoghue (Chapter 2) are correct, Bengtson's model of returning conodont elements to viable epithelial pockets between episodes of function is no longer tenable. Usually when odontodes erupt (e.g. in the case of teeth) the enamel organ is destroyed (although the odontoblasts can continue to secrete dentine), and even in those instances where the enamel organ continues to secrete enamel after eruption, this occurs only on the labial side of the tooth (e.g. in rodents). In the case of ozarkodinid conodont elements, post functional growth is more likely to have been facilitated by the growth of a new odontode around the pre-existing element. For this to occur, the element must have been returned to the epidermal layer, and the whole process of cell migration and cascades of epithelial-mesenchymal interactions repeated to form the new dental papilla, as though a new conodont element were to be grown. A similar scenario is envisaged for the growing scales of the extinct acanthodians (e.g. Reif 1982; Richter and Smith 1995). In conodonts ancestral to ozarkodinids, elements grew by

marginal accretion of odontodes which ultimately enveloped the existing element. In ozarkodinids, however, phases of growth subsequent to initial eruption, facilitated by the subsequent odontode, were restricted to first enveloping the existing element.

Many large Pa elements of various taxa that have been examined as part of this study exhibit a number of internal discontinuities reflecting periods of use (Fig. 4, 5). These are each separated by almost equal intervening phases of growth (Fig. 5). This alternation is paralleled by the cyclical variation in thickness of growth increments described from the crown tissue of conodont elements (Müller & Nogami 1971; Zhang *et al. in press*) which Müller & Nogami ascribed to resorption linked to seasonal variations of phosphate solubility in seawater. Zhang *et al.* proposed three alternative hypotheses to explain these growth patterns: a lunar cyclicity of days, weeks, or months entrained on the growth record; winter pauses in growth (*sensu* Müller & Nogami 1971); or alternating periods of growth and function. None of the elements thin-sectioned by Zhang *et al.* exhibited any evidence of repair in connection with the cyclical growth record, but the thin sections figured by Müller & Nogami (1971, pl. 22, fig. 1) do, thus supporting the hypothesis that the cyclical growth record in the layers of crown tissue is linked with alternating phases of growth and function. The regularity of the cyclicity in some of these examples (e.g. in the material figured by Zhang *et al. in press*, there are eleven incremental layers in each of the three cyclical units) indicates that the growth phases were of equal length.

The results of a biometric analysis of *Ozarkodina confluens* Pa elements by Jeppsson (1976) show a size distribution of elements segregated into three discrete clusters along a single line. Jeppsson explained the separate clusters by seasonal migration, but it is more likely that they represent ontogenetic stages, the generations remaining separated because growth was tightly regulated and took place over a very short period of time relative to the episodes of function. The implication of this is that size is a very good guide to the ontogeny of conodont elements. von Bitter & Norby (1994) have also noted possible cyclicity in the growth of conodont elements, albeit based on a small, statistically non-significant data set. However, out of a number of other biometric analyses (Barnett 1971; Rhodes *et al.* 1973; Murphy & Cebecioglu 1986, 1987; Purnell 1993a, 1994), the analysis of Jeppsson (1976) is the only one to exhibit clear clustering of data.

The obvious disadvantage of the conodont mode of growth is that while the elements were covered by soft tissue they were incapable of function. The alternate phases of growth and function suggest that cyclically (?annually) the conodont underwent a phase of fasting and perhaps dormancy. Therefore, as predicted by von Bitter & Norby (1994), it may in the future prove possible to recognise conodont-element growth stages and make population analysis a meaningful subject for research in palaeoecology.

CHAPTER 4

Mammal-like occlusion in conodonts

Abstract. - Recent analysis of conodont functional morphology has resolved the debate over element function in favour of the tooth hypothesis. However, our current perception of element function is still very poor; although we know that the elements performed grasping, slicing and crushing functions, we have little idea of exactly how those functions were performed. Here, I describe the analysis of a pair of *Idiognathodus* Pa elements dissected from a bedding plane assemblage, ensuring thereby that the elements are from a single individual, and have worked together in life. The opposing elements are not mirror images and exhibit a surprisingly high degree of asymmetry, allowing the elements to occlude. The degree of occlusion is comparable with mammalian molar teeth, and would have restricted the relative motion of the opposing elements to performing a crushing function. These conclusions are independently supported by microwear on the surface of the elements, which is described here for the first time from a bedding plane assemblage. Extrapolation of these results to more, and less closely-related taxa, indicate that P elements were supported by a structure which provided a degree of occlusal guidance comparable with jaws.

Introduction

Ever since Pander first discovered conodont elements in the Lower Ordovician greensands of the Baltic (Pander 1856), there have been two running debates in conodont palaeobiology, namely affinity and function. During the 127 years prior to the discovery of soft tissue remains of what we now know as the conodont animal (Briggs et al. 1983) the two debates remained inseparable as the elements themselves were the only key to affinity, and authors strove hopelessly to find homology through identifying functional analogues. With the benefit of soft tissue remains, the otherwise entirely soft-bodied animal has been established as a representative of an extinct group of chordates, although their exact phylogenetic position remains a matter of dispute. Some believe the animal to have been a protochordate, allied with the cephalochordates (Nicol 1987, 1995; Nowlan and Carlisle 1987; Kemp and Nicol 1995a, b, 1996), while others contend a vertebrate (=craniate) affinity (Aldridge et al. 1993; Gabbott et al. 1995; Janvier 1996a). I consider the latter to be the stronger hypothesis (Aldridge and Purnell 1996).

Discovery of the soft-tissue remains has been important not only in elucidating affinity, but also in separating the debates of affinity and function, and we are now, finally, in a position to examine independently the function of conodont elements without the added concern over affinity. These recent advances have opened the field of functional morphology to conodont specialists - a field perceived as closed, little more than fifteen years ago (Bengtson 1980).

Bengtson's 'basic questions of conodont [element] function' (Bengtson 1980) have now been resolved. Two competing hypotheses of element function persisted in recent years, the 'tooth' and 'filter-feeding' paradigms. The tooth hypothesis was largely based on comparative morphology of the elements, which exhibit a range of styles, many of which overlap with dentitions seen in a number of groups including arthropods and vertebrates (e.g. Müller 1981; Jeppsson 1979). However, the critical test which the hypothesis had persistently failed is the expectation of wear on the surfaces of elements, if they had indeed come into contact as envisaged by proponents of the tooth hypothesis (e.g. Purnell and von Bitter 1992). Although several workers had carefully examined collections of elements, none had observed any unequivocal evidence of *in vivo* wear (e.g. Hass 1941; Rhodes 1953, 1954; Pierce and Langenheim 1970; Jeppsson 1980; Nicol 1987). Various authors concluded from this that the elements must have been covered in life by soft tissue. This conclusion fits well with the observed outer-appositional mode of conodont element growth. The alternative hypothesis, where the conodont apparatus acted

as, or was the support of, a filter-feeding device (Nicoll 1977, 1987, 1995), has, however, suffered similar difficulties, failing a critical test of allometric growth. Animals which obtain their energy by filter feeding require their filtering device to exhibit significant positive allometry relative to growth of the animal (LaBarbera 1984). However, elements in the conodont feeding apparatus exhibited isometry and even negative allometry relative to increased body size (using the non-filtering posterior P elements as proxy for body size) (Purnell 1993a, 1994). So it appears that conodont animals could not have been filter-feeders.

The apparent deadlock between these competing hypotheses has recently been resolved by the description of patterns of microwear on the surfaces of conodont elements (Purnell 1995). This study provided the first direct evidence of element function, and unequivocal support for the tooth hypothesis. It has further enabled categorisation of microwear patterns by comparison with those shown by mammalian teeth that perform slicing and crushing functions.

Even with the benefit of conodont microwear, we know surprisingly little about how conodont elements interacted. Most of our knowledge concerns the two pairs of posterior 'P' elements which are known to have been disposed left-behind-right (Purnell 1995; Chapter 1), based on consistent disposition of the elements in bedding plane assemblages. These rare fossils represent the undisturbed skeletal remains of single animals, after death and decay of the supporting soft tissues. We also know that the P elements were capable of some degree of occlusion, because the P elements are often found in interlocking association in bedding plane assemblages and in specimens where the elements have been fused together by diagenetic minerals (e.g. Mietto 1982). Unfortunately, because the elements are fused, or held together by surrounding sediments, it is not easy to undertake detailed examination and assessment of the way in which the elements may have functioned during life. Attempts have been made to obviate this problem by reconstructing pairs of P elements from collections of isolated elements (Nicoll 1987, 1995). The way in which Nicoll articulated such elements was based on associations in fused clusters (Nicoll 1985), but his reconstructed pairs fitted together very poorly, and he used this as evidence to support his *a priori* assumption that the elements had been covered by soft tissue in life. Nicoll's conclusion was that the elements could have performed no function more intensive than 'gentle mashing'. However, it is just as likely that the poor degree of interlocking between the elements observed by Nicoll resulted from his use of discrete element collections; the elements almost certainly had not come from a single animal and had not worked together in life. Without suitable materials, it has not been possible to test Nicoll's hypotheses of function rigorously, although additional studies of conodont functional morphology and the description of microwear appear to contradict his conclusions (Purnell and von Bitter 1992; Purnell 1995).

Beside the issue of how accurately the elements interlocked, there has been the question of how the elements could have performed any 'tooth' function in the absence of jaws. We have no evidence of any supporting structure on which the elements articulated. A detailed and rigorous analysis of element interaction and articulation is now vital to determine the constraints on their function. In this study I have sought to contribute to the resolution of these questions through analysis of the functional morphology of a pair of the posterior Pa elements (Figs. 1A, B) dissected from a natural bedding plane assemblage of a single individual of *Idiognathodus* (*sensu* Baesemann 1973).

Material and Methods

The source materials for this study are natural bedding plane assemblages from the Pennsylvanian (Upper Carboniferous) Modesto Formation of Bailey Falls, Illinois. Together with coeval deposits in the vicinity, this

represents the source of the majority of known bedding plane assemblages (e.g. Du Bois 1943), and provided the material for the recent reconstruction of the ozarkodinid feeding apparatus (Chapter 1).

The shale is heavily indurated and resists disaggregation by traditional methods including hydrogen peroxide, petroleum ether, paraffin etc.. Elements were removed from the matrix using a modified version of a technique established by Norby (1976), where breakdown is achieved with approximately 10% sodium hypochlorite with 10 grams of sodium hydroxide added per 100 ml to promote the reaction. After 24 hrs or more, the shale surface had usually disaggregated and the conodont elements were readily removed from the matrix. Shale still adhering to the elements was removed by repeated treatment with sodium hypochlorite. Invariably, compaction during lithification of the shale had resulted in fracturing of the elements in the assemblages and all attempts at restoration using organic and dental bonding resins have failed. Particular attention was therefore paid to bedding plane assemblages with the least evidence of fracture, particularly at the point where the platform and blade join. Pairs of P elements removed from each assemblage were placed in opposition and held together with gum tragacanth. The analysis of occlusion presented below is based on one of these pairs, the Pa elements of specimen PCJD5.145.

Occlusion and Articulation in a Natural Pair of *Idiogoniatodus* Pa elements

Despite being arranged during life across the animal's axis of bilateral symmetry (Chapter 1) the opposing elements dissected from the bedding plane assemblage are not mirror images and deviate significantly in the morphology of their oral surfaces (Figs. 1A, B). The platform of the sinistral element (Fig. 1A) is over 17% longer than its dextral counterpart (Fig. 1B), which is 11% wider. Both platforms are strongly convex anteriorly (Figs. 2C, D), sharing a less convex, but more complex posterior margin (as used here, all such directional terms reflect the *in vivo* orientation of the elements, not arbitrary conventions as proposed by e.g. Sweet 1981). Between the asymmetrically raised margins, both elements have a medial trough which extends from immediately above the ventral blade to the dorsal tip. The anterior margins are 200-300% wider than the posterior and bear antero-posteriorly oriented asymmetrical ridges with steep ventral and shallow dorsal faces. The central area of the platform (i.e. above the apex of the basal cavity) is approximately flat, merging with the medial trough of the dorsal oral surface, and dominated by nodose ornament. The ventral portion of the platform surface, at the platform-blade junction, is dominated by a series of alternating ridges and furrows which lie in sub-parallel alignment on either side of the blade.

I manually placed the sinistral and dextral Pa elements in functional articulation (Figs. 2A-F) using data from fused clusters and bedding plane assemblages, where the blade of the sinistral element is disposed behind the dextral element (Purnell 1995; Chapter 1). Nicoll (1987) shows a similar disposition in his reconstructions based on fused clusters, but does not comment on it in his text. In this position, the blades of the opposing elements are offset, each fitting neatly into slots on their counterpart, on the anterior of the blade of the sinistral element and the posterior of the dextral platform (Figs. 2E, F). Even without prior knowledge from analysis of bedding plane assemblages (Chapter 1), this could have been ascertained directly because of the way in which the platforms lock into position.

Like the blades, the opposing platforms are offset so that the sinistral platform sits slightly posterior to its dextral counterpart (Figs. 2A, B). This slight anterior-posterior offset allows the ventral part of the oral surfaces of the platforms to interlock; the raised posterior margin of the dextral element and the raised anterior margin of the sinistral element each occlude with the medial trough of the opposed element. The anterior margin of the dextral

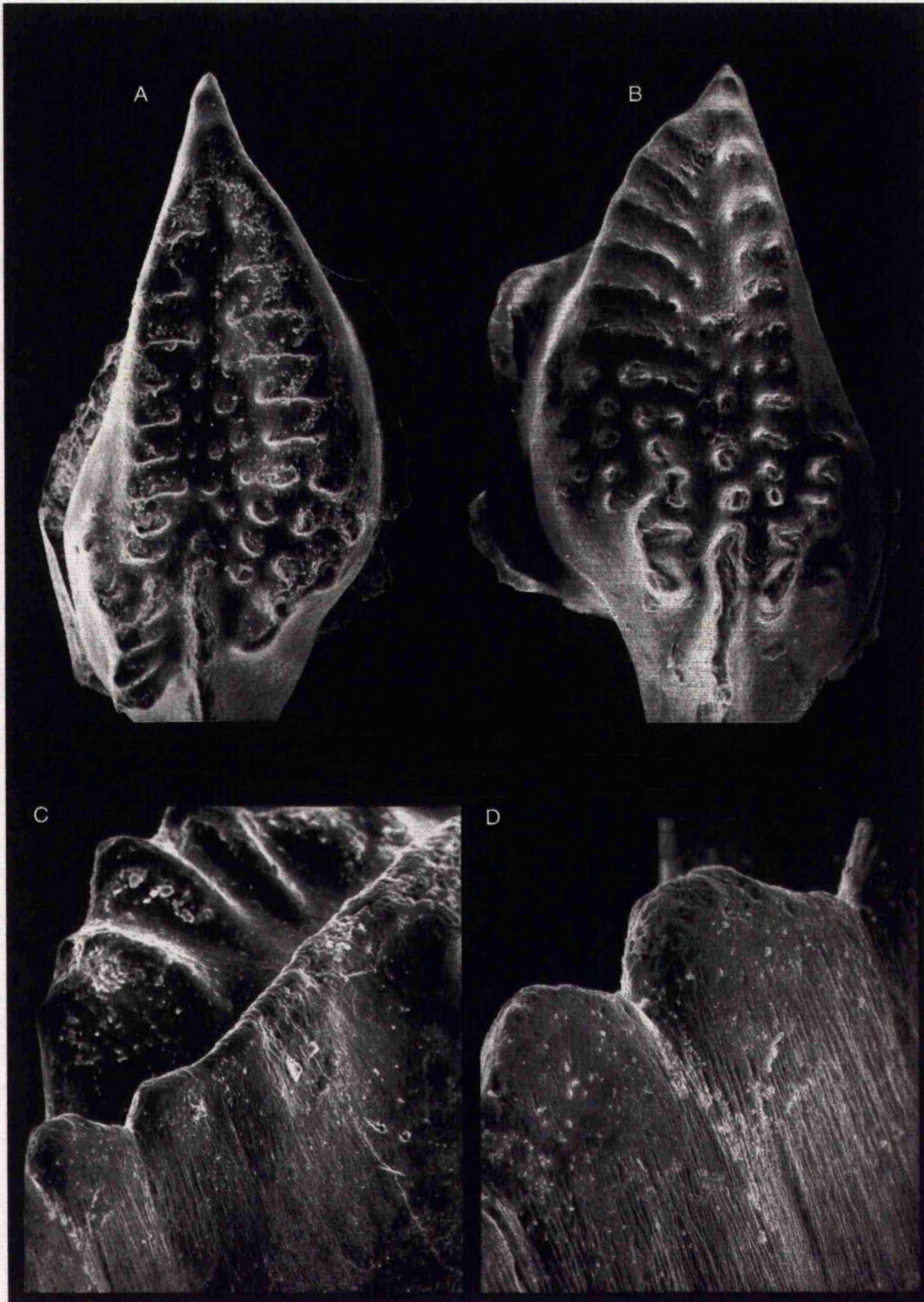


FIGURE 1. A. Platform component of the sinistral Pa element; dorsal up, posterior to left, anterior to right; PCJD 145L (x120). B. Platform component of the dextral Pa element; dorsal up, posterior to right, anterior to left; PCJD 145R (x120). C. Platform blade junction of the sinistral element exhibiting characteristic wear (x375). D. Detail of C, showing smooth polishing of the tips of the denticles on the anterior face of the blade, such that the fine striate ornament has been removed (x840).

element and the posterior margin of the sinistral element are non-occlusal, protruding anteriorly and posteriorly, respectively, from the occlusal surface (Figs. 2A, C, F). Upon articulation, the transversely oriented ridges of the opposing surfaces come into contact sufficiently precisely to facilitate accurate interdigitation.

The principal point of articulation between the opposing platforms is the area where the platform and the blade join. This portion is termed the 'platform-blade junction', and is often the most morphologically complex region of Pa elements within the *Idiognathodus* plexus. The complex morphology facilitates very precise articulation of the opposing platforms; they interlock much more closely than the dorsal-oral surfaces, largely because of the depth of the articulating components (Fig. 3). The axial ridge and furrow system, sub-parallel with the blade (Figs. 1A, B), incorporates a series of transverse structures which result in a more three-dimensional interlocking of the opposing platforms, restricting movement to simple opening and closure about the hinge. If the dorso-ventral axis is considered X, the anterior-posterior axis Y, and the left-right axis Z, the elements could only move in the X-Z plane, about the Y axis. Each morphological structure is mirrored by an 'inverted' or negative structure in the opposing element, so that each alternation of ridge and trough is matched exactly by a trough and ridge in the opposing element, and each node is matched by a pit (Fig. 3). The posterior margins of both platforms bear an accessory ridge as part of the platform-blade inter-area, composed from a linear arrangement of nodes (Fig. 2D). Again the morphology of opposing positions is inverted, providing an accessory articulating surface between the blade and the platform. The only area where positive morphological structures meet in opposing elements is in the relatively flat mid-oral region which is dominated by nodose ornament (Fig. 1A, B). The surfaces of these structures are heavily pitted, whereas the dorsal oral surfaces are comparatively pristine, with intact polygonal micro-ornament. The platform-blade inter-area shows evidence of the heaviest attrition, and the oral margin of the dorsal portion of the blade is almost flat owing to wear; originally it would have been denticulated.

The platforms are convex in anterior or posterior aspect and this prevents the whole oral surface from being in contact simultaneously (Figs. 2C, D). Instead the platforms come into contact by rocking from ventral to dorsal, the various matching morphological structures interlocking as they meet. Concomitantly, as the platform surfaces occlude from ventral to dorsal, the blades slice past each other then part; on the return motion the platforms occlude from dorsal to ventral and the blades cross (Figs. 2A-F, 4).

Microwear

As they come from a bedding plane assemblage the elements have undergone no transportation or sedimentary abrasion *post mortem* and the wear on their surfaces can reflect only *in vivo* attrition. This recognition of microwear is important because it corroborates Purnell's (1995) hypothesis of *in vivo* wear, which was based on discrete element collections which had become entrained by sedimentary processes prior to burial. In the *Idiognathodus* elements, the sinistral sides of denticle tips adjacent to the platform exhibit characteristic smooth polishing (Figs. 1C, D) comparable with that illustrated by Purnell (1995, fig. 2a), and is indicative of either enamel-on-enamel contact and/or processing of food with no hard particles. The platform-blade junction exhibits the highest degree of attrition and may have resulted either from crushing of prey containing hard particles, or poor alignment during occlusion (Fig. 1C).

Functional Morphology of the idiognathodontid Pa Element

The restricted movement of the opposing elements imposed by the occlusal structures at the platform-blade junction constrains interpretations of function. A grasping function is untenable because of element morphology,

and a shearing function is plausible for only the blade portion of the elements. Movement limited to opening and closure by rotational rocking also negates a chewing or grinding function for the platform, as this would require movement about more than one axis. However, the vertical motion of the opposing elements facilitated by rotational occlusion agrees well with a crushing function, which requires a simple opening and closure. This interpretation also accords with the microwear observed on the surfaces of this and congeneric taxa (e.g. Purnell 1995, fig. 2b); this is characteristically pitted, exhibits no evidence of translational motion, and is directly comparable with crushing wear observed on the surfaces of mammalian crushing teeth (e.g. Maas 1994; Gordon 1982). The surface morphology is also similar to that of mammalian crushing teeth (cf. Rensberger 1995). The raised ridges of mammal teeth act to reduce the surface area of tooth-food-tooth contact, concentrating applied stress into a much smaller area and increasing the efficiency of breakdown of brittle food particles (Rensberger 1995). However, there must be a trade-off between the apical angle of the ridges and the mechanical strength of the brittle tissue from which the elements are composed; the more acute the apical angle, the higher the concentration of applied stress, hence the greater the likelihood of brittle failure. A serious constraining factor is thus the rheology of enamel and its microstructure. Although enamel is the most hard-wearing of all vertebrate hard tissues, it is also one of the most brittle because of its low organic content in comparison with other dental hard tissues such as enameloid, dentine or bone. The problem is further amplified in this instance because unlike most vertebrate teeth, conodont elements were almost entirely composed of enamel. It is not surprising, therefore, that the elements described here have not developed the level of morphological complexity exhibited by some mammal crushing and shearing molariform teeth.

The asymmetry of the antero-posteriorly aligned platform ridges (e.g. Figs. 2C, D) provides further evidence of function. The pattern of occlusion and the steep ventral faces of the ridges together indicate that they acted to confine the movement of food particles preventing the food from moving dorsally during crushing. This asymmetry also indicates that the power-stroke in the occlusal cycle was ventral to dorsal, and not dorsal to ventral, or both (but see discussion on *Vogelgnathus*).

Occlusion of the complexity and detail described here is very rare amongst the vertebrates. Apart from a couple of Cretaceous crocodyliforms (Clark et al. 1989; Wu et al. 1995), a Palaeocene mammal-like reptile (Fox et al. 1992), a couple of Triassic reptiles (DeMar and Bolt 1981; Carroll and Lindsay 1985), a sauropod (Robinson 1957) and a pterosaur (Wild 1978), occlusion has rarely been recorded in the fossil record outside mammals. Some authors have even gone as far as suggesting that complex occlusal dentition is unique to mammals (Janis 1990; Smith 1993). Besides these reptiles and archosaurs, lungfish also bear complex dental plates which occlude (Kemp 1977), although in all these forms the occlusion is much less accurate than in mammal molars and the *Idiognathodus* platform elements. It is surprising that such a complex dental mechanism is present in a vertebrate of such antiquity, although simple dental functions may be mimicked by jawless fish, the possession of paired jaws is usually necessary to guide occlusion. During the early evolution of mammals, the group underwent changes in jaw structure, articulation, associated musculature, and brain programs to facilitate this (Young 1978). In the absence of jaws, the degree of occlusion attained by idiognathodontid conodonts is remarkable.

It is likely that the long ventrally developed blades were the main proxy for a pair of jaws in idiognathodontids and provided the primary means of element alignment. If the blades were also involved in the processing of food, the type of microwear developed on the surfaces of blade denticles indicates that the prey contained no hard particles. However, microwear of this kind could also be indicative of enamel-on-enamel contact with no intervening prey items. Pitted crushing facets on the surfaces of the platforms are similarly equivocal, indicating either the processing of prey containing hard particles, or else repeated contact between crushing

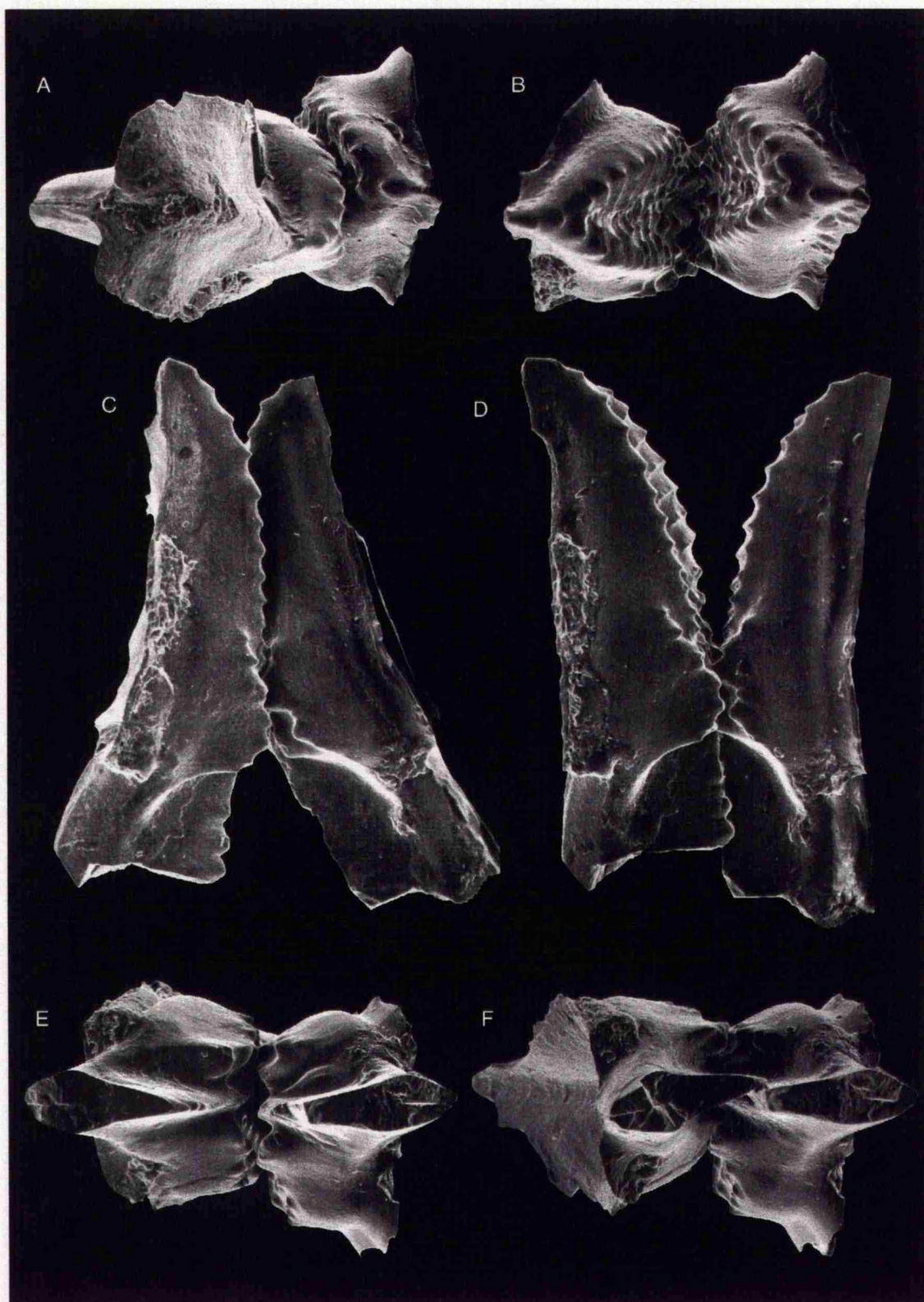


FIGURE 2. A, C, E platforms occluded, B, D, E blades occluded. A, B dorsal surfaces (x78). C, D caudal surfaces (x78). E, F ventral surfaces (x78). Sinistral to the left and dextral to the right in all cases.

surfaces without intervening abrasives. Unlike true jaws, the hinge arrangement of the elements about a pivotal point, the platform-blade junction, adjacent to the main functional surface means that the blades could have provided little leverage, as the occlusal power-stroke in the platforms was ventral to dorsal. Instead, the blades and platforms were alternately occluded in antagonistic fashion, causing most wear in the hinge area (Figs. 4B, C and Purnell 1995, fig. 2a).

However, this paradigm of element movement precludes the main occlusal surface, the platform-blade junction, from performing a function analogous to mammalian molar teeth because it is acting primarily as a hinge. This structure would therefore not, at least not primarily, have been involved in the breakdown of food particles. It is pertinent at this point to consider the functional morphology of other *Idiognathodontid* Pa elements which lack development of the platform-blade junction. Such taxa lack the intrinsic control over articulation seen here, but the morphology of the element indicates that their dorsal oral surfaces too were occlusal and were articulated to the same degree of accuracy. There was, therefore, no need for any intrinsic control over element articulation, as occlusion must have been guided by some additional but unpreserved supporting structure. A primary hinge function is thereby contradicted. Evidence from microwear (Fig. 1C) also supports a hypothesis that the platform-blade junction did not represent (at least wholly) an intrinsic adaptation to alignment, but was instead truly analogous in function to molar-type dentition. If it had acted solely as a hinge, one would expect only to observe smooth polishing resulting from enamel-on-enamel contact with no intervening food particles. However, the heavy attrition and pitted surfaces of the platform-blade junction are more likely to be the result of either breakdown of prey including hard parts, and/or damage due to misaligned occlusion. In either case, the platform-blade junction would have to have been parted (Fig. 4A) to allow prey items to be inserted between the occlusal surfaces or for misalignment to occur, and could not, therefore, have been the sole means of element articulation. The development of the platform-blade junction was primarily an adaptation which performed a function analogous to mammalian crushing molars. Nevertheless, this complex did have hinge-like qualities that prevented translational motion and would thus have enhanced the effectiveness of the elements during crushing.

The results of this study highlight significant errors in the paradigms proposed in both current interpretations of Pa element function. The hypothesis of a tooth-like function has largely been based on inference (Jeppsson 1971, 1979; Aldridge et al. 1986; Purnell and von Bitter 1992; Purnell 1995; Weddige 1990). Jeppsson's interpretation of *Idiognathodus*-like Pa element function is largely hypothetical, but relies on line drawings by Lindström (1964, figs. 43f, g) of taxa with very similar morphology to the natural pair here described. Purnell's reconstruction is based on patterns of microwear, but both incorrectly reconstruct the element platform-pairs with an anterior-posterior offset such that the medial troughs of the opposing elements would have been directly opposed during use (Jeppsson 1971, fig. 3; Purnell 1995, fig. 1). In this position the elements could not have articulated so that the occlusal surfaces came into contact.

Nicoll's interpretation of element function is based on real specimens (Nicoll 1987), but, as in some of Jeppsson's (1971) reconstructions, the main functional surfaces of the platforms did not come into close contact. However, the accurate occlusion shown by the present study leaves no room for soft tissue between the opposing elements. The lack of close articulation and occlusion in Nicoll's pairs of discrete elements does not agree with the natural element pair used in this study nor with interlocked elements in some bedding plane assemblages. This disparity results from his selection of elements that almost certainly did not come from a single individual, thereby not allowing for the dissimilarity in size and shape of opposing elements in natural pairs documented here.

Weddige's (1990) interpretation although largely hypothetical, is closer to that of Purnell (1995), being

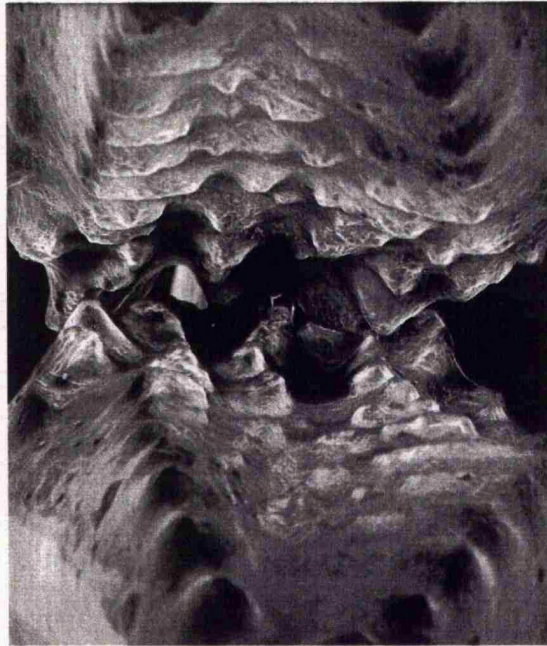


FIGURE 3. Dorsal view of the sinistral and dextral element occluded just ventral of the platform-blade junction. Note the complex complementary occlusal structures at this junction; sinistral above dextral (x193).

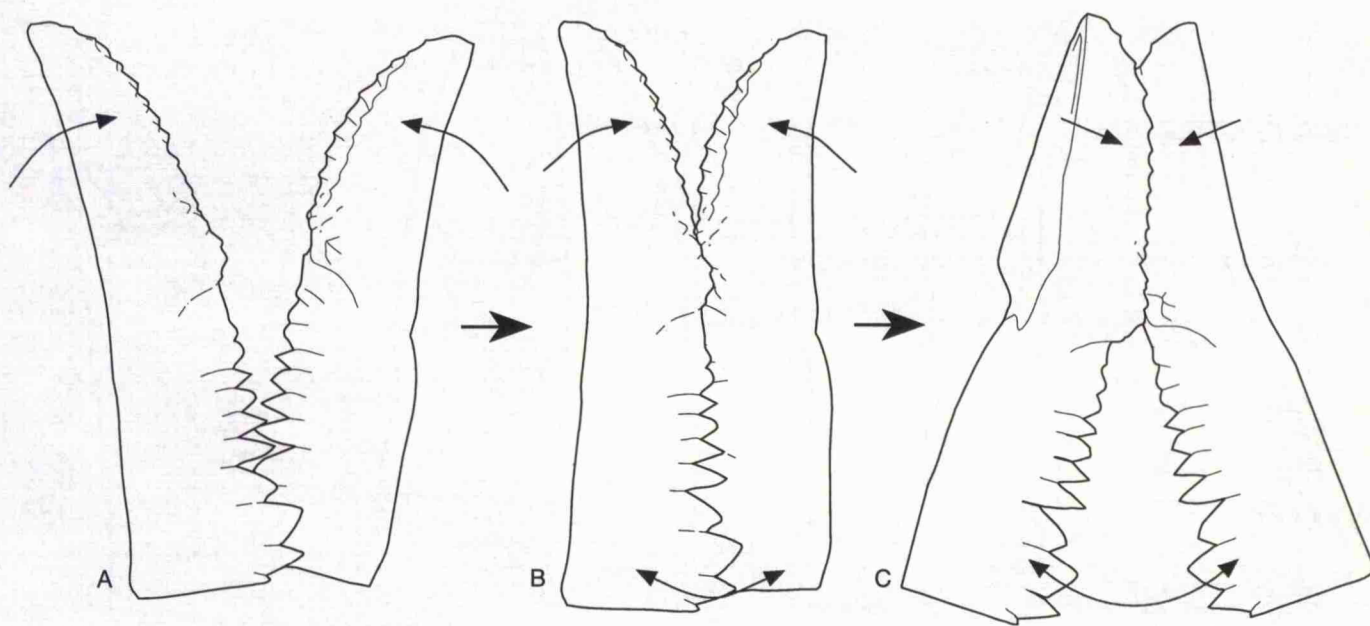


FIGURE 4. Operation of *Idiognathodus* Pa element during function. A. Blades partially occluded B. Blades fully occluded. C. Platforms occluded. Only the first phase of occlusal cycle is depicted here, the second phase is the reverse of the first.

based on surface indications of *in vivo* function. Weddige draws upon previous studies (Jeppsson 1979; Nicoll 1987) in proposing an antagonistic mechanism by which the elements ‘see-saw’ about the cusp, in the same manner later proposed by Purnell and von Bitter (1992) for *Vogelgnathus*, and demonstrated here in *Idiognathodus* (Figs. 2A-F, 4). However, the limits of element movement demonstrated by the natural element pair in this study indicate that Weddige’s perception of the degree of movement was an overestimate. Although his models are based on another ozarkodinid genus, *Polygnathus*, this also possesses a complex platform-blade interarea which would have controlled element alignment and articulation. It is unlikely that the ventral surfaces would have parted to the considerable degree portrayed by Weddige (1990, text-fig. 15b).

The Function of the Pa Element in Other Taxa

The most important morphological complex in constraining element movement in *Idiognathodus* is undoubtedly the axial ridge and furrow system of the platform-blade junction. Similar complexes can be found in numerous other conodont taxa including gnathodids, and some polygnathids, particularly *Siphonodella*, which developed as many as three or four ridges and intervening troughs parallel with the blade. These would have provided an unmatched constraint over movement of the platforms to the X-Z plane once occluded. The lack of transverse structures in the complex may have led to axial slippage between the elements unless this was prevented by the antero-posteriorly oriented ridges on the dorsal oral surface.

Many taxa exhibit little evidence of element alignment features other than the blade (e.g. *Palmatolepis*). Nicoll (1987, 1995) has suggested that the blade-shaped Pa elements of *Ozarkodina eosteinhornensis* gently mashed food particles between their lateral faces. This interpretation assumes that the orientation of these elements in fused clusters, reflects their true functional orientation, even though he rejects the orientation of elements of other taxa that he figures in fused association. Microwear described from an older species of the same genus, *O. confluens* (Purnell 1995), indicates that the posterior portions of the elements met in a manner very similar to those of *Idiognathodus*. The denticles of the opposing elements must have intermeshed, producing shearing. There is no obvious means of alignment of the elements other than the elongate ventral blades, although the consistency of scratch orientation within the wear facets (Purnell 1995) appears to indicate as much control as that exhibited by *Idiognathodus*. This suggests that supporting structures must have been present to guide articulation and alignment of elements in taxa with less ornate surfaces. The existence of supporting structures has been proposed previously, for example in the *Panderodus* apparatus (Smith et al. 1987), and for the anterior grasping array of ozarkodinids including *Idiognathodus* (Chapter 1).

In most cases it is clear that it was the dorsal oral surface that processed food. One exception is the Pa element of *Vogelgnathus*, which bears lateral nodes on the ventral portion of the sinistral side only, facilitating occlusion. The morphology of the dorsal denticles, however, indicates that they were performing a slicing/crushing function. It is possible that *Vogelgnathus* adapted the ventral blade for use in food processing so that the power stroke was both ventral to dorsal (as in all taxa described above) and dorsal to ventral.

Asymmetry

Gross asymmetry between sinistral and dextral conodonts of the same species has been widely recognised in the past, although all previous examples have been based on criteria such as common range and co-occurrence. This is the first demonstration of asymmetrically paired elements from an individual conodont. Identification of element-pair asymmetry has many important implications, particularly for taxonomy where sinistral and dextral

elements have often been given different specific names, only sometimes subsequently recognised as asymmetrical pairs from a single species (e.g. Voges 1959; Lane 1968; Klapper 1971; Klapper and Lane 1985; Sandberg and Ziegler 1979; Kuz'min 1990).

Lane's (1968) conodont symmetry classification scheme provides a simple and convenient means of distinguishing between different styles of Pa element pairing. Out of his four categories and various sub-categories, the natural element pair described here belongs to category III. All categories were based on gross element morphology, but if small morphological details are considered, particularly those which have functional significance such as sinistral blade asymmetry which allows the blades to slice past each other, all P elements are asymmetrical both as individuals and as pairs, and all the different classes of symmetry become condensed into class III.

From a functional perspective, the importance of recognising asymmetry in element-pairs cannot be understated. So, although Lane's symmetry classification scheme has proven useful and convenient in taxonomy, more importance should be attached to the finer details of element asymmetry; these relate directly to function and will help determine evolutionary relationships between taxa. Asymmetry in element morphology does not imply asymmetrical feeding behaviour in conodonts as contended by Babcock (1993), but is related to their complex bilaterally-operating function in a bilaterally symmetrical organism. Perfect mirror image pairs of elements could not perform an efficient tooth-like function requiring occlusal contact. A degree of asymmetry between the functional pairs is necessary to allow them to interlock; this has been termed 'complementary occlusion' by Weddige (1990). Babcock (1993) rationalises this by identifying a 'lead side' which results from anterior and posterior disposition of bilaterally opposed structures. Preliminary work indicates that conodont elements evolved a consistently sinistral asymmetry, (dextral lead side) disposing the elements left-behind-right, (Purnell and von Bitter 1992; Purnell 1995; Chapter 1). The apparent absence of intrapopulation variation in asymmetry indicates that this phenomenon is not a manifestation of handedness. Only one example of a dextral asymmetry in conodont elements has so far come to light (Stamm 1996, and not *Icriodus* as reconstructed by Weddige 1990), and has been used as the basis on which to erect a new species of *Idiognathodus* (*Idiognathodus* sp. A. of Grubbs 1984). The possibility that this represents intraspecific variation, and thus handedness, should first be ruled out by identification of other diagnostic characters; other explanations could include *situs inversus*, or reversal due to injury of the germ (e.g. Reif 1976, 1980, and c.f. Bergman 1990). It would be interesting to know whether the sinistral or dextral P elements appeared first in conodont ontogeny.

Growth

The Pa elements of *Idiognathodus* underwent considerable morphological change during ontogeny (Purnell 1994) and this will have affected element function. Juvenile *Idiognathodus* Pa elements bear greatly reduced platforms relative to their adult counterparts and are broadly blade-shaped with secondary ridges above the basal cavity aligned parallel to the blade, more closely resembling ancestral taxa (e.g. Purnell 1994, fig. 4f). This morphology may have facilitated overlapping occlusion similar to that displayed by *Gnathodus bilineatus* (e.g. Nicoll 1987, pl. 5.3, fig. 2) but could not have performed a crushing function as efficiently as in mature specimens with complex platforms. This must have influenced prey selection. The smallest recognisable juvenile may not, however, represent a functional stage. Some studies of the internal structure of conodont elements indicate periodic growth (Müller and Nogami 1971, 1972; Zhang et al. in press), and use may have been restricted to the end of each growth cycle (Chapter 3). Mature platform morphology is attained with very little increase in element size,

indicating that it developed very rapidly in ontogeny (see Purnell 1994, figs. 4f-j). The smallest forms may, thus, represent an animal that died during initial growth of the feeding elements prior to eruption. However, this can only be rigorously evaluated by analysis of microwear with relation to ontogeny.

Cyclical growth of the feeding elements causes enormous problems in modelling histogenesis, because it requires that the elements be returned to the epidermis for subsequent growth to occur (Chapter 2, 3). But how does this tissue-cover hypothesis stand up to our current view of element function? Bengtson (1976, 1983a) proposed a means of accommodating a necessity for soft tissue cover with a proposed tooth function, contending that elements were everted during function and subsequently retracted into the same epithelial pocket. However, recent advances in the understanding of conodont element growth (Müller and Nogami 1971; Sansom 1996; Chapter 2) and long-standing criticisms (Conway Morris 1980) render Bengtson's paradigm untenable and we must now view elements as either permanently, or only periodically covered by soft tissue in a manner analogous to growing scales (Chapter 2).

Homology

The biting action of the conodont feeding apparatus was clearly bilateral and, therefore, differed fundamentally from the bite of gnathostomes which is dorso-ventral. However, both groups of extant agnathans bear feeding apparatuses which also acted bilaterally, as did the extinct agnathan *Gilpichthys* (Bardack and Richardson 1977). Given the phylogenetic position of these taxa (Forey and Janvier 1994; Forey 1995; Janvier 1996a), it is likely that bilateral, and not dorso-ventral, action is plesiomorphic for the Craniata (Janvier 1981; Jefferies 1986; Smith 1990; Purnell 1994). Furthermore, the anterior array of the ozarkodinid feeding apparatus has recently been re-evaluated as a complex grasping structure which acted in a manner similar to the lingual teeth of extant agnathans, supported and articulated by a cartilage complex which may have been homologous with that of hagfish and lampreys (Chapter 1). The posterior portion of the apparatus including the Pa element pair has no analogue in the extant agnathans, and Janvier (1996a) has proposed that it was situated on 'a transversely moving structure derived from a velum of larval lamprey type'. However, it is more likely that the differentiated feeding apparatus was derived phylogenetically from an apparatus that was architecturally, as well as morphologically, undifferentiated.

Concluding Remarks

Definitive functional analyses are best based on elements dissected from bedding-plane assemblages. However, collections of discrete elements can be used provided consideration is taken of the way in which elements occur in fused and bedding-plane associations, and of studies such as this one. Microwear is also an invaluable tool in recognising the points of contact between elements and resolving the types of function performed in life. The most exciting prospect from this work arises from its demonstration of the functional significance of the various morphological structures that comprise the oral surface of platform elements. It may now prove possible to determine the driving forces behind conodont evolutionary patterns through analogies with the relationship between mammalian molar morphology and function (e.g. Rensberger 1995).

CONCLUSIONS

Although it is over 140 years since conodont elements were first discovered we still have little understanding of the relationships between taxa. The first serious multielement suprageneric treatment of conodonts was undertaken less than ten years ago (Sweet 1988) and we can only progress from this by identifying homologies, provided by bedding plane assemblages. Analysis of the ozarkodinid apparatus architecture, presented here, goes some way to refining the bauplan of this major group which has in the past provided the template for all conodonts. This analysis of ozarkodinid architecture also indicates that, although this group was the most diverse of all conodont orders, it shows little evidence of architectural disparity. Perhaps most importantly, the refined architectural model provides the best data set yet on which to base a functional interpretation of the ramiform array. This portion of the feeding apparatus is probably homologous to the bilaterally-acting rasping apparatus of the living agnathans, although the elements themselves are not. The S and M elements were probably integrated in performing a rasping and/or grasping function. An analysis of the orientation of collapse of all available ozarkodinid bedding plane assemblages has also revealed surprising results relating to conodont taphonomy. The conodont animal is generally perceived to have been laterally compressed, and so most bedding plane assemblages should represent lateral collapse where the conodont carcass came to lie on its side; however, the majority of bedding plane assemblages represent angles of collapse where animal was more than thirty degrees to the bedding plane. This may not be telling us anything new about conodont palaeobiology, but rather that the sea floor was either very 'soupy', or else the conodont animal may have lived within burrows in poorly compacted sediments, as do hagfish at the present day.

My analysis of conodont histology has been aimed at resolving the current confusion in the recent debate over homology of conodont hard tissues, confusion which has arisen from the lack of attention to earlier classical histological studies. I have also gone some way to resolving our long-standing ignorance of conodont element growth, and I have achieved this without making any *a priori* assumptions over the affinity of the hard tissues. My study has concentrated on the relationships of the tissues and their component structures during growth, recorded by the periodic punctuations in the tissues. By identifying homology within the different patterns of growth in conodont elements I hope that we can look at conodonts in a new way, and that patterning may provide a means of discriminating homology in phylogenetic analysis. Conodont hard tissues are homologous to the hard tissues of other vertebrates and grew in combination in the same way. Conodont elements are composed from a number of odontodes and can be considered as odontocomplexes, or possibly as tooth families. Successive odontodes were added periodically, providing a mechanism for the resolution of Jeppsson's (1979) paradox of conodont element growth and function. My evaluation of the competing hypotheses of element retention indicates that conodonts must have retained their feeding elements throughout life, periodically repairing and enlarging their elements to keep pace with the increasing energy needs of the growing animal. Evidence critical to this debate arises from the recognition that internal discontinuities in the lamellar growth record of the hard tissues relate to functional episodes in the life of the animal.

During conodont phylogeny, evolution appears to have taken advantage of the specialised strategy of growth, allowing complex occlusal dentition. Without this mode of growth conodonts could not have maintained the intricate articulating surfaces that are required for occlusion. The functional morphological analysis of *Idiognathodus* Pa element pairs in chapter four demonstrates that at least some conodonts were capable of a degree of dental occlusion unparalleled before the rise of mammals. However, without consideration of other taxa, it is unclear whether these occlusal surfaces were adapted to assist articulation or to perform a food-processing

Conclusions

function. Published studies of microwear on the surfaces of less morphologically complex conodont elements indicate that they too were capable of a degree of occlusal guidance comparable with *Idiognathodus*, without the facility for complex interlocking occlusion. This indicates that conodont elements must have been supported by an additional but unpreserved supporting structure which performed a similar function to jaws, though the two are not homologous. The morphology of *Idiognathodus* Pa elements restricted their function to crushing as the elements could only move in a single plane. This compares very well with independent evidence of microwear.

Future research into conodont functional morphology should build on this study and try to identify the changing dietary habits which are recorded in the phylogeny of closely related taxa. Recognition of internal discontinuities and fused denticles may also provide additional evidence in identifying points of repeated contact between opposing elements during function, particularly in the absence of microwear.

My contribution to conodont hard tissue histology is by no measure intended as a final treatment in the way that many earlier classical works have been regarded (e.g. Müller and Nogami 1971). There is much work to be done in this area; we still have no measure of the variability of dentine and enamel microstructure, and the true affinities of white matter are yet to be resolved (although I would lean heavily in favour of an interpretation as a primitive enameloid). Analysis of enamel microstructure in the conodont crown indicates that complex prismatic enamel is present only in conodont elements that are predicted to have performed intensive mechanical functions such as crushing, and that this level of complexity evolved many times in conodont phylogeny. The evolution of enamel in conodonts appears to mirror its evolution in jawed vertebrates, particularly among the mammals (e.g. Rensberger 1995); increasing complexity is not a measure of phylogenetic advancement, but rather occurs iteratively within a group in response to increases in imposed dental stresses. If this relationship can be convincingly demonstrated, enamel microstructure may provide a further means of deducing element function.

The greatest problem remaining in conodont palaeobiology is the absence of a coherent suprageneric classification scheme. The most promising means of overcoming this is by employing a cladistic analysis of the Conodonta. The most sensible group to begin with is the Ozarkodinida as they are the most comprehensively understood of all the conodont orders. Although the prioniodinid bauplan is very similar to that of ozarkodinids (Purnell 1993b), identifying homology is hampered by the similarity in morphology between the P, M, and S elements (Purnell and von Bitter 1996). Similarly, the prioniodontids are a highly problematic group and our only clue at present to their bauplan is the apparatus of *Promissum pulchrum*; other evidence suggests that *P. pulchrum* is not typical of the entire order (Stewart 1995). The four coniform orders are even more problematic and our only evidence for identifying homology within and without these groups rests with the apparatus of *Panderodus* (Sansom *et al.* 1994), evidence for which is extremely poor.

Although evidence for the craniate affinity of the conodont animal is now overwhelming, particularly as cephalochordates must now also be considered craniates (Williams and Holland 1996), their exact placement within the Craniata relies on the discovery of more specimens preserving the soft tissue remains, particularly from different deposits with different taphonomic histories, preserving different aspects of soft tissue anatomy. More and more *Konservat-lagerstätte* are being discovered within the long range of the conodont fossil record, and prospecting for conodont remains in these new deposits is of vital importance considering the impact conodont palaeobiology has had on research into early vertebrate evolution in recent years.

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APPENDIX 1

Conodonts: a sister group to hagfish?

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Abstract

Conodonts are an extinct group of naked agnathan fish which range in age from Cambrian to Triassic. The conodont animal is almost exclusively represented in the fossil record by the phosphatic elements of the feeding apparatus, which was the only mineralised component of the skeleton. Only twelve specimens have been found which preserve the soft tissue anatomy of the animal.

The animal possessed a notochord, myomeres, caudal fin, paired sensory organs (optic and possibly otic) and extrinsic eye musculature; these characters indicate that the animal was a vertebrate. Just posterior of the eyes and ventral of the notochord lay a feeding apparatus of varying complexity that acted bilaterally as in hagfish, differing from the dorso-ventral arrangement and action of gnathostome jaws.

The hard tissues from which the feeding apparatus is composed are comparable with those of vertebrates, particularly other fossil agnathans and corroborate the phylogenetic position established on the basis of the soft tissue anatomy. Although conodont soft tissues suggest a relationship to hagfishes, the elements cannot be homologised with hagfish lingual 'teeth' because of fundamental differences in the modes of growth of these structures.

KEY WORDS: Conodont, hagfish, agnathan, vertebrate, palaeobiology

Conodonts are an extinct group of chordates, represented in the fossil record almost exclusively by the phosphatic elements of their feeding apparatuses. They possessed no other biomineralized skeleton, and remained enigmatic until the discovery of the first of a number of fossils with preserved soft tissues in 1982 (Briggs *et al.*, 1983). Conodont soft tissues are now known from three separate localities: the Ordovician Soom Shale of South Africa (Aldridge & Theron, 1993; Gabbott *et al.*, 1995), the Silurian Brandon Bridge dolomite of Wisconsin, U.S.A. (Mikulic *et al.*, 1985a, 1985b; Smith *et al.*, 1987), and the Carboniferous Granton Shrimp Bed of Edinburgh, Scotland (Briggs *et al.*, 1983; Aldridge *et al.*, 1986, 1993). The single Silurian specimen from Wisconsin is very poorly preserved and provides little information about conodont anatomy, but the Soom and Granton specimens preserve several features of the trunk and head. It must be emphasised, however, that the preservation of particular tissues and organs has been highly selective, and the processes of replacement that led to the preservation of non-biomineralized tissues are currently poorly understood. Replacement of muscles by calcium phosphate, as displayed by the Granton specimens, has been replicated in the laboratory by Briggs *et al.* (1993), but the preservation of muscle fibres by clay minerals, evident in the Soom Shale, is problematic, although it may involve an intermediate phase of phosphate replacement (Gabbott *et al.*, 1995). Whatever the preservational history of these specimens, it is clear that each exhibits only part of the soft anatomy of the original organism, biased by the particular characteristics of the chemical and microbiological environment in which it died and decayed. Using information gleaned from several specimens, however, it has proved possible to reconstruct many of the characters of the living conodont animal, although details of features of low preservation potential remain obscure.

Conodont soft-tissue anatomy

Ten specimens from the Granton Shrimp Bed exhibit features of the trunk of the animal (Fig. 1); two of these also preserve the tail, and two show structures in the head (Aldridge *et al.*, 1993). A single giant specimen (Fig. 2) from the Soom Shale displays part of the trunk and head region (Gabbott *et al.*, 1995), while at least forty have been found in which lobate structures, interpreted as eye cartilages by Aldridge & Theron (1993), are associated with complete feeding apparatuses. All of these fossils were subject to some decay before the processes of replacement which preserved the tissues commenced, but experimental examination of the pattern of decay in extant primitive chordates, principally *Branchiostoma* (Briggs & Kear, 1994), provides a basis for interpretation of the structures that remain. These features can be compared with those of living and fossil cephalochordates and agnathans to develop hypotheses regarding the phylogenetic position of the Conodonta in relation to the Myxinoidea.

(a) General features

The conodont animal specimens from the Ordovician and Carboniferous are all from taxa that possessed complicated feeding apparatuses comprising pectiniform and ramiform elements. These taxa represent at least two conodont orders: seven of the specimens from the Granton Shrimp Bed can be assigned to *Clydagnathus*, an ozarkodontid (Aldridge *et al.*, 1993), and the Soom Shale specimen is of the prioniodontid genus *Promissum* (Gabbott *et al.*, 1995). General features of the anatomy are remarkably constant; all are elongate with a short head and a laterally compressed trunk made up of somites (Fig. 1.1). These are apparently V-shaped in all specimens, although preservation may be incomplete; they are thus simpler than the W-shaped myomeres of adult hagfish and lampreys, but comparable with the chevron muscle blocks of *Branchiostoma* and some fossil agnathans, (e.g. *Sacabambaspis*, see Gagnier *et al.*, 1986; *Mayomyzon*, see Bardack & Zangerl, 1968, 1971; *Gilpichthys* and *Pipiscius*, see Bardack & Richardson, 1977). The *Clydagnathus* specimens are all small, with the largest a little over 55 mm in total length (Aldridge *et al.*, 1993), whereas the preserved portion of the *Promissum* specimen is 109 mm and the entire length may have approximated 400 mm (Gabbott *et al.*, 1995).

(b) The trunk

Paired axial lines occur along the trunk of most of the Granton specimens (Fig. 1.3) and represent the margins of the notochord (Aldridge *et al.*, 1993); the notochord of *Branchiostoma* is one of the most decay-resistant features of this animal and collapses to a pair of lateral ridges comparable with those shown by the fossil conodonts (Briggs & Kear, 1994). Preferential preservation of the notochord is also apparent in a number of fossil agnathans from other deposits, including *Gilpichthys* (Bardack & Richardson, 1977) and *Mayomyzon* (Bardack & Zangerl, 1968, 1971) from the Carboniferous Mazon Creek fauna. The notochord is not preserved in *Promissum*, but its position is indicated by a 2 mm gap in preservation within the myomeres (Gabbott *et al.*, 1995). A dorsal nerve cord may be represented on two of the Granton specimens by a medial darker trace apparent along the anterior portion of one wall of the notochord, although this interpretation remains equivocal (Aldridge *et al.*, 1993). Details of the structure of the trunk muscles are best preserved in the *Promissum* specimen, in which each myomere displays sets of fibril bundles, together with possible sarcolemmic membranes and collagenous connective tissues (Gabbott *et al.*, 1995). The fibres do not show the extreme flattening characteristic of *Branchiostoma*, and appear more circular in cross-section than those of agnathans and fishes; their size (5µm in diameter) is consistent with their being slow muscle fibres (Gabbott *et al.*, 1995). Larger, fast muscle fibres have not been recognised, although these may be present outside the plane along which the fossil has split.

(c) The tail

Closely spaced fin rays are apparent at the posterior end of two of the Granton fossils (Briggs *et al.*, 1983, figs. 4, 5; Aldridge *et al.*, 1986, fig. 4; Fig. 1.4), but their configuration is not clear on either. From one of the specimens it is evident that fins occur on both the dorsal and ventral margins; more examples are required before we can ascertain for certain if the disposition is symmetrical, or if the apparent extension of the fin further on one of the margins is genuine. There is no evidence of articulating musculature at the base of the fin rays, suggesting that they resemble the unsupported fin folds of myxinioids (Aldridge *et al.*, 1993).

(d) The head

Apart from the phosphatic feeding apparatus, the most commonly preserved features of the head are the two lobate structures interpreted by Aldridge & Theron (1993) to represent sclerotic cartilages which surrounded the eyes (Fig. 1.2, 2.2). In specimens from Granton and from South Africa, these are evident as apparently carbonised impressions, commonly thickened marginally and with some phosphatisation; they can be reconstructed as deep, inwardly tapering hollow rings (Aldridge *et al.*, 1993). They are positioned above and immediately anterior to the feeding apparatus and are closely comparable morphologically with structures that have been interpreted as eye capsules in fossil agnathans, for example *Jamoytius* (Ritchie, 1968), and as altered retinal pigments in the hagfish *Myxinihela* (Bardack, 1991), the lampreys *Mayomyzon* (Fig. 2) and *Hardistiella* (Bardack, this volume), and larval gnathostomes such as *Esconichthys* (Bardack, 1974), *Bandringa* and *Rhabdoderma* (Richardson & Johnson, 1971). Optic capsules in living craniates are embryologically derived from ectodermal placodes (Gans & Northcutt, 1983).

The most complete *Promissum* specimen displays solid white oval patches anterior to and above the feeding apparatus, in a similar position to the sclerotic rings on other specimens (Fig. 2.1). These patches have a fibrous texture and were interpreted as representing extrinsic eye musculature by Gabbott *et al.* (1995); the development of such muscles is entirely patterned by connective tissue derived from neural crest (Noden, 1991; Couly *et al.*, 1992).

Other than indistinct and indecipherable patches, only the first specimen discovered from Granton has additional soft-tissue features in the head region (Briggs *et al.*, 1983, figs 2C and 3A; Aldridge *et al.*, 1993; Fig. 2). A pair of small subcircular dark patches behind the sclerotic rings may represent the otic capsules, similar to those reported in the Carboniferous lamprey *Mayomyzon* (Bardack & Zangerl, 1971) and hagfish *Myxinihela* (Bardack, 1991). The presence of otic capsules is further supported by the occurrence of a phosphatic structure, strongly resembling the statoliths of modern lampreys, in the vicinity of the feeding apparatus in the head of another of the Granton conodont animals (Fig. 4.2). Transverse traces posterior to the eyes of the first specimen may be branchial structures, comparable with features so interpreted in *Mayomyzon* (Bardack & Zangerl, 1968, 1971). There is no preserved evidence of pharyngeal slits.

The relative arrangement of the structures in the head of the conodont animal is closely comparable with that shown by fossil and recent lampreys and hagfish (Fig. 2.2, 2.3). The otic capsules are positioned just posterior of the optic capsules, and the putative gill pouches are located very close to the head structures, as in *Mayomyzon*. The first Granton conodont animal also preserves an indistinct organic trace surrounding the head structures that resembles the unmineralized head cartilage of the fossil lampreys from the Mazon Creek fauna.

The feeding apparatus is only partly exposed in most of the specimens from Granton, but its architecture has been reconstructed using additional evidence from undisturbed assemblages of elements found occasionally on Carboniferous shale surfaces. The apparatus was bilaterally symmetrical, comprising a set of 11 ramiform

elements that formed an anterior basket, behind which lay two pairs of pectiniform elements with their long axes directed dorso-ventrally (Aldridge *et al.*, 1987; Purnell & Donoghue, *in press*; Fig. 3). The anterior half of the apparatus has been interpreted as an oral raptorial array (Aldridge & Briggs, 1986; Purnell & von Bitter, 1992), but this has recently been challenged (Mallatt, 1996). Mallatt contended that the position of this portion of the apparatus posterior of the eyes suggests that it lay in the pharynx. However, if the interpretation of gill pouches in the first Granton specimen is correct (Fig. 2.2), the position of the anterior array, anterior of the first gill pouch, and the pectiniform elements posterior, implies that the two portions of the apparatus were located in the oral cavity and pharynx respectively, thus falling into the 'old' and 'new' mouths of Mallatt (1996).

The *Promissum* apparatus was similar to that of ozarkodinids, but more complicated, with 11 ramiform elements positioned below an array of four pairs of pectiniform elements (Aldridge *et al.*, 1995). Both types of apparatus are more complex than those found in any other agnathan, and they do not compare with the jaws of fishes. However, more primitive conodonts, and their putative ancestors the paraconodonts (Szaniawski & Bengtson, 1993), had simpler apparatuses made up of conical elements which may be more readily comparable with the lingual and palatal teeth of hagfish. The multicuspid lingual laminae of some lampreys (Potter & Hilliard, 1987) also bear a broad resemblance to some ramiform conodont elements.

(e) Phylogenetic interpretations

Of the preserved soft tissues, the notochord and the chevron-shaped myomeres clearly show that the conodonts belong within the euchordates (Cephalochordata + Craniata) (although for a contrary view see Dzik, 1995). Their precise affinities are controversial, with some authorities still maintaining that they are closest to the protochordates (Urochordata + Cephalochordata) (Kemp & Nicoll, 1995), although the radials in the caudal fin, the presence of eyes and the termination of the notochord behind them, the bilaterally operative feeding apparatus, and the phosphatic skeletal biomineralization are all craniate characters (Aldridge *et al.*, 1993; Janvier, 1995).

The possession of paired external sensory organs and a distinct head anterior of the notochord are also indications of vertebrate grade. The 'new head' hypothesis for the origin of the vertebrates (Gans & Northcutt, 1983) recognises that most of the functional and morphological differences between vertebrates and other chordates are located in the head, and contends that the vertebrate head is a new structure. Most of the new structures in the vertebrate head are embryologically derived from neural crest and ectodermal placodes.

More recently, a single collinear cluster of *hox* genes has been identified in amphioxus, the traditional proxy for a vertebrate ancestor, matching four paralogous clusters in gnathostomes (Garcia-Fernández & Holland, 1994; Holland & Garcia-Fernández, 1996). The expression of these clusters in mice never occurs more anteriorly than the rhombomeres of the hindbrain, and expression of *hox* genes in amphioxus too has distinct anterior limits, indicating a significant portion of the animal equivalent to the craniate head. Furthermore, the single cluster in amphioxus also points to a gene duplication at the acraniate-craniate transition, emphasising the fundamental importance of this event in chordate evolution. Determination of *hox* gene clusters in hagfish and lampreys is at a preliminary stage, but multiple clusters, up to four in number, appear to be present in each group (Holland & Garcia-Fernández, 1996).

Much of the opposition to the interpretation of conodonts as vertebrates stems from the lack of consensus over what constitutes a vertebrate or a craniate; many workers consider these to be synonymous (Kardong, 1995; Nielsen, 1995; Young, 1995). The 'new head' hypothesis for the origin of the vertebrates places myxinioids as the first crown-group vertebrates (Gans, 1993). Janvier (1981, 1993) however, considered the lack of

arcualia in hagfish to exclude them from the vertebrates, placing them in the craniates; the lampreys were regarded to be crown-group vertebrates. On this basis, much of the controversy surrounding the interpretation of conodont affinities becomes semantic. In the present context, it is pertinent to assess the evidence for and against a close relationship between the conodonts and the hagfish.

Aldridge *et al.* (1986) forwarded two possible phylogenetic positions for the conodonts on the basis of the soft tissue characters: as a sister group to the Myxinoidea, or immediately crownwards of them. Other placements have been suggested (see Aldridge & Purnell, 1996), including immediately anti-crownwards of the Myxinoidea, as stem-group craniates (Peterson, 1994). Conodonts differ from myxinoids in having eyes with apparent extrinsic musculature and in bearing phosphatic, not keratinous, oral elements. Large eyes with extrinsic eye muscles are a vertebrate characteristic, but their absence in myxinoids may be degenerate rather than primitive (Northcutt, 1985). The lack of a phosphatic skeleton in hagfish may also be secondary, or it might be argued that the development of phosphatic structures in conodonts was a separate, convergent feature, unrelated to the origin of skeletons in other craniates. The mode of growth of conodont elements and the nature of their phosphatic tissues are of crucial importance in resolving this particular question.

Conodont hard tissues

A typical euconodont ("true conodont") element is constructed of two structurally distinct components, a basal body and an overlying crown, which grew by the addition of calcium phosphate on their outer surfaces (Furnish, 1938; Hass, 1941). Post-Devonian elements do not have a basal body, suggesting that its function was fulfilled by unmineralized tissue in more derived forms. The crown is composed of a crystalline, hyaline tissue punctuated by numerous incremental growth lines (Fig. 4.5); in most conodonts the crown also includes areas of opaque tissue, traditionally known as "white matter" because it appears albid in incident light. The cores and tips of the cusps and denticles of conodont elements are commonly composed of this white matter (Fig. 4.4), which is relatively fine-grained and massive, but contains numerous cavities and fine tubules (see Lindström & Ziegler, 1981). The basal body is also finely crystalline, but much more variable in structure; it commonly displays growth increments and may show spherical or tubular features (Fig. 4.6).

(a) Lamellar crown tissue

A homology between conodont crown tissue and the enamel of vertebrates has been suggested several times (e.g. Schmidt & Müller, 1964; Dzik, 1986; Sansom *et al.*, 1992). Although only a few taxa have as yet been examined in detail, there is considerable variability in the orientation of crystallites in the hyaline lamellae with respect to the incremental growth lines. In most, the crystallites are more or less perpendicular to the growth increments (*contra* Schultze, 1996), as in true enamel, whereas one area of the crown tissue figured by Sansom *et al.* (1992) from *Parapanderodus* (fig. 3F) showed crystallites arranged at a shallower angle and this was considered outside the range of known enamel types by Forey & Janvier (1993). However, crystallite arrangement in enamel is known to vary, particularly in primitive forms of prismatic enamel (Smith, 1989, 1992), and Sansom (1996) has described a prismatic form of lamellar crown tissue that compares directly to primitive prismatic enamel from the teeth of a sarcopterygian fish. As is the case with enamel, the lamellar crown of conodont elements exhibits variation in crystallite arrangement within a single specimen.

The interpretation of the conodont tissue as enamel has been contested by Kemp & Nicoll (1995, 1996) on the grounds that etched surfaces are stained by picosirius red, a stain specific for collagen. True enamel does not contain collagen. However, the validity of such histochemical tests on fossil material remains to be established, as

they have not been applied to unequivocal fossil vertebrate material. It is possible that the etching of the element surface increases porosity and permits retention of the stain which 'fixes' by electrostatic attraction; further work is required to test the results of this technique. The presence of fibrous tissues, claimed to be collagen, in conodont elements has also been reported by Fahraeus & Fahraeus-van Ree (1987, 1993), who demineralized Silurian conodont hard tissues then fixed, dehydrated, sectioned and stained the residue. They commented that the most remarkable result of their study was that tissue more than 400 million years old could remain histochemically intact (Fahraeus & Fahraeus-van Ree, 1987, p. 106). There is, however, no certainty as to which of the conodont hard tissues housed the soft tissue they recovered.

(b) White matter

Many of the vacuoles within white matter closely resemble the lacunae of odontocytes or osteocytes (Fig. 4.4), and together with evidence of associated canaliculi this led Sansom *et al.* (1992) to interpret this tissue as dermal bone. The vesicles are ubiquitous in white matter and are repeatedly observed in thin sections (*contra* the assertion that they are artefacts, Schultze, 1996); the nature of the tissue is different to cellular dermal bone in other vertebrates, and it is likely that white matter represents a tissue unique to conodonts.

Histochemical staining of the white matter with picosirius red failed to indicate the presence of collagen (Kemp & Nicoll, 1995, 1996), which is present in the dentine and bone of extant vertebrates. However, it is unusual for any fossil bone or dentine to preserve collagen, which normally disintegrates shortly after death, leaving at best degradation products in the form of amino acids (Fahraeus & Fahraeus-van Ree, 1987). Detectable amino acids have been reported in conodont elements by Pietzner *et al.*, (1968) and Savage *et al.*, (1990), but see Collins *et al.*, (1995). 9

(c) The basal body

Schmidt & Müller (1964) suggested that the basal body of conodonts was homologous with the dentine of vertebrate sclerites, and branched or unbranched tubules representing different forms of dentine have been described in the basal bodies of a number of Ordovician taxa (Barnes *et al.*, 1973; Barskov *et al.*, 1982; Dzik, 1986; Sansom *et al.*, 1994). Basal bodies of other species, including most post-Ordovician elements examined, show regular lamination without tubuli or comprise a homogenous alamine mass, the former having been interpreted as a form of atubular dentine (Sansom, 1996). In some early conodonts, for example *Cordylodus*, the basal material comprises a mass of fused spherical bodies and this has been compared with the globular calcified cartilage of the Ordovician vertebrate *Eriptychius* (Smith *et al.*, 1987; Sansom *et al.*, 1992), although it is just as likely to be an atubular dentine (Fig. 4.3, 4.6). Such apparent diversity of tissue types in conodonts is unexpected, but parallels experimentation with different tissue combinations by other coeval agnathans (Halstead, 1987).

As with the white matter, basal bodies examined by Kemp & Nicoll (1995, 1996) failed to stain positively for collagen, although they tested positive for mucopolysaccharides.

(d) Histogenesis of conodont elements

Published ontogenetic studies of conodont elements have concentrated on the development of the lamellar crown and basal body, which are known to have grown synchronously (Müller and Nogami, 1971). The pattern of divergent appositional growth between the basal body and the crown is comparable with that of the dentine and enamel of extant vertebrate teeth, and Schmidt and Müller (1964), Dzik (1976, 1986) and Smith *et al.* (1996) have argued for a homology between conodont elements and vertebrate odontodes. Odontodes are the basic building blocks of the dermal skeleton in vertebrates and are formed by interaction of the epithelium, which forms the enamel, and ectomesenchymal cells, derived from the neural crest, which ultimately form the dentine,

dermal bone and cartilage. Odontodes are almost exclusively composed of a complex of enamel, dentine and underlying bone of attachment. The bone of attachment is absent in conodonts, but this is also the case in the dermal denticles of thelodonts and in the oral teeth and skin denticles of chondrichthyans (Smith *et al.*, 1996).

(e) Comparison with hagfish toothlets

Both conodonts and myxinioids possess a feeding apparatus comprising a bilaterally symmetrical array of cusped elements, and a homology between conodont elements and hagfish lingual toothlets has been proposed by Krejsa *et al.* (1990a, b). Evidence comes from a similarity in overall morphology between simple conodont elements and myxinioid teeth, and an overlap in size range between conodont elements and juvenile hagfish toothlets. The hypothesis requires that the phosphatic lamellar crown of conodont elements should be a mineralized homologue of keratin, with the pores in white matter interpreted as moribund remnants of pokal cells. The basal body is considered to be a developing replacement tooth (Krejsa *et al.*, 1990a, 1990b).

Evidence such as analogous morphology and similarity in size is regarded as weak and circumstantial, and this interpretation of conodont elements has been severely criticised (Szaniawski & Bengtson, 1993; Smith *et al.*, 1996). Histogenetic and ontogenetic studies of conodont elements show that the crown and basal body of conodonts grew synchronously, with appositional growth increments passing confluent between the two structures (Müller & Nogami, 1971); the basal body is clearly not a replacement tooth. Indeed, except in the simplest of conical conodont elements, the upper surface of the basal body bears no morphological resemblance to the upper surface of the crown it would putatively replace.

Discussion

Possible phylogenetic positions of the conodonts relative to the extant euarchodonts are illustrated in Figure 5. Kemp & Nicoll (1995, 1996) contended that their histochemical tests prove that the hard tissues of conodont elements are not homologous with those of vertebrates, and concluded that conodonts were therefore more closely related to cephalochordates than to craniates. This is not a necessary conclusion from their arguments, even if they were correct. If conodont hard tissues were developed independently from those of vertebrates, then this could have happened at any stage in early chordate history, for example as an offshoot from the myxinioids or from the petromyzontids. The evidence from conodont soft tissues suggests that either of these positions would be more parsimonious than a sister group relationship with the cephalochordates.

How strong, then, is the evidence for the Conodonts to be considered as a sister group to the Myxinoidea? There are two hypotheses to be examined here: either conodont characters are plesiomorphic for this group and have been secondarily lost in the hagfish, or conodont hard and soft tissue features are derived and synapomorphic for the Conodonts. The latter proposal does not seem parsimonious; not only would the enamel- and dentine-like skeletal tissues of conodonts represent a completely independent and fortuitously analogous development from that in other craniates, but the development of eyes with extrinsic muscles would be similarly homoplastic.

It is perhaps more likely that myxinioids separated from the conodonts by secondary loss of conodont characters. The eyes of hagfish are connected to the brain and sensitive to light (Wicht & Northcutt, 1995) and are probably responsible for the entrainment of the circadian rhythm (Ooka-Souda *et al.*, 1993). They are nevertheless of very limited function, and despite the formation of a lens placode during development, a lens, iris, extrinsic musculature and associated nerves fail to develop (Wicht & Northcutt, 1995). The most likely interpretation is that hagfish represent a condition degenerate from that of, for example, conodonts, with characters lost in

response to their specialised mode of life (Fernholm & Holmberg, 1975; Northcutt, 1985). However, it is quite feasible that the failure of the lens placode to form a lens is a primitive condition (Wicht & Northcutt, 1995), since the placode is ultimately responsible for the formation of a number of other structures, including the cornea, which are present in hagfish.

The conversion of phosphatic hard parts to keratin may be more problematic. The recognition of enamel-like antigens (putatively enamelin) in the pokal cell cone beneath the tip of the keratin toothlet of hagfish (Slavkin *et al.*, 1983) may be of relevance here, and Kresja *et al.* (1990a, 1990b) used this to support a proposal that conodonts were ancestral hagfish that switched from secreting mineralised keratin to keratin. The occurrence of the fossil hagfish *Myxinihela* in the Mazon Creek (Bardack, 1991) shows that the two groups were distinct by the Carboniferous. The case is weakened, however, by the lack of any demonstrable homology between conodont elements and hagfish toothlets. Smith *et al.* (1996) also cited the lack of developmental support for a switch from an apatitic system to one secreting keratin.

Relatively, few myxinoid embryos have been recovered, and there is little evidence to indicate the degree of neural crest involvement in the formation of hagfish skeletal head structures. Conel (1942), however, suggested that neural crest played no role in hagfish cranial skeletal development. If hagfish neural crest is indeed restricted to neuronal derivatives (Langille, 1987), the evidence for neural-crest derived tissues in conodonts would indicate that the conodonts are the more derived.

The placement of the conodonts immediately anticrownwards of myxinoids (Peterson, 1994) suffers from similar drawbacks, involving loss in the myxinoids of the phosphatic tissues, the muscularized eyes and migratory neural crest, and their re-evolution in the post-myxinoid craniates. A position crownwards of the myxinoids poses fewest problems with current evidence of conodont soft and hard tissues (Aldridge *et al.*, 1993). Their precise placement will be influenced by resolution of the controversial relationships between extant and fossil agnathans. If hagfish and lampreys form a natural group (Yalden, 1985; Stock & Whitt, 1992) or if the hagfish and lampreys are successive paraphyletic groups (Forey & Janvier, 1994; Forey 1995), then conodonts may well occupy a position crownwards of both myxinoids and petromyzontids (Gabbott *et al.*, 1995). However, Langille (1987) has described neural crest involvement in the formation of the head skeleton of lampreys, and the ability of petromyzontids to mineralize their skeleton has been demonstrated by *in vivo* (Bardack & Zangerl, 1971) and *in vitro* studies (Langille & Hall, 1993). This evidence, and the possession of arcualia by lampreys, suggests that of the two groups, the conodonts are the more primitive.

Janvier (1996) recently completed the first full cladistic analysis of the Agnatha to incorporate conodonts. Lack of soft tissue characters and equivocation over the interpretation of some characters largely resulted in tree imbalance. However, Janvier's text-fig. 5c, the best resolved of the relevant trees, places the conodonts as a sister group to lampreys, with which they form a sister group to all other agnathans with a mineralised exoskeleton; hagfish are a sister group to all other craniates. This intriguing solution awaits testing by additional cladistic analyses. Further, the speculation by Janvier (1995, 1996) that conodonts might be closer to the gnathostomes than all the ostracoderms apart from the osteostracans currently seems difficult to sustain, as it would involve secondary loss in the conodonts of the exoskeleton and the paired fins.

Whatever the final position of conodonts within craniate phylogeny, they have clearly influenced recent debates on vertebrate origin and generated a new impetus into long-standing controversies regarding the origin and early evolution of the vertebrate skeleton.

Conodonts as living animals

Aldridge *et al.* (1993) reconstructed the conodont animal as an elongate and laterally-compressed eel-shaped agnathan (Fig. 5) capable of an anguilliform mode of swimming. Lack of muscle fibres of a size comparable with 'fast' white muscle in the Soom specimen may indicate that conodonts were adapted to sustained swimming and incapable of rapid bursts (Gabbott *et al.*, 1995). However, examination of the musculature in this specimen is at a preliminary stage, and other muscle tissue may be present.

Conodonts had a complex feeding array which performed a number of tooth functions (Aldridge & Briggs, 1986; Purnell & von Bitter, 1992; Purnell, 1995; Purnell & Donoghue, *in press*). Early forms possessed only conical elements which were capable of grasping and perhaps slicing food (Aldridge & Briggs 1986; Purnell, 1995); later forms developed more highly differentiated feeding apparatuses which separated grasping from slicing and crushing elements. The great variation in conodont apparatuses suggests that the group adopted a number of different ecological strategies, although with their locomotive capability and differentiated nervous system (including eyes with associated musculature) many would have made effective hunters (Purnell *et al.*, 1995).

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FIGURES:

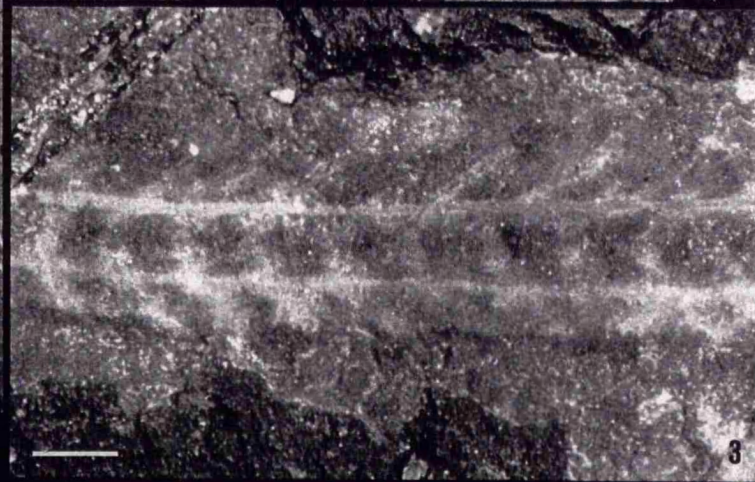
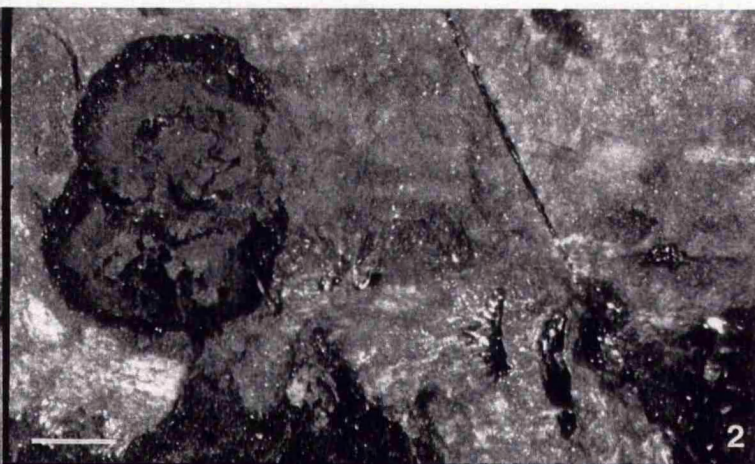
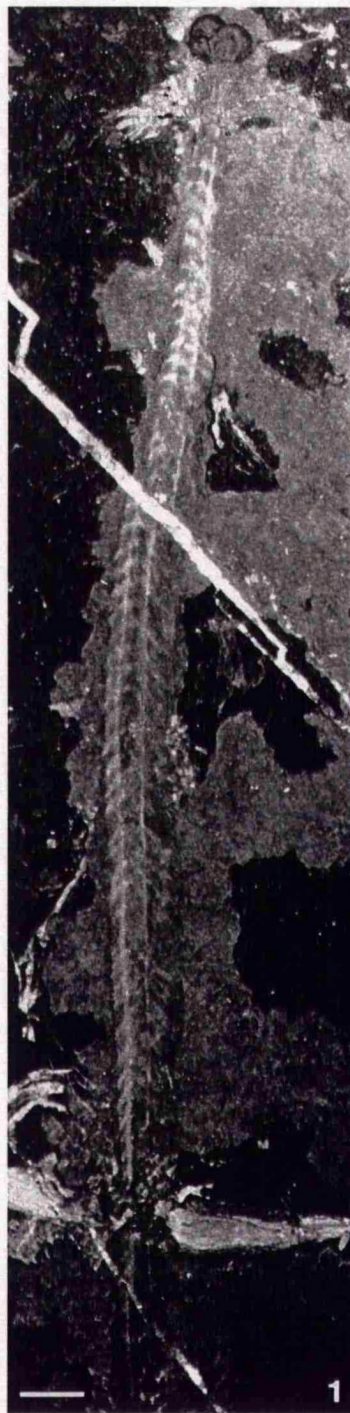
Figure 1. *Clydagnathus windsorensis* (Globensky), 1.1-1.3 RMS GY 1992.41.1 (refigured from Aldridge *et al.* 1993, with permission); 1.4 IGSE 13822 (refigured from Briggs *et al.* 1983, with permission). 1.1. Complete specimen, anterior at top and ventral to left; scale bar 2000µm. 1.2. Anterior portion showing eye cartilages, feeding apparatus (only partially uncovered) and anterior part of trunk with notochord; scale bar 500µm. 1.3. Detail of trunk at mid-length showing the notochordal sheath and shrunken myotomes; scale bar 500µm. 1.4. Posterior portion of trunk and tail showing closely set ray supports and tail asymmetry; scale bar 500µm.

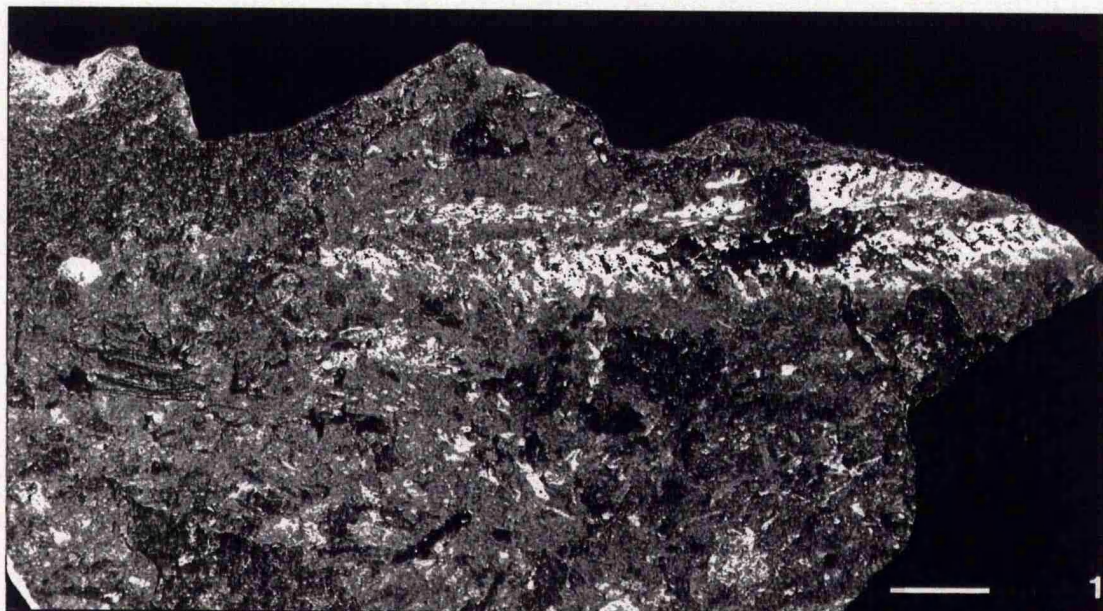
Figure 2. 2.1. *Promissum pulchrum* Kovács-Endrödy (GSSA C721a; refigured from Gabbott *et al.* 1995, with permission), complete specimen (counterpart) showing the trunk, extrinsic eye musculature and feeding apparatus; anterior to left; scale bar 10mm. 2.2. Head of *C. windsorensis* (IGSE 13822; refigured from Briggs *et al.* 1983, with permission) showing eye capsules, otic capsules, possible traces of gill pouches, and feeding apparatus, anterior at top (soft tissues preserved in dorso-ventral orientation); scale bar 500µm. 2.3. Head of *Myomazon pieckoensis* Bardack (FMNH PF 8167) a fossil lamprey from the Carboniferous Mazon Creek lagerstätte, showing nasal and eye capsules, gill pouches and trace of notochord, preserved orientation as 2.2; scale bar 500µm.

Figure 3. Model of the conodont (ozarkodinid) feeding apparatus in oblique antero-ventral view. From Purnell and Donoghue (*in press*).

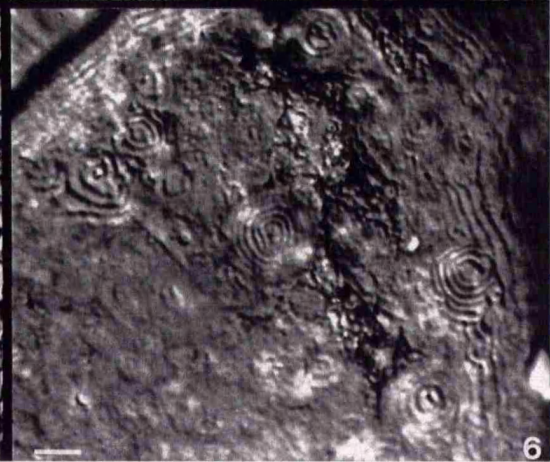
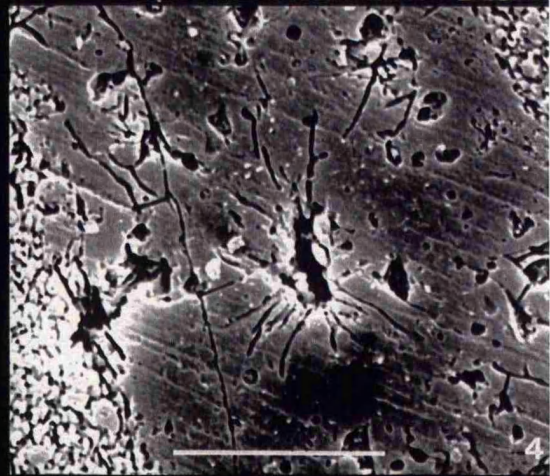
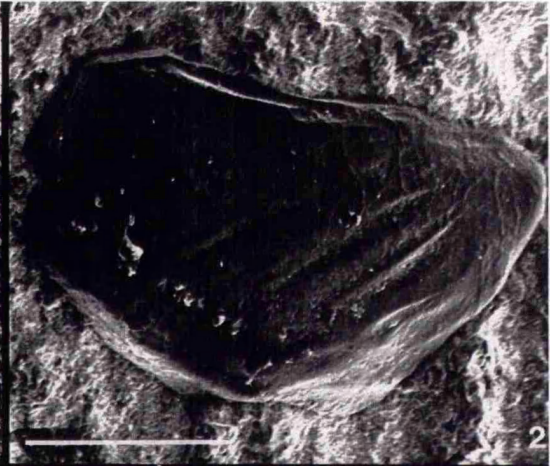
Figure 4. 4.1. Feeding apparatus from one of the Scottish conodont animals (RMS GY 1992.41.3), still partially covered by matrix. The small black asymmetric structure to the upper left of the frame is the putative statolith; scale bar 1000µm. 4.2. Close-up of possible statolith, concentric grooves may represent the limit of annual growth increments; scale bar 100µm. 4.3. Thin section of *Cordylodus*, a Lower Ordovician conodont, Maardu Beds, Estonia (BU 2614), micrograph taken using differential interference contrast, showing crown (to right) and basal body (to left). The hyaline crown tissue incorporates 'white matter' upper right; scale bar 100µm. 4.4. SEM micrograph of an etched thin section through an element of *Ozarkodina* Upper Silurian, Gotland (BU 2615), showing fine grained ground mass and enclosed cell and cell-process spaces characteristic of white matter; scale bar 10µm. 4.5. SEM micrograph of an etched thin section through the enamel crown tissue of an element of *Scaliognathus* Carboniferous, North America (BU 2613), showing incremental growth lines and crystallites organised into protoprisms; scale bar 10µm. 4.6. Micrograph of detail of 4.3 taken using differential interference contrast, showing lamellar and spheroidal structures in the basal body; scale bar 10µm.

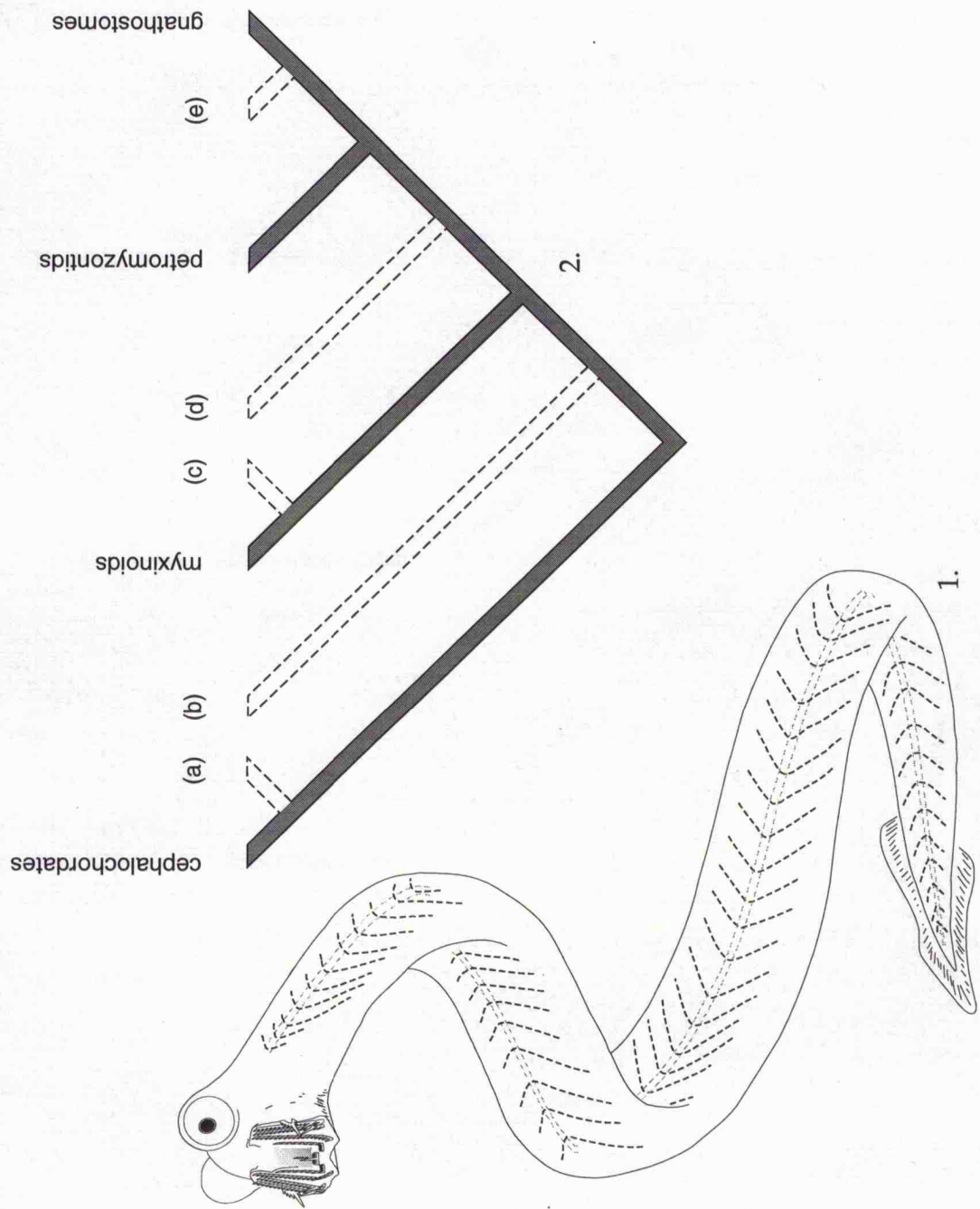
Figure 5. 5.1. reconstruction of a conodont animal, based on current evidence; the feeding apparatus is shown in the 'everted' position according to Purnell and Donoghue (*in press*). 5.2. Cladogram of possible conodont relationships; solid branches represent phylogenetic positions of extant groups, dashed lines represent some of the proposed positions of conodonts: (a) Kemp and Nicoll (1995, *in press*), (b) Peterson (1994), (c) Krejsa (1990a, b), Aldridge *et al.* (1986), (d) Aldridge *et al.* (1986, 1993), and (e) Gabbott *et al.* (1995), Janvier (1995).











Conodonts and the first vertebrates

Mark A. Purnell, Richard J. Aldridge, Philip C.J. Donoghue and Sarah E. Gabbott

More than 500 million years ago the first vertebrate made its appearance in the sea. It had no hard skeleton and fossil specimens are consequently unknown. Because of this, theories of vertebrate origins are controversial, but recently new light has been shed on this old problem. The evidence comes from research into the fossilized remains of conodonts, a long-extinct and enigmatic group of animals.

The remains of conodonts are among the most abundant and widespread animal fossils known. A fist-sized chunk of limestone deposited in the sea any time between the Late Cambrian and the latest Triassic (520 to 205 million years ago) will probably contain microscopic conodont elements (Figure 1), possibly in their thousands. But these spiky phosphatic remains are also among the most problematic and controversial of fossils. From the time of their discovery almost 150 years ago, the question of what conodonts were has intrigued almost everyone who has encountered them. Both the nature of the organism to which conodont elements belonged, and the function of the elements have been the subjects of wide-ranging speculation, and as recently as 1981 the identity of conodonts was considered to be one of the most fundamental unanswered questions in palaeontology [1].

Since 1981, however, there has been a revolution in our understanding of conodonts. The discovery of fossils preserving not just the conodont elements but also the remains of the soft-bodied animal that bore them [2] has at last enabled reconstruction

of conodont anatomy and provided firm ground on which their relationships can be assessed [3]. Parallel research has led to a re-evaluation of the structure and function of the elements [4–7], with important and unexpected implications for hypotheses concerning the origin of vertebrates and their skeletons.

The first vertebrates and the importance of feeding

Some time ago, probably during the early part of the Cambrian Period (~520 million years ago; see Figure 2), a new type of animal appeared. It was small, a few centimetres in length, and elongate; it had no hard skeleton, but a stiffening rod of cartilage

along its back and V-shaped blocks of muscle along its sides; it had paired eyes, a brain and tail fins. It was the first vertebrate. Unfortunately, the potential for totally soft-bodied organisms to be fossilized is close to zero; consequently, there is no direct fossil evidence of this evolutionary milestone, and scenarios that seek to explain how and why vertebrates evolved are controversial. Surprisingly, few authorities disagree about the likely anatomy of the earliest forms. Their characteristics must lie somewhere between those of the amphioxus, the closest living invertebrate relative of vertebrates, and the hagfish, the most primitive extant vertebrate. Beyond this, however, agreement fails and issues are hotly debated: how did

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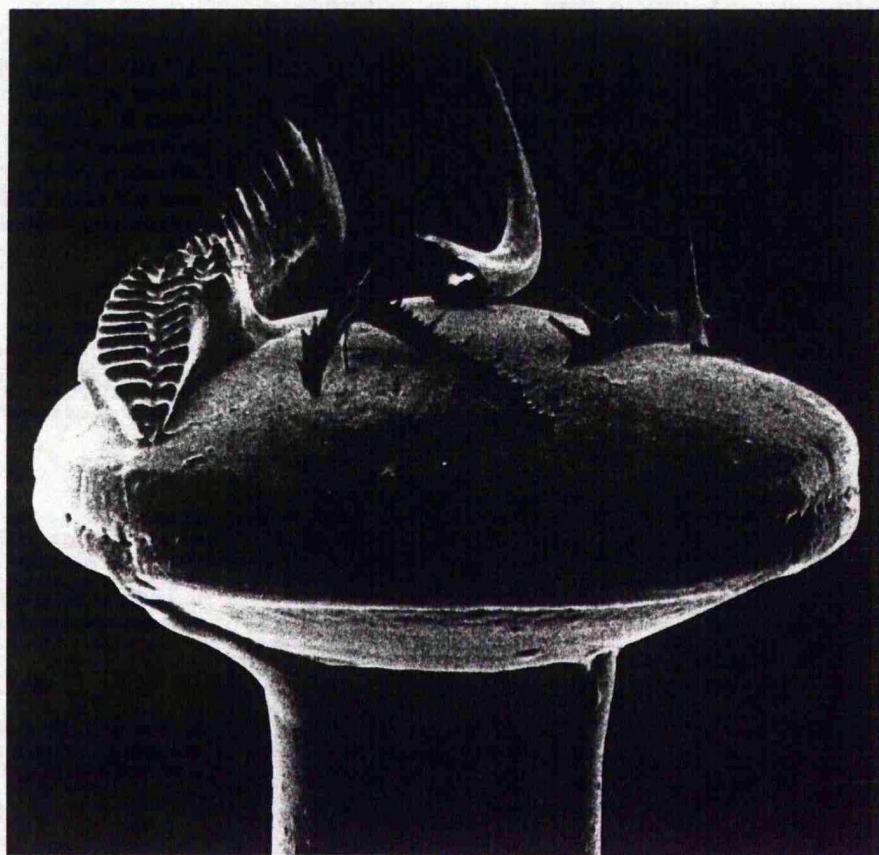


Figure 1 Scanning electron micrograph of four conodont elements mounted on a pinhead. The elements are (from left to right) *Idiognathodus* Pa element (Carboniferous); *Gnathodus* Sa element (Carboniferous); *Panderodus graciliform* element (Silurian); and *Ozarkodina* Sc element (Silurian).

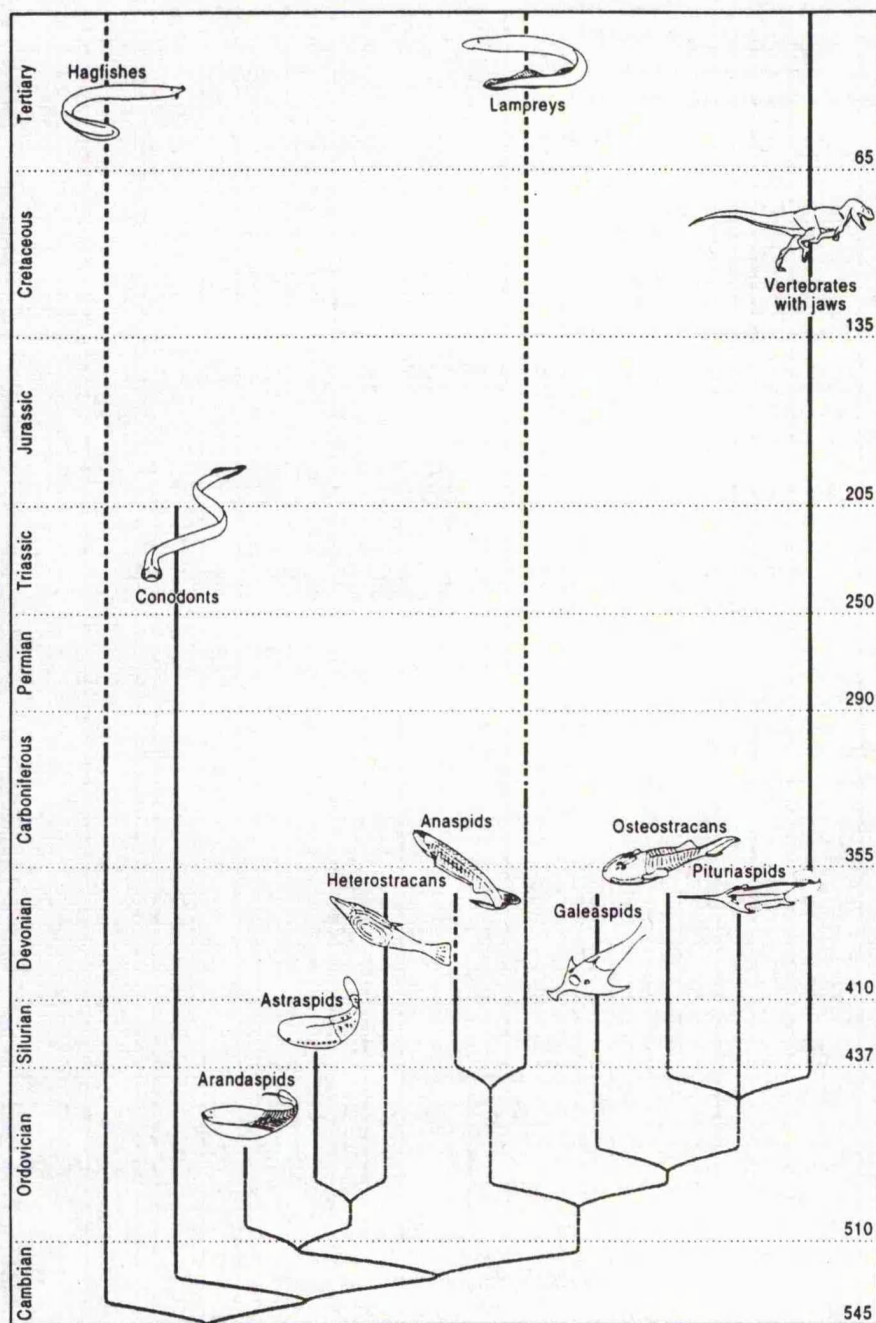


Figure 2 The fossil record of vertebrates, and their evolutionary relationships (modified from [23]). The solid black lines show the known fossil record of each group, the grey lines indicate the relationships between them. Arandaspid, astraspids, heterostracans, anaspids, galeaspids, osteostracans and pituriaspids are collectively known as ostracoderms.

the first vertebrates feed, and what was the evolutionary significance of their feeding strategies? In what kind of environmental setting did they first appear, fresh water or marine? What were the selective pressures involved in the evolution of one of the most characteristic of vertebrate features, the phosphatic skeleton of bones and teeth [8–11]?

The question of feeding is particularly contentious. According to the traditional, textbook view, the first vertebrates were relatively inactive, suspension-feeding organisms [10,12], ecologically comparable with the living amphioxus and larval

lampreys, which feed by collecting microscopic food particles with a filter. Champions of this view consider that it was only with the evolution of jaws, 100 million years later, that vertebrates were able to become predators. Others have contended that many of the definitive characters of vertebrates, such as the paired eyes and muscular and skeletal adaptations for active life, would not have evolved unless the first vertebrates were predatory [8,9]. According to this theory, the shift from suspension-feeding to predation was one of the most important innovations of the first vertebrates, and provides the key to under-

standing the evolutionary pressures responsible for their appearance. Evidence for feeding mechanisms in early vertebrates is obviously crucial in the resolution of this debate.

There is a firmer consensus regarding the environment in which vertebrates arose. All close relatives of the vertebrates live in shallow coastal waters, and all the oldest vertebrate fossils are found in rocks deposited in marine conditions, clearly indicating a marine origin. The idea that at least part of the life cycle of the first vertebrates was spent in fresh water has recently been resurrected [11], but there is little evidence to support this.

The origin of the vertebrate skeleton has often been regarded as being linked to defence. The first, soft-bodied vertebrates would have been easy prey for the numerous invertebrate carnivores of the Cambrian and Ordovician, especially if they were sedentary suspension feeders. So, it is argued, these animals began to armour themselves by producing extensive coverings of bony scales or plates. Indeed, external skeletons of this type are common in the well-known fossils of jawless vertebrates of Ordovician to Devonian age (Figure 2). Other suggestions are that phosphatic mineralization of skin tissues was primarily an adaptation to enhance electroreception [9] or that phosphate was first deposited as a means of regulating calcium and phosphate levels [11]. According to all these hypotheses, teeth are secondary features, adapted from bony scales that migrated into the mouth over millions of years of evolution and were co-opted into a feeding function. However, if teeth were more primitive than external armour, and the earliest vertebrates were predators, then this entire scenario collapses. This is where the conodonts are making their contribution to the story.

Conodonts: from enigma to ancestor?

For many years conodonts were an insoluble palaeontological puzzle. It was widely recognized that their remains were very useful to geologists, especially in providing ages for rocks, but because they were known only as scattered, disarticulated skeletal elements, interpretation of their biology proved impossible. In the 1930s fossils were found which indicated that a number of elements of different shapes belonged together during life, but it took another 30 years before conodont specialists had even worked out how to recognize which elements came from the same species, let alone how they were arranged in life. By this time it was clear that whatever conodonts were, they were not closely related to anything living, so modern organisms could be of only very limited help in rebuilding them. The breakthrough came in 1982 with the discovery of the first of a number of fossils preserving whole conodont animals (Figure 3) [2]. These fossils

provided the information required to rebuild conodonts and to interpret them as animals.

Only 12 conodont animal fossils are known and almost all of these come from one locality of Carboniferous age (330 million years) on the outskirts of Edinburgh [2,3,13]. The rarity of these fossils is not surprising when one considers that the only hard parts of the animal are the conodont elements in its mouth. The rest of the body is composed of soft tissues which fossilize only under exceptional conditions, protected from scavengers and decay. The conodont specimens from Scotland died in such circumstances and preserve a remarkable calcium phosphate replica of the muscle and cartilage of the conodont body. These tissues normally decompose rapidly after an animal dies and the process of replication in these fossils probably began within hours of death.

The Scottish specimens show that the conodont was a small, eel-shaped animal with fairly large eyes, a stiffening notochord along its back, V-shaped muscle blocks running along the sides of the body, and posterior tail fins (Figure 3) [3,13]. This suite of characteristics matches those of the hypothetical first vertebrate closely and identifies conodonts as chordates, the phylum to which vertebrates belong. Indeed, some of these features indicate that conodonts might themselves have been vertebrates.

This suggestion has been tested by a re-investigation of the microstructure of the skeletal elements of a number of species. This work has been pioneered by a team from Birmingham and Durham Universities, and Guy's and St Thomas's Hospitals, London [4,5]. The techniques involved include high-resolution optical and scanning electron microscopy of thin, polished slices of conodont elements, revealing the complexities of their internal structure (Figure 4). In the past, interpretation of these features has been speculative, but now that conodonts are known to be chordates, we can make comparisons with phosphatic tissues in related living and fossil organisms. These indicate that conodont elements are made up of hard tissues that compare closely with enamel, cellular bone, calcified cartilage and dentine, all of which are unique to vertebrates [4,5].

The combined evidence from soft-part anatomy and element microstructure strongly indicates that conodonts are among the most primitive of vertebrates. The lack of any mineralized skeleton apart from the elements in the mouth indicates that they are more primitive than the armoured jawless fishes such as the ostracoderms, but they are more advanced than the hagfish, which possess no phosphatic skeleton at all [3]. Although interpretation of the relationships between early vertebrates continues to be difficult, Figure 2 illustrates current theory, with the conodonts placed in their appropriate position [3]. The extent of the conodont fossil record is also evident from

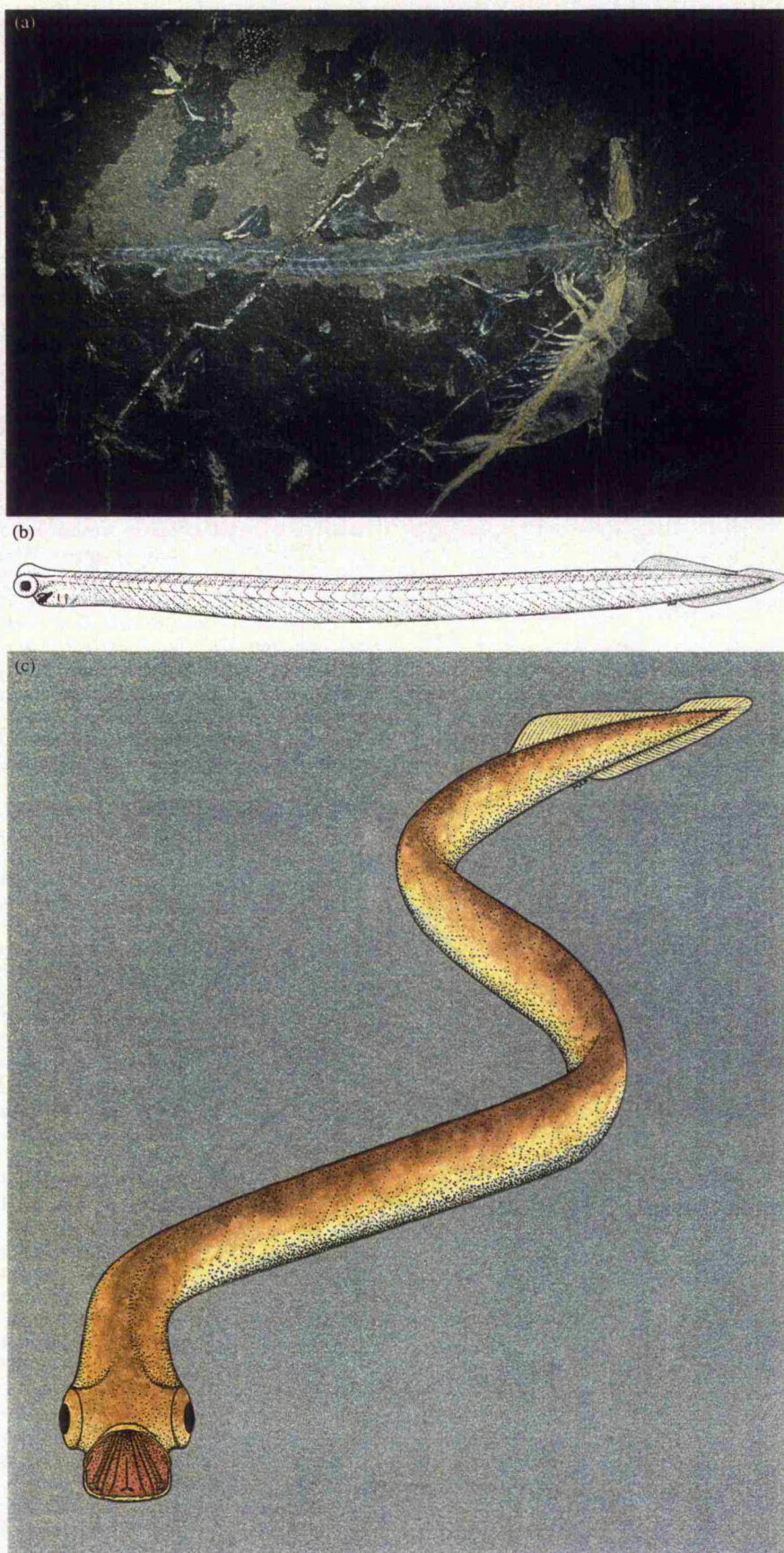


Figure 3 The conodont animal. (a) Fossil from the Carboniferous of Edinburgh (Royal Museum of Scotland specimen 1992.41.1), preserving 38-mm long body; (b) a reconstruction of the conodont animal based primarily on the specimen shown in (a); (c) the animal as it may have looked in life, with its mouth open, swimming.

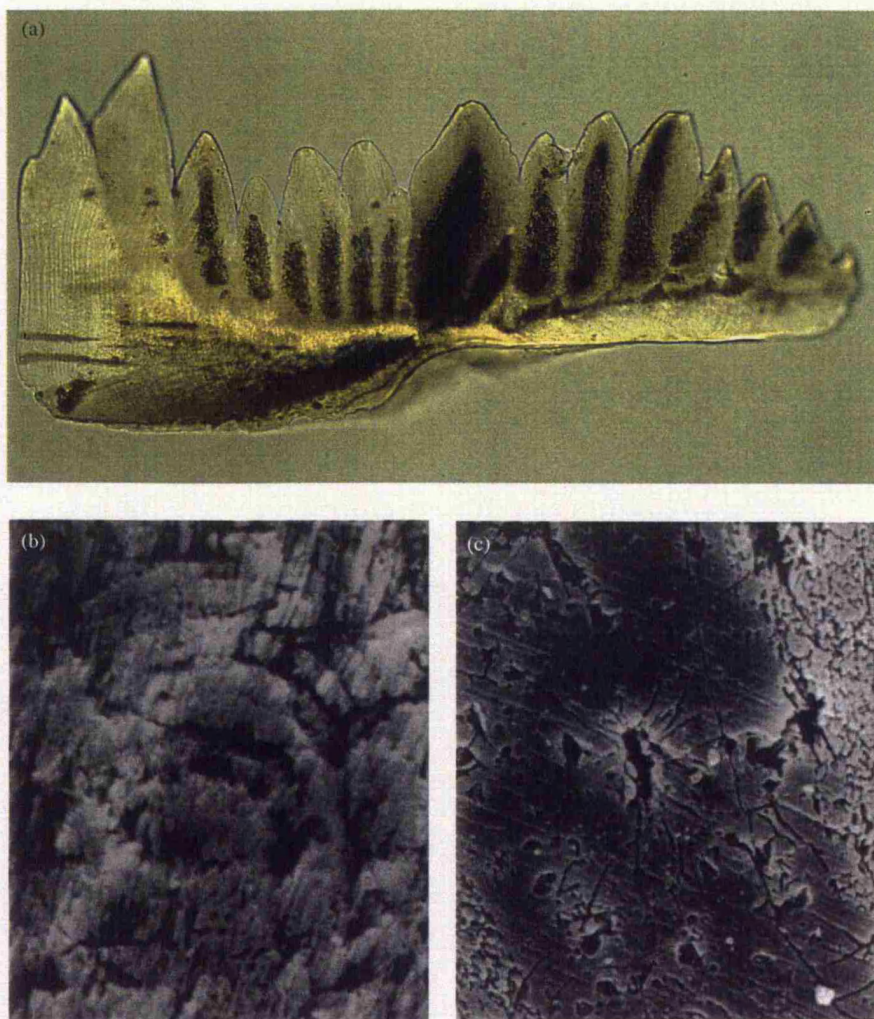


Figure 4 Conodont microstructure. (a) Internal structure of a Pa element of *Ozarkodina*. The structure of the lamellar tissue evident at the left side of the element and shown in (b) is very similar to enamel, and may be homologous. The dark tissue at the core of the element, also shown in (c) contains small spaces which once housed the cells that secreted this tissue; it has been interpreted as a type of bone. (a) Light photomicrograph of 1 mm long element, (b) and (c) scanning electron micrographs (original magnifications $\times 2440$ and $\times 1770$ respectively).

this diagram. Not only did they appear at least 30 million years before the ostracoderms, they outlasted them. Clearly, although they were primitive in an evolutionary sense, conodonts were a well adapted and successful group of animals.

Conodont skeletons and functional morphology

The fossil record of conodonts is not only longer than that of other early vertebrates, it is much less patchy. It also contrasts with the record of the ostracoderms, in which there is no direct evidence of feeding mechanisms, by consisting almost entirely of phosphatic elements from the mouth. After the death and decay of a conodont, these elements usually became disarticulated and were scattered over the sea floor by currents and scavengers, and after they were buried in sediment, burrowing organisms often caused even further disruption. Only very rarely did conditions conspire to allow conodont

carcasses to be buried without disturbance, preserving the skeletal elements in their original arrangement. As the enclosing sediment turned to rock, the skeletons became flattened onto planes parallel to the original sediment surface. These 'bedding plane assemblages' (Figures 5–7) have been known since the 1930s, but only since the discovery of the complete conodont animals has it been possible to interpret them fully.

The mouth of each conodont contained a number of different elements. Bedding plane assemblages show them to have been arranged in groups, and the animal fossils indicate that an array of elongate comb-like elements lay in front of pairs of shorter, more robust elements. To understand how they operated, however, we need to know the arrangement of the elements in three dimensions, not just the two displayed by the flattened fossils. This information can be deciphered through careful study of the

bedding plane assemblages. Each assemblage reflects the collapse of the conodont skeleton onto the sea floor as the supporting soft tissues decayed, and the resulting arrangement of the elements will be affected by the orientation of the conodont carcass on the seabed. Each bedding plane assemblage therefore conforms to one of a small number of recurrent patterns of element arrangement, depending on whether the dead animal was lying on its side, on its back or at an angle. To rebuild the full architecture of the skeletal apparatus we simply need to 'uncollapse' the assemblage out of the rock surface by constructing actual physical models of the skeleton and testing them against the assemblages we find in the rock. If the model can be matched to a variety of different patterns of collapse, then its three-dimensional structure must be correct [14–16].

This approach has been successfully applied to bedding plane assemblages of two groups of conodonts (Figures 5–7). Most assemblages belong to the conodont order Ozarkodontida, and Figures 5 and 6 show two ozarkodontid bedding plane assemblages, together with explanatory drawings and photographs of our three-dimensional model. The photograph in Figure 5 was taken from the side and slightly above; it closely matches the pattern of element arrangement exhibited by the fossil, indicating that the carcass of the animal which bore the apparatus lay on its side. Photographing the model from above and behind simulates the pattern of elements seen in the specimen in Figure 6, indicating that the dead animal lay on its belly.

From this model we have worked out that the ozarkodontid apparatus comprised an anterior array of nine comb-like S elements arranged as two opposed sets of four elongate elements, stacked on either side of a symmetrical element. These S elements were flanked by a pair of pick-shaped M elements, and behind lay two opposed pairs of P elements, arranged with their long axes perpendicular to the axis of the animal (Figure 5).

A second type of apparatus, belonging to the order Prioniodontida, is illustrated in Figure 7. It was more complex than the ozarkodontid apparatus, but in terms of element arrangement and morphology it was very similar. It had a set of nine symmetrically arranged S elements, accompanied by a pair of M elements. As in ozarkodontids, the P elements were arranged as opposed pairs, but there were four pairs, and they lay above rather than behind the S elements.

These reconstructions of skeletal architecture have allowed us to investigate how the conodont apparatus worked, as they make it possible to formulate sensible and testable hypotheses of element function. In the past, numerous ideas of function have been forwarded, mostly purely speculative, but when the spatial arrangement of the

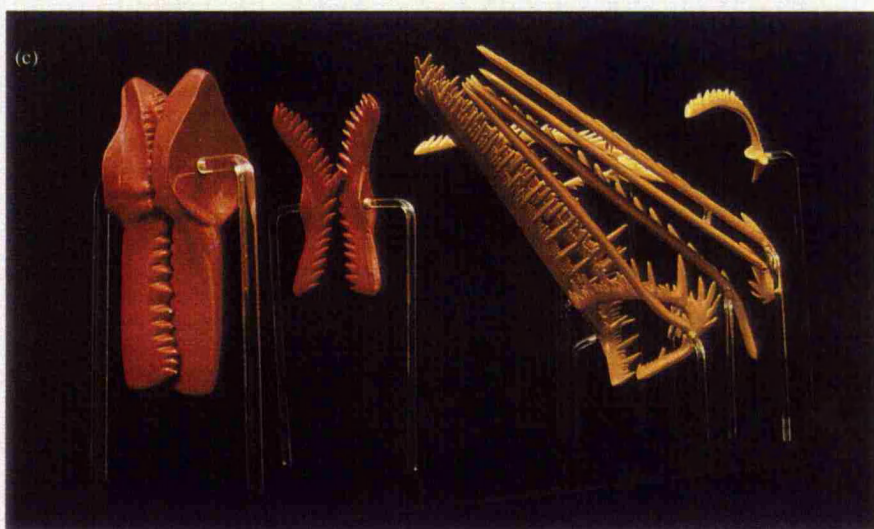
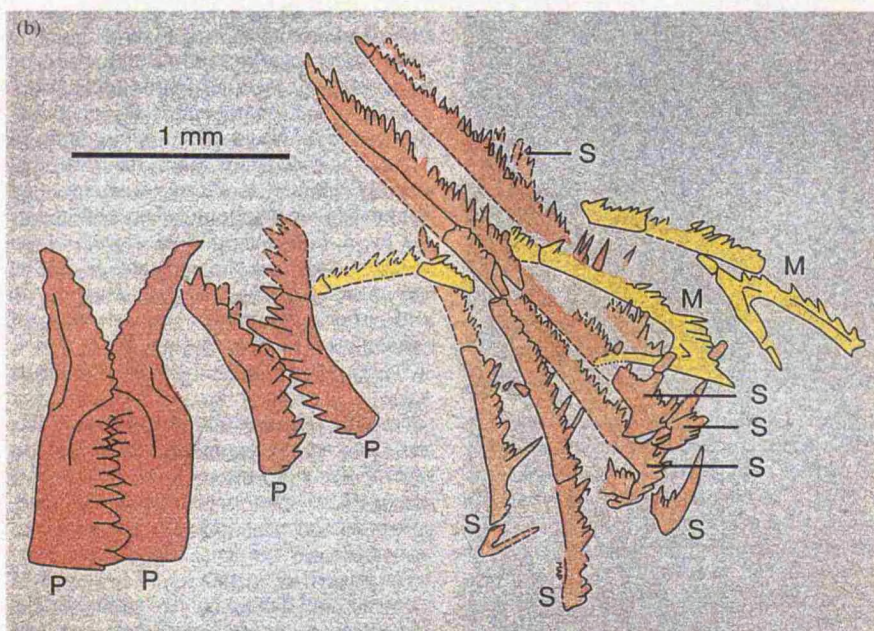


Figure 5

Figures 5 and 6 (facing page).

Reconstructing the ozarkodinid conodont apparatus. Figures 5(a) and 6(a) show fossil bedding plane assemblages of the ozarkodinid genus *Idiognathodus* from the Carboniferous of Illinois, USA. The positions of the different elements of the apparatuses are clarified in 5(b) and 6(b). Figures 5(c) and 6(c) show our model of the original 3D structure of the apparatus of *Idiognathodus* before burial and fossilization. In 5(c) the model has been photographed from the side and slightly above, simulating the fossil shown in 5(a) and 5(b); in 6(c) the model has been photographed from above and slightly behind, simulating the fossil shown in 6(a) and 6(b).

elements in the conodont mouth is taken into account, only two remain plausible. Firstly, the S and M element array has been interpreted as a tissue-covered, ciliated suspension-feeding system which trapped microscopic particles of food to be passed to the P elements for gentle mashing and bruising [17,18]. Alternatively, the S and M elements may have been a raptorial apparatus with which food was grasped. The P elements, according to this hypothesis, sliced and crushed the captured prey in a manner closely analogous to the teeth of higher vertebrates [15,26].

One way of testing these alternative hypotheses is to consider how the apparatus must have increased in size to maintain the food supply to the growing conodont. If the animal grasped food, then comparisons with living organisms suggest that the elements of the apparatus need only have increased in size at the same rate as the rest of the body. If they provided food by filtering, however, the physical principles governing suspension-feeding indicate that the length of the S and M elements would have had to increase at a greater rate than the length of the animal. This is because surface areas, increase at a rate below that of a growing organism's energy requirements, and a suspension-feeding animal that does not alter its proportions soon has a food-gathering surface that is too small to provide it with enough food. Proportional increase in size is shown, for instance, by the suspension-feeding system of larval lampreys. The test of conodont function, therefore, is simple: if the suspension-feeding hypothesis is correct, then the S and M elements should be proportionately larger in larger apparatuses [7,19].

Careful measurements of element lengths in ozarkodinid bedding plane assemblages reveal that the S and M elements are not relatively larger in larger apparatuses. Thus ozarkodinid conodonts could not have been suspension feeders [7,19]. However, the alternative hypothesis, that conodonts actively grasped their food, has been rejected in the past because wear has not been recognized on the element surfaces (for example, [18]). If the elements functioned as teeth they should exhibit similar wear

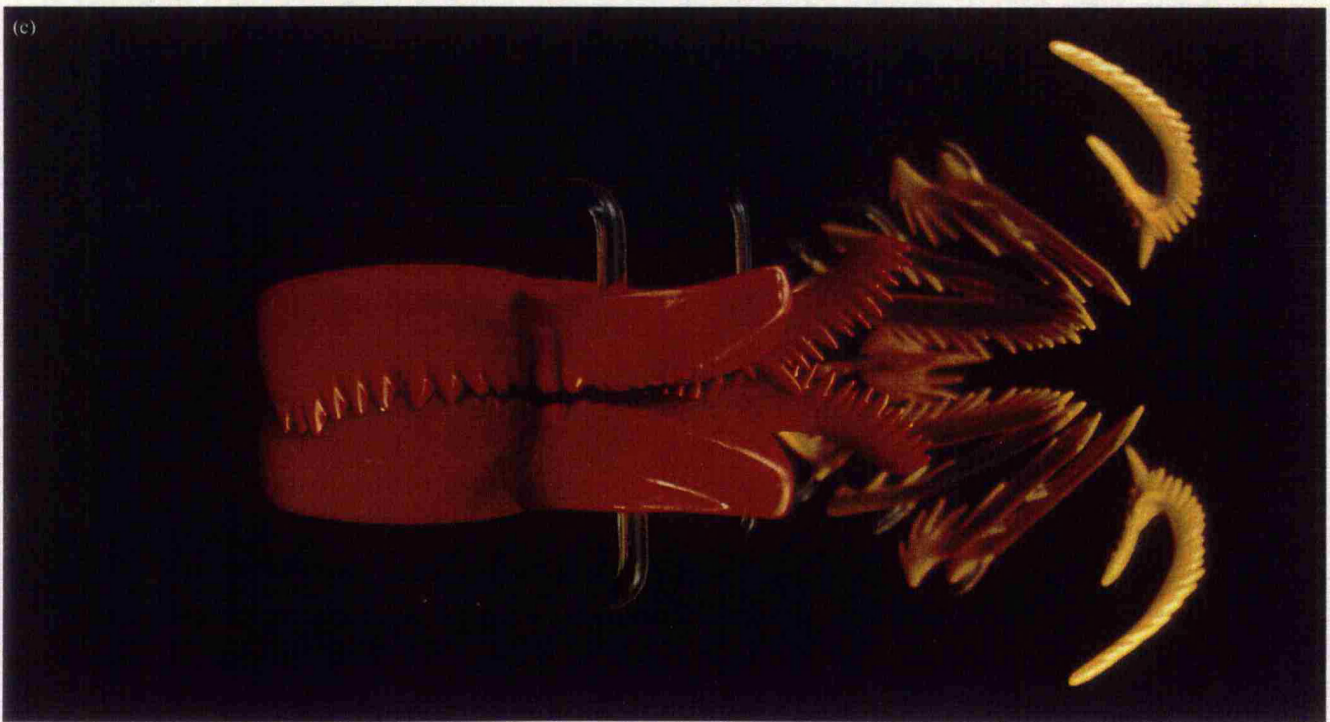
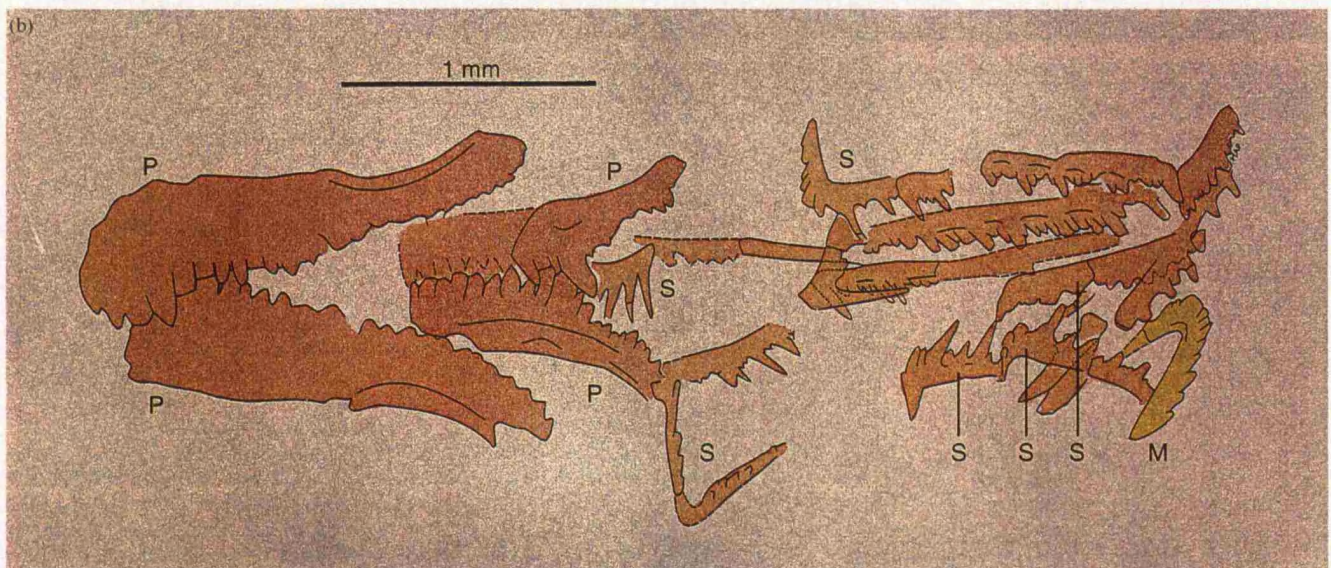


Figure 6

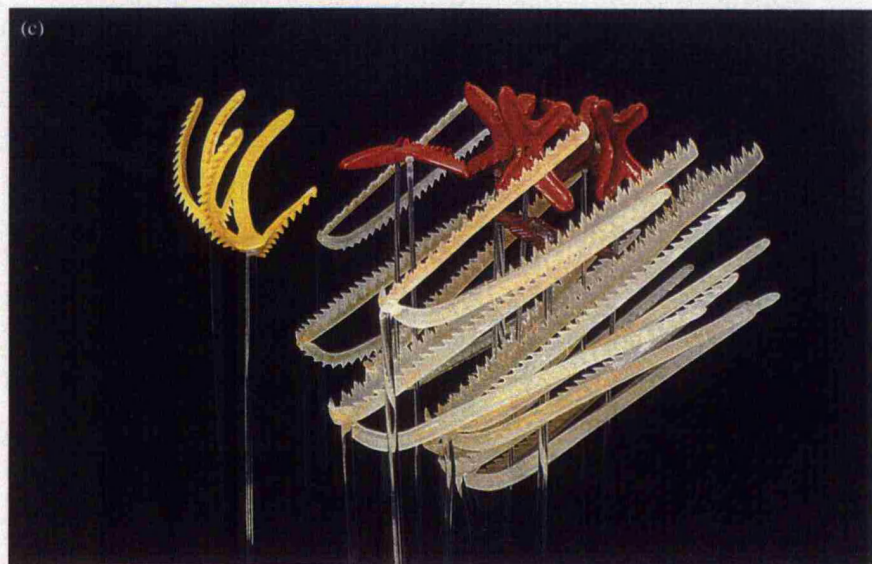
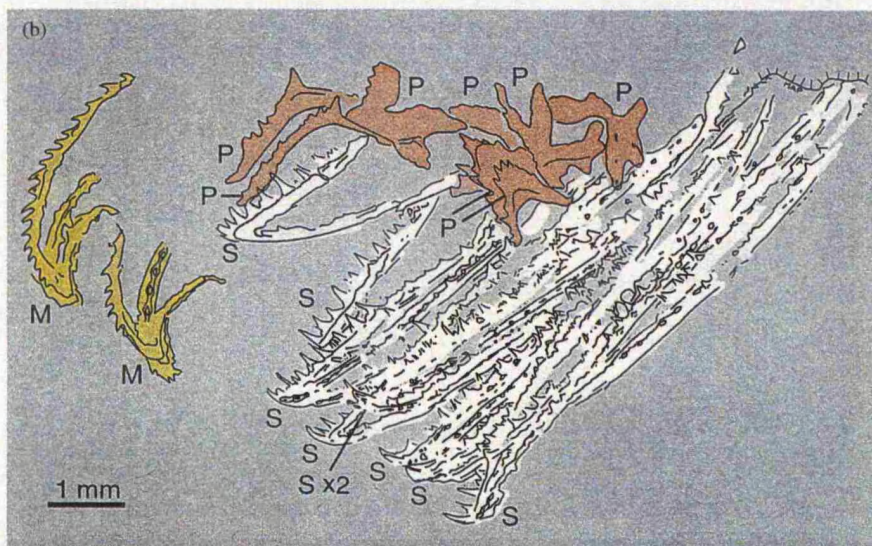


Figure 7 Reconstructing the prioniodontid conodont apparatus. (a) A fossil bedding plane assemblage of the prioniodontid genus *Promissum* from the Ordovician of South Africa. The positions of the different elements of the apparatus are clarified in (b). (c) Our model of the original 3D structure of the apparatus of *Promissum* before burial and fossilization. The model has been photographed from the side and slightly above, simulating the fossil shown in (a) and (b). (Reproduced with permission from [16].)

patterns to those found in the teeth of higher vertebrates.

Wear would occur on the functional areas of the element surface that came into contact during the grasping and mastication of food. Our new understanding of the, detailed architecture of the conodont apparatus enables these points of contact to be identified and specifically examined for evidence of wear. Scanning electron microscopy has recently revealed wear patterns on the functional surfaces of several different types of conodont element (Figure 8) caused by their use as teeth [20]. Several different patterns occur, but perhaps the most significant is scratching, which is diagnostic of a shearing or scissor-like motion of the elements. This method of food breakdown is not effective on microscopic food particles, so conodonts probably ate food that was relatively large. Thus there is increasingly strong evidence that conodonts were predators or scavengers.

Conodonts and the nature of the first vertebrates

The oldest conodont remains are at least 30 million years older than the earliest uncontested ostracoderm fossils, and conodonts appear to have been the first vertebrate group able to build hard parts composed of calcium phosphate. Our interpretation of such conodont elements as teeth challenges established hypotheses concerning the evolution of the vertebrate dental and skeletal system, with the idea that teeth are secondarily evolved organs derived from bony scales clearly called into question. It now appears that hard parts first evolved in the mouth of an animal to improve its efficiency as a predator, and that aggression rather than protection was the driving force behind the origin of the vertebrate skeleton. If it can be demonstrated that there is a direct evolutionary link between conodont teeth and the teeth of the jawed vertebrates that appeared 100 million years later, then the entire scenario of early vertebrate evolution is open to re-evaluation [21].

What else can we say about the nature of the first vertebrates? Conodonts had good vision [3,22] and were probably capable of rapid, eel-like swimming [3]. It is likely that many were active hunters, although in such a successful group it is probable that a wide diversity of ecological strategies was adopted. The teeth of the earliest conodont animals, alive during the Cambrian period, were simple conical elements that could grasp and slice food, but could not process it in the sophisticated manner developed later by the ozarkodinids and prioniodontids. The ancestry of these early conodonts probably extends back into the major radiation of multicellular animals in the early Cambrian, at which time an ecological shift from suspension feeding to predation marked the origin of the vertebrates and set in motion the course of evolution that eventually produced, among other things, ourselves.

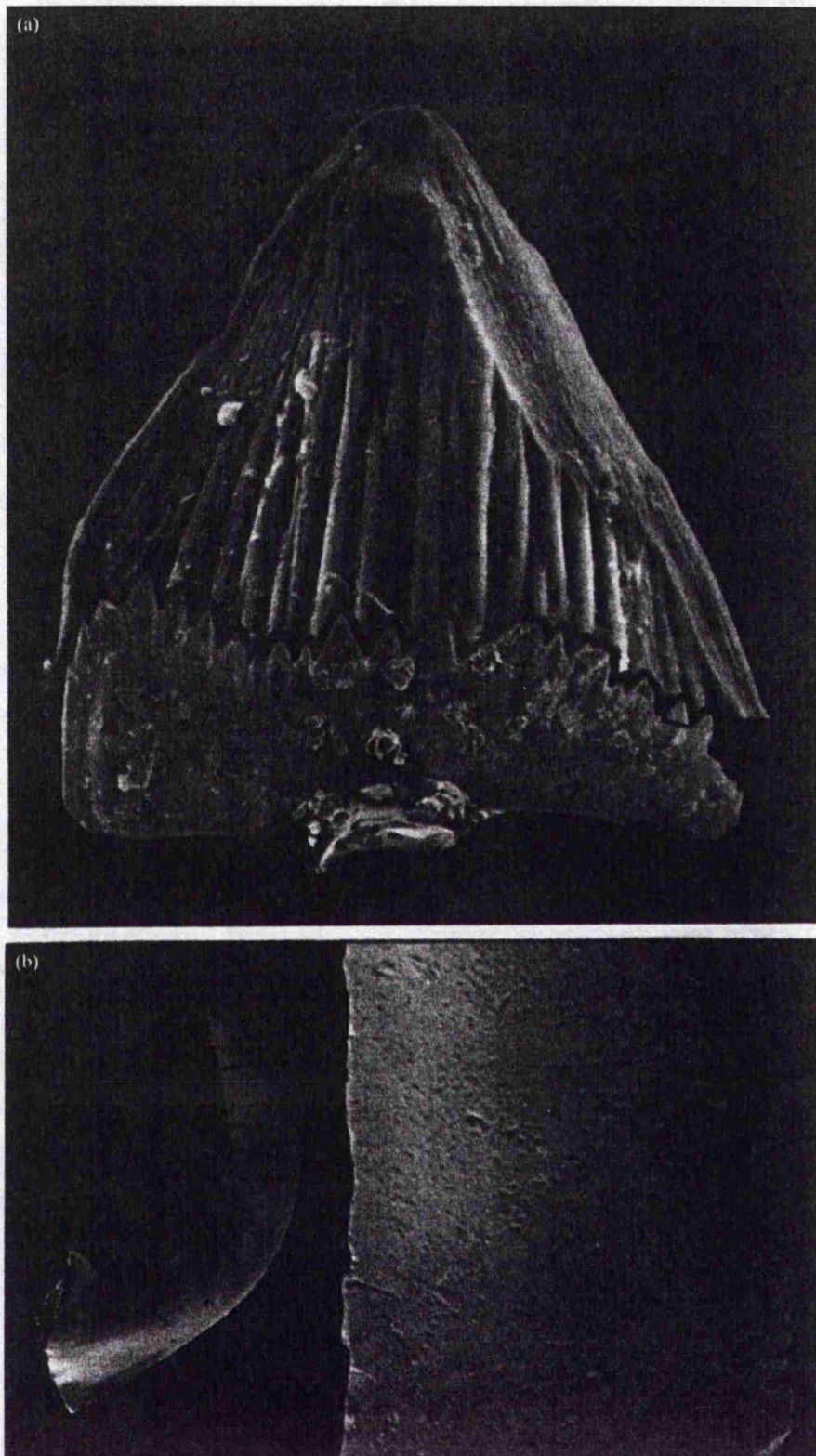


Figure 8 Wear on conodont elements. (a) A well-developed wear facet on a Pa element of *Ozarkodina*; this was formed by repeated contact with another element during feeding; the fine scratching on the surface of the facet indicates that it was caused by shearing movements. The wear illustrated in (b) is also characteristic of shearing; this is an element of *Drepanoistodus*, a conodont which bore only cone-shaped elements and belongs to one of the oldest conodont orders, dating back to the Late Cambrian. The elements shown are approximately 1.5 mm long. Modified from [20].

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APPENDIX 3

An Early Triassic conodont with periodic growth?

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ABSTRACT

Elements of a new Triassic conodont genus *Parapachycladina*, from the Lower Triassic Beisi Formation of western Guangxi Province, China, show a characteristic pattern of lamellar edges in the recessive basal margin. The lamellae are grouped in sets of 8-10, with broad interlamellar spaces between each set. If this apparent periodicity reflects annual cycles, the specimens were not more than four years old when they ceased growing.

INTRODUCTION

Lower Triassic conodonts were first described by Müller (1956), and have subsequently become quite well known. One characteristic member of the fauna is the genus *Pachycladina*, which occurs in shallow-water deposits in Europe, North America and China. Founded by Staesche (1964) as a form genus, with *P. obliqua* Staesche as type species, the multielement nature of *Pachycladina* was recognized by Sweet (1981) in the *Treatise on Invertebrate Paleontology*. Sweet (1981, p. W154) regarded the apparatus as seximembrate, with a carminate to palmate Pa element, digyrate Pb, M and Sb elements, a bipennate Sc element and an alate Sa element with no posterior process. All the elements are "hyaline, with thick growth axes in all denticles"; the aboral surface on each has a small basal pit and a broad zone of recessive basal margin, forming a scarlike area on the inner and outer sides of the Pa element but only on the inner side of other elements. In Sweet's (1988) classification, the genus is placed in the family Ellisoniidae of the order Prioniodinida.

Zhang (in Zhang & Yang, 1991, 1993) reported four species of *Pachycladina* from western Guangxi, China: *P. obliqua*, *P. bidentata* Wang & Cao, *P. erramera* Zhang and *P. peculiaris* Zhang. The last species departs from the diagnosis of *Pachycladina* given by Sweet (1981) in having an Sa element with a posterior process, which bears one or two reclined denticles on some specimens. A similar Sa element from the Thaynes Formation of Utah was illustrated as *Pachycladina* sp. by Solien (1979, pl. 1, figs 16, 18). Zhang (in Zhang & Yang, 1991) therefore revised the diagnosis to include Sa elements with a denticulate or adenticulate posterior process as well as those without a posterior process.

We have restudied specimens of *P. peculiaris* and compared them with those of other species referred to *Pachycladina*. In addition to the distinctive Sa element, specimens of *P. peculiaris* display surface microstriae and a characteristic structure in the lamellae of the crown, revealed in the recessive basal margin. We use these features to diagnose a new genus, *Parapachycladina*, and speculate on the growth history recorded by the coronal lamellae.

SYSTEMATIC PALAEONTOLOGY

Class *Conodonta* Pander, 1856Order *Prioniodinida* Sweet, 1988Family *Ellisoniidae* Clark, 1972Genus *Parapachycladina* nov.

Type species. *Pachycladina peculiaris* Zhang, (in Zhang & Yang 1991), sample YT228, Beisi Formation (Lower Triassic), Taiping, Pingguo, Western Guangxi Province, China.

Diagnosis. Apparatus seximembrate, composed of ramiform elements with intergrading morphology. Pa extensiform digyrate, Pb extensiform to breviform digyrate, M breviform digyrate, Sa alate with posterior process, Sb breviform digyrate, slightly asymmetrical, Sc bipennate. All elements robust, with discrete peglike denticles containing white matter. Aboral surfaces of all elements with small basal pit and broad zone of recessive basal margin. Cusp and denticles of all elements with longitudinal microstriae.

Remarks. The genus is currently monospecific. It differs from *Pachycladina* in the arched and bowed processes of the P elements, the posterior process of the Sa element, in the grouping of the lamellae in the recessive basal margin into sets and in the presence of longitudinal surface striations. Surface striations are clearly apparent at a magnification of 300x on the specimens illustrated as *Pachycladina* sp. and *P. symmetrica* Staesche by Solien (1979, pl. 1, figs 18, 20) and these are assigned here to *Parapachycladina peculiaris*. The denticle surfaces of Chinese specimens of *P. obliqua*, *P. bidentata* and *P. erromera* are very smooth, even at magnifications as high as 3000x. These observations suggest that surface microstructure is a valuable character in the reconstruction of the apparatuses of Triassic ellisoniids.

The recognition of *Parapachycladina* as a separate genus removes the necessity for the revised diagnosis of *Pachycladina* provided by Zhang (in Zhang & Yang 1991).

Parapachycladina peculiaris (Zhang, in Zhang & Yang 1991)

(Pl. 1, figs 1-4; Pl. 2, figs. 1-6; Pl. 3, figs. 1-12)

1979 *Pachycladina symmetrica* Staesche; Solien: 304, pl. 1, figs 17, 20 (Sb element).

1979 *Pachycladina* sp. Solien: 304, pl. 1, figs 12, 13 (Pa), figs 16, 18 (Sa).

1990 *Pachycladina peculiaris* sp. n. Zhang: pl. 2, figs 4 (Pa), 7 (Sa).

1991 *Pachycladina peculiaris* sp. n. Zhang; Zhang & Yang: 40-42, pl. 3, figs 1-12 (all elements).

1993 *Pachycladina peculiaris* Zhang; Zhang & Yang: pl. 5, figs 1-7 (all elements).

Diagnosis. Pa with faint ribs along processes; Sa with denticulate or adenticulate posterior process.

Material. Pa element 22, Pb element 17, M element 26, Sa element 17, Sb element 19, Sc element 23. From sample YT228, lower part of Beisi Formation, Taiping village, Pingguo County, western Guangxi Province, China; Lower Triassic *Pachycladina obliqua* - *Parachirognathus delicatulus* Assemblage Zone (see Zhang, 1990).

Repository of specimens. Natural History Museum, London.

Remarks. The elements of *P. peculiaris* were described by Zhang & Yang (1991). Additional characters are the striae (Pl. 3, Figs 1, 3, 5, 7, 12), the grouping of lamellae revealed in the recessive basal margins of all elements (Pl. 1, figs 1-4; Pl. 2, figs 1-6; Pl. 3, Figs 9, 10) and the presence of white matter in the cores of denticles. Longitudinal

microstriae are present on the cusp and all denticles of every element of *P. peculiaris*; only the sharp denticle margins are smooth. The scale (<0.7 mm) places them in the fine striation category of Lindström & Ziegler (1981). The striae are continuous for the entire denticle length, running parallel for considerable distances but also bifurcating and anastomosing, particularly near the base.

CONODONT ELEMENT STRUCTURE

Conodont elements are characteristically constructed from two basic units, the crown and the underlying basal body. Mineralised basal bodies are, however, unknown in Triassic conodont specimens. The aboral surface of the crown is, therefore, always exposed, and the edges of the coronal lamellae are usually visible on the basal attachment area of the element. In *P. peculiaris*, as in other ellisoniids, the aboral surface of all elements displays a central pit surrounded by a scar-like recessive area, where the edge of each lamella did not extend as far basally as its predecessor. The shape of this recessive area varies with the morphology of the element, but all specimens show a consistent arrangement of the edges of the coronal lamellae. Each visible lamella is separated from its neighbours by an interlamellar space, with the lamellae further grouped into sets by markedly broader intervening spaces. Four such sets are evident in most specimens; except for the outermost, in which the number is variable, each set comprises 8-10 lamellae (Pl. 1, figs 1, 3, Pl. 2, figs 1, 3, 6, Pl. 3, fig. 9).

HARD TISSUE HISTOLOGY

The crowns of conodont elements are constructed of concentric apatite lamellae, which grew through outward secretion, each successive lamella enveloping much of the exterior surface (see Lindström & Ziegler, 1981). The arrangement of crystallites in the lamellae and the incremental lines led Sansom *et al.* (1992) to compare this crown tissue with the enamel of vertebrates.

The specimens of *Parapachycladina* have been thermally altered to CAI 5 (in excess of 300°C), but transmitted light and scanning electron microscopy of whole elements and of etched thin sections has allowed identification and differentiation of histological tissues. Etched thin sections show elements to be heavily fractured internally, and in most specimens this masks the histological structure. However, the best-preserved specimens clearly display the lamellar structure, reflecting the pattern observed in the recessive-basal margin (Pl. 4, figs. 1-7). The cores of denticles in *Parapachycladina* also contain 'white matter', a relatively etch-resistant, fine-grained tissue, interpreted by Sansom *et al.* (1992) as cellular bone (Pl. 4, fig. 3). The blocks of white matter fill the tips of each denticle, flanked by lamellar crown tissue (Pl. 4, fig. 3, 5). Between the batches of lamellae are blocks of white matter which form the denticle core (Pl. 4, fig. 1). The figured section is cut slightly obliquely to the true axis of the curved cusp, so the true extent of the subsumed denticles represented by blocks of white matter cannot be seen.

INTERPRETING THE GROWTH PATTERN

Episodic growth of conodont crowns is evident from their intrinsic lamellar structure, but the lamellar pattern in *Parapachycladina* suggests that a broader periodicity may also be represented. Episodic structures separating groups of lamellae have previously been recognized in thin sections of conodont elements by Müller & Nogami (1971, p. 27, text-fig. 17), who attributed them to resorption. In their examples, the zones of postulated resorption do not coincide with the zones of accretion, thereby producing internal truncations in the lamellar structure. No such truncations are apparent in our specimens of *Parapachycladina*. Müller & Nogami's figures also show

differing numbers of lamellae between each postulated resorption layer. Their interpretation of these features as due to resorption may or may not be correct, but in any event they do not appear to be comparable with the structures we describe here.

There is now a substantial body of evidence indicating that the systematic position of the conodonts lies among the primitive vertebrates, and that the elements functioned as teeth (Briggs, 1992; Sansom *et al.*, 1992; Aldridge *et al.*, 1993; Janvier, 1995; Purnell, 1995; Gabbott *et al.*, 1995). It is therefore appropriate to consider the occurrence of episodic patterns in the skeletal structures of other vertebrate groups. For example, periodic growth of skeletal elements in fishes has long been known, and the resulting structures are commonly used to determine fish ages (e. g. Hartley, 1947; Panella, 1971; Tesch, 1971). Fish scales in particular, may show wide rings at the beginning of a season's growth, becoming narrower and slightly irregular towards the end of the season, with a well-marked boundary before the resumption of the next season's rapid growth. In many fish these ring-line boundaries are formed at the end of the spawning season (Hartley 1947, p. 8).

Otoliths are also commonly used in ageing fish and show comparable 'check marks' on an annual scale. Such structures are, however, continuously grown through the life of the animal and so may not be useful in a detailed comparison with conodont teeth which were at least periodically in use.

Incremental layers in vertebrate enamel (the striae of Retzius) were interpreted by Schour & Hoffman (1939a, b) as representative of a daily rhythm of secretion. Subsequent studies have led to suggestions that cross-striations perpendicular to the axes of the enamel prism reflect a circadian rhythm, whereas the striae of Retzius, which are oblique lines through the enamel, record an approximate seven-day rhythm (see Dean, 1987; Rozzi, 1994). Growth bands at several spatial scales have been described in mammalian dentine, reflecting days, months, seasons or years (see e.g. Laws, 1952; Carlson, 1990). Phillips *et al.* (1982) found a high variability in the pattern of incremental lines in the dentine and cementum of living bats and urged caution in using them to determine age; they did, however, conclude that there generally is a loose correlation between the number of lines and age.

The incremental layers of the *Parapachycladina* enamel could, therefore, represent daily or weekly rhythms rather than monthly or annual cycles. However, conodonts are so distantly related to the other vertebrates studied that interpretations must be equivocal. The more closely related myxinooids do not have biomineralized skeletal elements, but do episodically shed the functional keratinous coverings of their lingual teeth (Krejsa *et al.*, 1990a, b). We can find no record of the frequency patterns of this shedding. Similar problems exist with lampreys, and there are no extant biomineralizing agnathans. Little work has been undertaken on growth patterns in the skeletal hard parts of extinct agnathans. Märss (1992) described rhythmicity in thelodont dermal denticles from the Silurian of the Baltic but offered no specific interpretation.

A few models exist that seek to explain the mode of growth of conodont elements. Krejsa *et al.* (1990a, b), for example, proposed a homology between the growth of myxinooid teeth and those of conodonts. However, the lingual teeth of the hagfish do not compare with conodont elements in composition or internal histology.

Another model, proposed by Bengtson (1976, 1983), suggested that each individual lamella represents a single phase of growth interrupted by eversion of the 'tooth' from the phosphate secreting epithelial pocket. The tooth was then retracted and another phase of growth began. If this is the case, any broader cycles would represent a longer-period physiological cyclicality imposed upon the animal, possibly by environmental changes. Müller & Nogami (1972) interpreted variation in lamellar thickness within an individual as a response to seasonal variations in phosphate solubility in sea water. An annual winter pause in secretion would be a possible

explanation of the broader interlamellar spaces shown by *Parapachycladina*; our specimens show three such pauses in their growth history and might possibly have been no more than four years old when the animal died or shed its teeth.

Bengtson's growth model has been questioned on the basis of space problems (Conway Morris 1980) and is not fully compatible with improved understanding of conodont element function (Purnell and von Bitter 1992, Purnell 1995). It has become clear that this hypothesis is too simplified, and full interpretation of the lamellar structures we describe here probably awaits the development of a more comprehensive growth model. However, we can review alternative possible explanations. These would differ if conodont elements were either a) shed and replaced, or b) retained as permanent teeth.

The hypothesis that conodont elements were deciduous, as is common in vertebrates, was first argued by Carls (1977). In this event, replacement teeth would grow quickly and the episodicity recorded by the lamellae would represent short-term cyclicity prior to eruption, possibly daily, weekly, monthly, or combinations of these. There is currently no direct evidence that conodonts repeatedly shed and replaced their teeth; indeed, most evidence suggests an alternative view (Jeppsson 1976; Purnell 1994). If, however, shedding has occurred in *Parapachycladina*, then the presence of comparable sets of lamellae in all elements would indicate discarding of the whole apparatus at one time.

If the elements were grown then erupted as a permanent tooth, the lamellar pattern would be open to the same interpretation; the episodicity could be regarded as daily, weekly or monthly.

A third possibility is that alternate periods of function and growth occurred, in which the permanent but worn tooth was repaired and enlarged repeatedly during ontogeny. The latter interpretation is essentially an amendment of the original Bengtson (1976, 1983) model, with each lamella interpreted as a single growth stage recording a possible daily increment, during a much larger growth phase. Such phases may be recorded in *Parapachycladina* by the prominent 'sets' of lamellae.

Size distribution analysis of Silurian ozarkodinid conodont elements carried out by Jeppsson (1976) also indicated three growth cycles in mature specimens. If these cycles were annual, then the age of the mature Silurian ozarkodinid specimens compares closely with that suggested for our Triassic *Parapachycladina*. The growth/resorption patterns described by Müller & Nogami (1971, 1972) also record up to four complete cycles.

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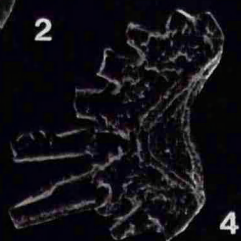
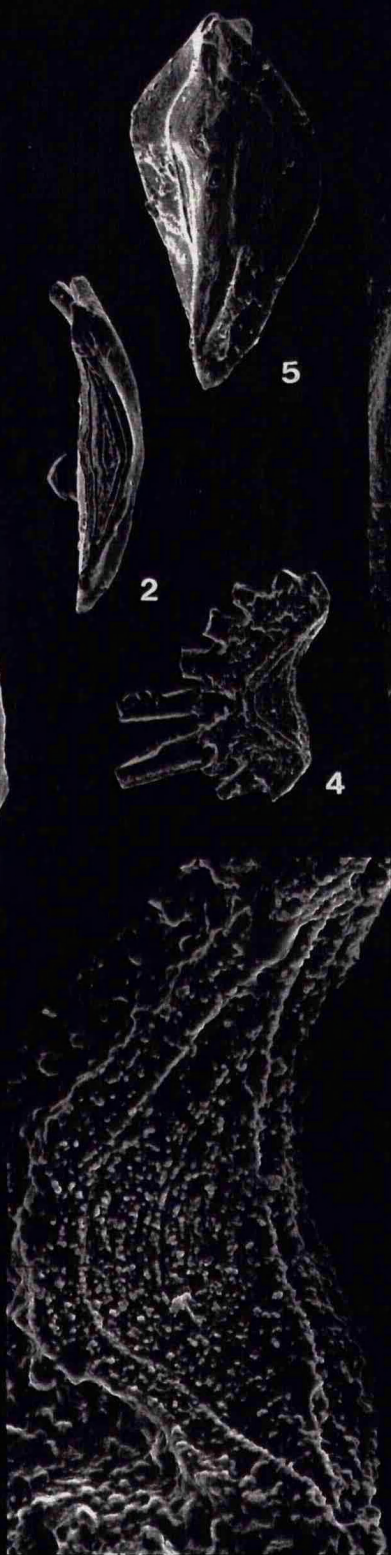
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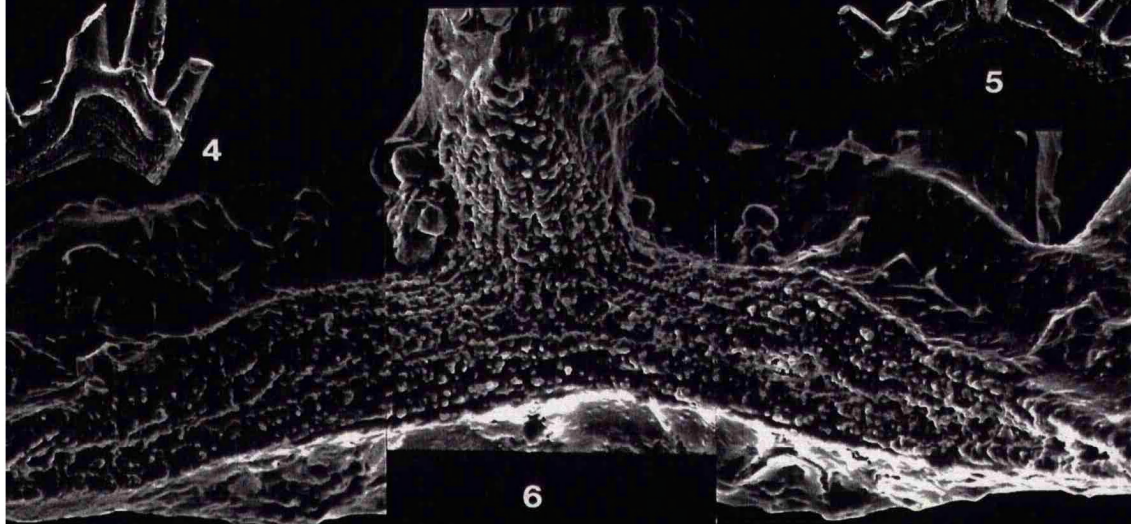
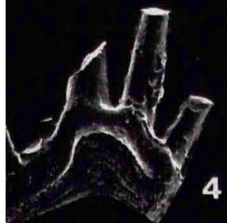
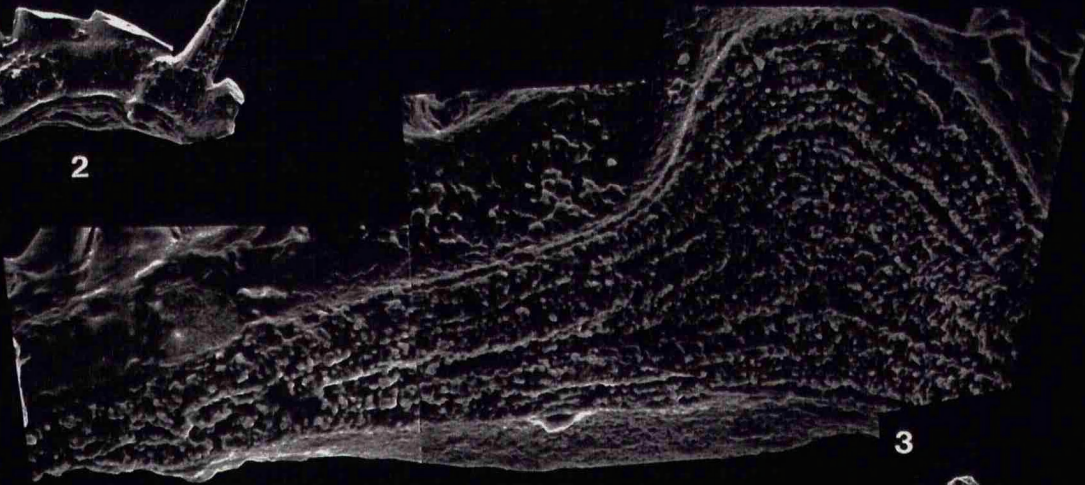
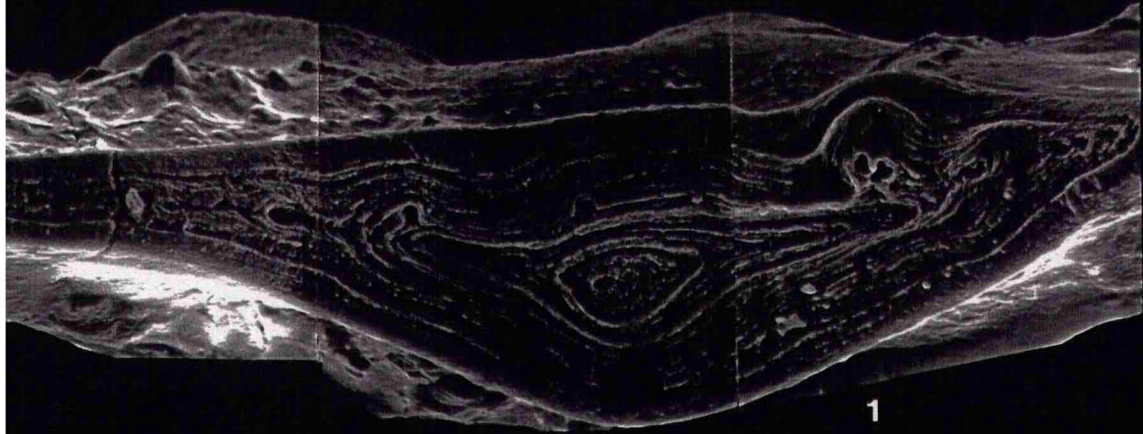
Explanation for Plate 1

Figs 1, 2. *Parapachycladina peculiaris* (Zhang in Zhang & Yang 1991), Pa element, specimen SEM 00041, Beisi Formation, sample YT 228. **Fig. 1.** Aboral surface detail, X424. **Fig. 2.** Aboral view, X73. **Figs 3, 4.** *Parapachycladina peculiaris* (Zhang in Zhang & Yang 1991), Pb element, specimen SEM 000004, Beisi Formation, sample YT 228. **Fig. 3.** Lateral view of basal margin, X424. **Fig. 4.** Lateral view, X73. **Figs 5, 6.** *Pachycladina obliqua* Staesche, 1964, Pa element, specimen SEM 000024, Beisi Formation, sample YT 246. **Fig. 5.** Aboral view, X73. **Fig. 6.** Detail of aboral surface, X424.



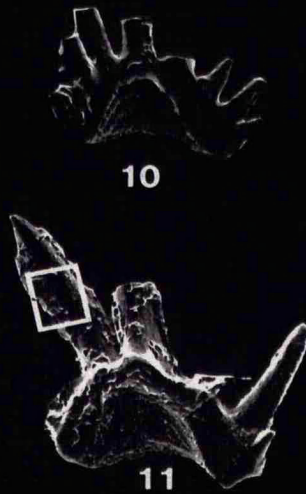
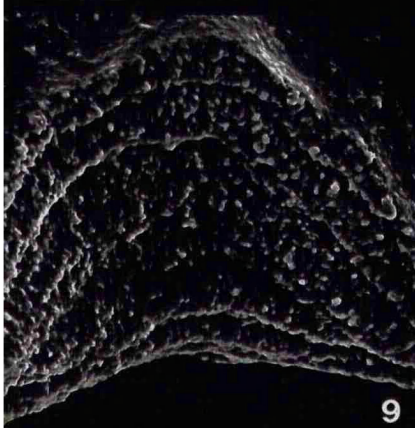
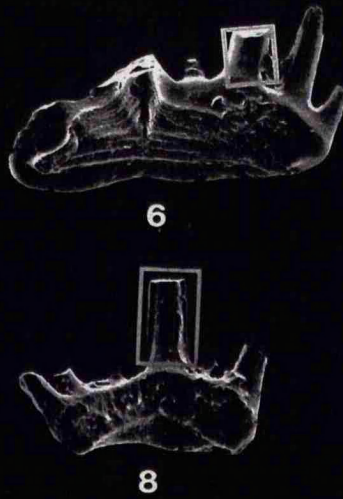
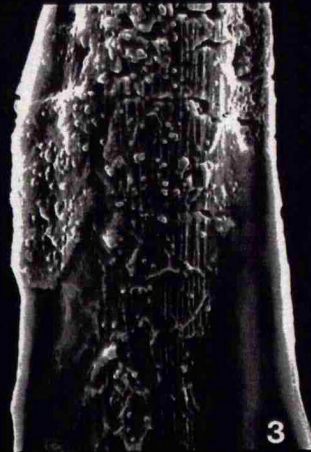
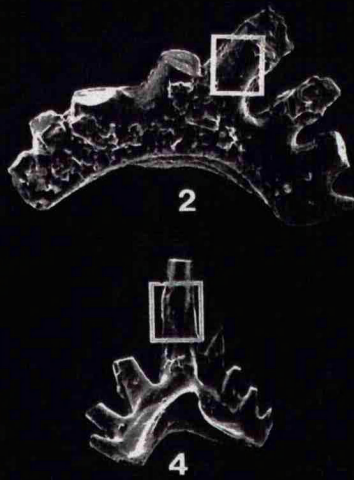
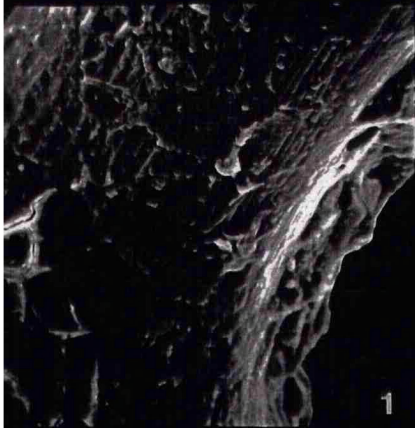
Explanation for Plate 2

Figs 1-6. *Parapachycladina peculiaris* (Zhang in Zhang & Yang 1991), Beisi Formation, sample YT 228. **Fig. 1.** Pa element, specimen SEM 000005, detail of aboral surface, X424. **Fig. 2.** Pa element, specimen SEM 000005, lateral view, X73. **Fig. 3.** M element, specimen SEM 183008, posterior view of basal margin, X424. **Fig. 4.** M element, specimen SEM 183008, posterior view, X73. **Fig. 5.** Sa element, specimen SEM 183001, posterior view X73. **Fig. 6.** Sa element, specimen SEM 183001, posterior view of basal margin, X424.



Explanation for Plate 3

Figs 1-12. *Parapachycladina peculiaris* (Zhang in Zhang & Yang 1991), Beisi Formation, sample YT 228. **Fig. 1.** Pa element, specimen SEM 183002, detail of cusp (shown in box in Fig. 2), X605. **Fig. 2.** Pa element, specimen SEM 183002, lateral view, X73. **Fig. 3.** M element, specimen SEM 183009, detail of cusp (shown in box in Fig. 4), X605. **Fig. 4.** M element, specimen SEM 183009, posterior view, X73. **Fig. 5.** Sa element, specimen SEM 183011, detail of denticle (shown in box in Fig. 6), X605. **Fig. 6.** Sa element, specimen SEM 183011, posterior view, X73. **Fig. 7.** Sb element, specimen SEM 183014, detail of cusp (shown in box in Fig. 8), X605. **Fig. 8.** Sb element, specimen SEM 183014, posterior view, X73. **Fig. 9.** Pb element, specimen SEM 183005, lateral view of basal margin, X424. **Fig. 10.** Pb element, specimen SEM 183005, lateral view, X73. **Fig. 11.** Pb element, specimen SEM 183006, lateral view, X73. **Fig. 12.** Pb element, specimen SEM 183006, detail of denticle (shown in box in Fig. 11), X605.



Explanation for Plate 4

Figs. 1-7. *Parapachycladina peculiaris* (Zhang in Zhang & Yang 1991), Beisi Formation, sample YT 228. **Fig. 1.** Slightly oblique transverse section through the cusp of Sb element, exhibiting three sets of growth lamellae (arrowed) with intervening white matter, X302. **Figs. 2-4.** Transverse section through Pb element, exhibiting at least two sets of growth lamellae, **Fig. 2.** X212, **Fig. 3.** The relationship between the lamellar tissue (left) and the finely crystalline, porous white matter (right), X1028, **Fig. 4.** X424. **Fig. 5.** Transverse section through Pb element, showing the white matter core to the cusp, X302. **Fig. 6, 7.** Transverse section through Pb element, at least two sets of lamellae can be discerned, **Fig. 6.** X484, **Fig. 7.** X212.

