

# SKELETAL ARCHITECTURE, HOMOLOGIES AND TAPHONOMY OF OZARKODINID CONODONTS

by MARK A. PURNELL *and* PHILIP C. J. DONOGHUE

**ABSTRACT.** Conodonts are generally found as disarticulated skeletal elements, yet almost all aspects of conodont research rely on knowledge of the original arrangement of these elements in the apparatus. Analysis of rare, articulated 'natural assemblages' of taxa assigned to the order Ozarkodinida reveals that there was no significant variation in the skeletal architecture within this major group of extinct agnathans. The apparatus comprised 15 elements: a pair each of bilaterally opposed Pa and Pb elements; an anterior, axial Sa element, flanked on each side by a group of four close-set, inward and forward inclined Sb and Sc elements; and above and outside each S group, an inward and forward pointing M element. We identify the S positions in the ozarkodinid apparatus as Sa, Sb<sub>1</sub>, Sb<sub>2</sub>, Sc<sub>1</sub> and Sc<sub>2</sub>.

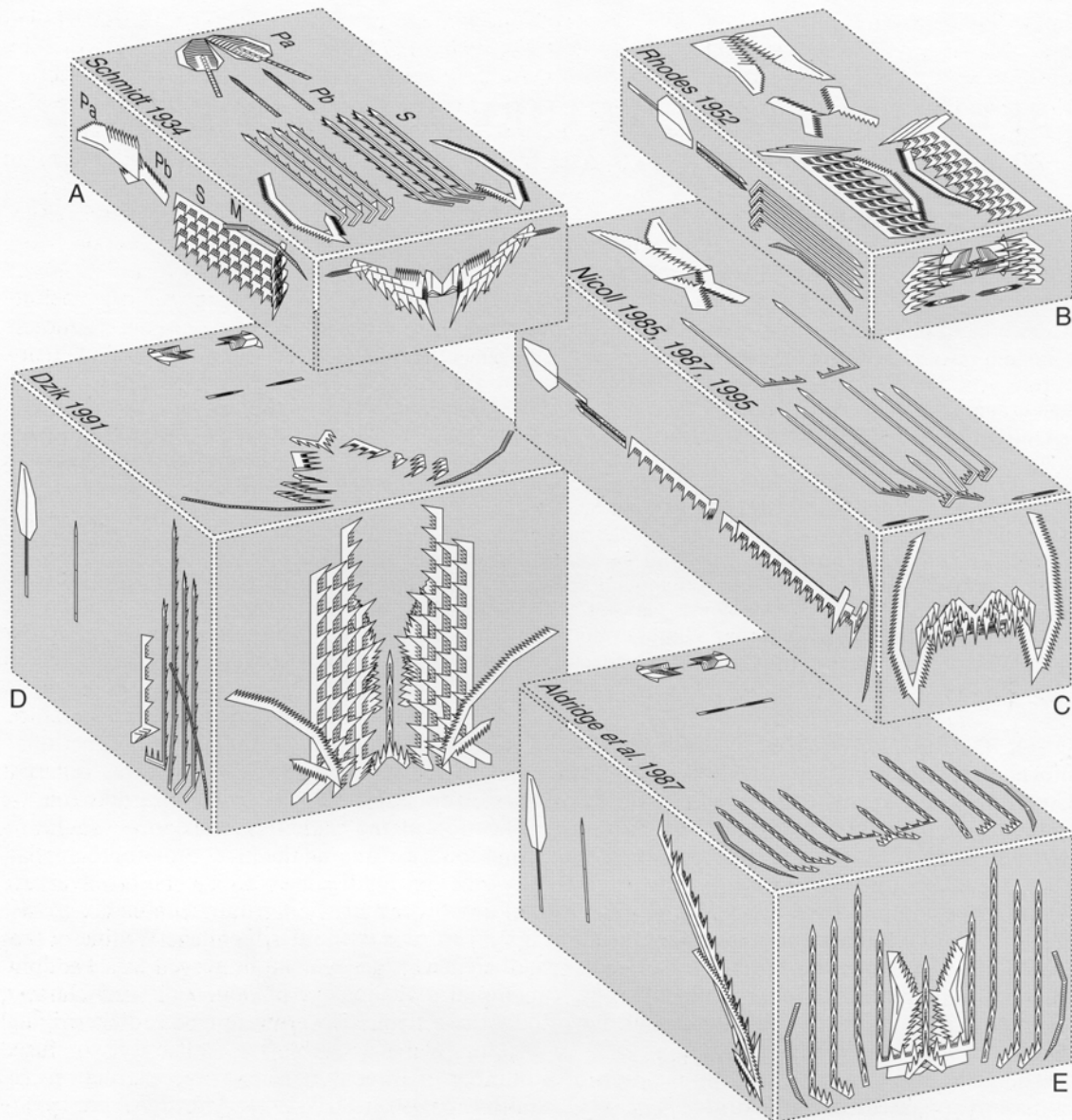
Architectural analysis sheds new light on the taphonomy of conodonts, indicating that the majority of natural assemblages represent ozarkodinid carcasses that did not lie parallel to the sea floor. Our new apparatus model also goes some way to removing some of the more significant architectural barriers that have hampered the recognition of homologies between conodont clades. There are many similarities between the apparatuses of ozarkodinids, prioniodinids, prioniodontids, and panderodontids; it is possible that the Conodonta was rather more conservative architecturally than current hypotheses suggest.

OVER the last 15 years, our understanding of conodont anatomy, affinities and functional morphology has changed beyond recognition (see Aldridge and Purnell 1996 for review). 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 1995; Janvier 1996). Conodonts are among the first craniates to appear in the fossil record, and are far more diverse than any other group of jawless fish. Their fossil record is also more complete and better known than that of any other agnathan group. That is not to say that understanding and analysis of the conodont fossil record is without difficulties. With very few exceptions, conodonts are found as isolated skeletal elements, yet almost all aspects of conodont research, including taxonomy, palaeobiology, functional morphology, phylogenetic analysis and suprageneric classification, rely on knowledge of how these elements were arranged together in the conodont oropharyngeal apparatus.

The last few years have seen publication of a number of three-dimensional reconstructions of conodont apparatuses (e.g. Aldridge *et al.* 1987; Smith *et al.* 1987; Dzik 1991; Aldridge *et al.* 1995), and recently we have produced a new, precise model of the ozarkodinid skeletal apparatus. This model has been widely illustrated (e.g. Palmer 1995, 1996; Purnell and Donoghue 1995; Purnell *et al.* 1995; Abrams 1996) and our aim here is to provide a discussion of our methodology and the wider significance of our model in understanding the taphonomy and homologies of the ozarkodinid apparatus. Aspects of apparatus function are dealt with elsewhere (Purnell and Donoghue 1997).

## *Architecture and natural assemblages*

The development of ideas about conodont skeletal arrangement (see Text-fig. 1) has closely paralleled hypotheses of biological affinity and functional morphology (see Aldridge 1987 for a review). Rigorous analysis of functional morphology requires knowledge of apparatus architecture,



TEXT-FIG. 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 used in text. 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,  $Sb_1$  elements (his Sd) 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 of Dzik (1991) (modified from Dzik 1976, 1986); M elements anterior, dorsally directed ends of elements are 'posterior' according to conventional designation. E, arrangement of Aldridge *et al.* (1987); S and M elements anterior. Text-figure modified from Purnell and Donoghue (1997).

but architecture cannot be based on hypotheses of function. Unfortunately, some studies have fallen into this trap (e.g. Schmidt 1934; Lindström 1964, 1973, 1974; Nicoll 1995) and have thereby contributed to the diversity of alternative and sometimes speculative models of skeletal architecture that have been proposed (see below). However, the lack of consensus regarding architecture also reflects a paucity of good fossil material and a consequent lack of morphological constraint.

Because conodonts were primarily soft bodied organisms, the skeletal elements of their feeding apparatus became scattered in the sediment on the death and decay of the animals. Fortunately, however, there are fossils that preserve together different types of conodont elements, either associated on bedding-planes or as a cluster of elements fused together by diagenetic minerals. More than 1000 of these 'bedding-plane assemblages' and 'fused clusters' are now known, and although several conodont orders are represented in collections from around the world, the majority belong to taxa assigned to the order Ozarkodinida. These specimens represent a range of biostratigraphic histories (see Appendix for a review), and some are undoubtedly accumulations of elements representing the faecal matter or stomach ejecta of animals that preyed upon conodonts. Such specimens may contain elements belonging to more than one individual and more than one taxon (e.g. Hinde 1879; Schmidt and Müller 1964, fig. 9) and generally they preserve very little of the original arrangement of the elements. Many clusters and bedding-plane assemblages represent the remains of a single dead conodont, but the amount of architectural information they preserve 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 process to have affected the apparatus is passive gravitational collapse as the soft tissues of the conodont body decayed (e.g. Pls 1-3; Text-figs 2-16). In such assemblages, post-mortem movement is limited to minor rotations of element long axes as they ultimately came to rest parallel to bedding. 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 separated 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 include a higher proportion of faecal associations, simply because the process of coprolite formation often brings elements into closer juxtaposition. Enhanced levels of phosphate in faecal material may also have increased the probability of elements becoming diagenetically fused.

Compared with 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 spatial arrangement of skeletal elements in the oropharyngeal feeding apparatus. 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, in the interpretation of evolutionary pathways and relationships, and in the construction of meaningful suprageneric classification.

## RECONSTRUCTION OF THE CONODONT APPARATUS

Suprageneric classification of conodonts has yet to stabilize fully, but up to seven orders are currently recognized (Sweet 1988; Dzik 1991; Aldridge and Smith 1993). They all bore apparatuses composed of a number of different elements, with four orders characterized by morphologically simple elements. Of these, the architecture of some taxa assigned by Sweet (1988) to the Bellodellida and the Panderodontida has been reviewed recently by Sansom *et al.* (1994). Three orders (*sensu* Sweet 1988) bore an apparatus typically composed of more complex elements: Prioniodontida (see Aldridge *et al.* 1995 for a discussion of architecture), the Prioniodinida (architectural analysis in preparation (MAP)), and the Ozarkodinida (*sensu* Sweet 1988). Ozarkodinid taxa dominated conodont faunas through most of the Palaeozoic, in terms of both abundance and diversity. Most bedding-plane assemblages and clusters are ozarkodinids, and almost all attempts at reconstructing the conodont apparatus have dealt primarily with ozarkodinid taxa.

*Linear reconstructions*

A few studies have based architectural hypotheses on interpretations of function. Lindström's (1964, 1973, 1974) reconstructions were based primarily on his functional interpretation of the conodont apparatus as a lophophore support, with spatial constraints imposed by the dimensions of the conodont eater *Typhloesus*. They are not considered further here. Similarly, the approach adopted by Nicoll (1995) is 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'. However, almost all analyses of conodont apparatus arrangement have adopted one of two distinct approaches which rely on data from bedding-plane assemblages and clusters. Both recognize that the extremely rare natural assemblages that preserve bilaterally symmetrical arrangements of elements (e.g. Text-figs 2–3) record primary architectural information, but the approaches differ in the way they treat asymmetrical assemblages (e.g. Pls 1–3; Text-figs 4, 5A, 6A, 9, 10A, 11A, 12, 13A, 14A, 15, 16A). Most analyses have assumed that deviations from symmetry reflect post-mortem movement of the elements, and that recurrent asymmetrical 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 (Schmidt 1934; Scott 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 (Text-fig. 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 Text-figures 7–8, 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 20 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 *Lochriea* 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*) (Text-fig. 1B). Rhodes stated explicitly 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, pl. 25, fig. 14; Text-figs 2–3) 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 successive editions of the conodont *Treatise* (Moore 1962; Robison 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. Pl. 2; Text-figs 9–11) to be a better approximation of the original arrangement in the conodont animal than most previously described material. They recognized 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 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 (Text-fig. 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 process.

The emphasis placed on symmetrical assemblages, the interpretation of asymmetrical assemblages as 'unnatural', and the consequent need to invoke systematic post-mortem effects to explain recurrent asymmetrical patterns represent significant weaknesses in the approach to apparatus reconstruction adopted by many of these authors. Several authors, however, realized 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 (1974) recognized 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*).

#### *Three-dimensional reconstructions*

Observations such as these led to the development of a more rigorous approach to apparatus reconstruction which, in contrast to the methodology outlined above, aimed to construct an hypothesis of apparatus architecture that could account for a variety of natural assemblage patterns without recourse to *ad hoc* post-mortem effects. Norby (1976, 1979), for example, suggested that a reconstruction with elements oriented side by side with their long axes vertical was more compatible with asymmetrical assemblage patterns than were linear models. Dzik (1976; later modified a little by Dzik 1986, 1991, 1994; Text-fig. 1D) proposed a similar arrangement to account for the different patterns exhibited by the natural assemblages illustrated by Rhodes (1952, pl. 126, fig. 11; Text-figs 2–3) and Mashkova (1972, pl. 1; Text-figs 12–13).

This approach was further developed (Aldridge *et al.* 1987) by incorporating techniques derived from Briggs and Williams (1981). The apparatus of the first-discovered conodont animal specimen (IGSE 13822) was taken as the primary data for a physical model of element arrangement (Text-fig. 1E) which was then tested by photographic simulation of a variety of recurrent patterns of

apparatus collapse (Aldridge *et al.* 1987). The resulting architectural model was utilized in several subsequent papers (e.g. Purnell and von Bitter 1992; Aldridge *et al.* 1993, 1994, 1995; Purnell 1993a, 1994), and similar methods have since been used to reconstruct the apparatus of the prioniodontid conodont *Promissum pulchrum* (Aldridge *et al.* 1995).

### *Outstanding problems*

Rigorous architectural interpretation of bedding-plane assemblages and clusters is based on the recognition that, firstly, some associations of elements 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 on to a two-dimensional bedding-plane. Different patterns of element arrangement in natural assemblages therefore represent different orientations of apparatus collapse, and the limited number of recurring patterns reflect the attitude of the dead conodont on the sea floor (cf. Dzik 1986). For example, symmetrical patterns (e.g. Text-figs 2–3) were produced by decomposition of a carcass lying on its belly (or belly-up). A carcass on its side produced one type of asymmetrical pattern (Pl. 2; Text-fig. 11), and a carcass lying head down (or up) in the sediment produced another (e.g. Purnell and Donoghue 1997, figs 6–7).

If one accepts that hypotheses that invoke *ad hoc* post-mortem movements of elements to explain element arrangements in symmetrical and asymmetrical natural assemblages are inferior to those that do not, then testing of reconstructions is simple. All linear models (e.g. Schmidt 1934; Rhodes 1952; Jeppsson 1971; Nicoll 1977, 1985, 1987, 1995; Walliser 1994; Text-fig. 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) (Text-fig. 1D–E) are in much closer accord with observed patterns, and they have clarified important architectural features, such as the orientation of the P elements, and the anterior posterior spatial differentiation within the apparatus. But, there are still a number of discrepancies.

Aldridge *et al.* (1987) were aware of a number of limitations of their model: the elements were more widely spaced than in nature, and details of the model, especially the relative positions of the ramiform elements (particularly the M elements) were in need of further refinement. Dzik (1991) also highlighted some of these difficulties with the orientation of S elements; in particular, it is difficult to account for the consistent inward inclination of S element denticles in collapse orientations approaching dorso-ventral (e.g. Pl. 3; Text-figs 2, 3A, 7, 8A, 14A). Dzik's own model (Text-fig. 1D), however, is also a poor match for the arrangement of S elements in natural assemblages: the vertical orientation of the S elements is not seen in lateral or oblique lateral collapse patterns (e.g. Pls 1–2, Text-figs 4, 5A, 6A, 9, 10A, 11A, 12, 13A, 15, 16A), 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. It is these difficulties, together with the acquisition of new material and re-examination of existing collections, that prompted us to produce our new model of ozarkodinid architecture. Furthermore, both Aldridge *et al.* (1987) and Dzik (1991) based their models on only a few taxa; we have attempted to test the degree to which our model can be applied to the ozarkodinids as a whole, and thereby to assess the architectural stability of the apparatus through time and across taxonomic distance.

### *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 material from the Carboniferous of 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 stratigraphical and locality details) and from the Devonian Cleveland Shale of Ohio, USA. Repository abbreviations are as follows: BM and PM, The 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.

Our architectural reconstruction is based primarily on *Idiognathodus* (*sensu* Baeseman 1973; Grayson *et al.* 1991). Natural assemblages of *Idiognathodus* outnumber those of all other taxa, and in order to produce the most accurate reconstruction possible, we used regressions derived from measurements of bedding-plane assemblages (Purnell 1993a, 1994) to produce 1:50 scale models of all of the elements in an apparatus with Pa elements 2 mm long. These elements, made using epoxy putty modelling combined with moulding and casting techniques, were then used to produce our three dimensional reconstructions. 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 compared visually 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 collapsed 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. Modelling techniques similar to these have been used previously 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.

The results of the final photographic testing of the model and a detailed description of the *Idiognathodus* apparatus are published elsewhere (Purnell and Donoghue 1997). Here, we provide three examples (Pl. 1; Text-figs 2–6) in order to demonstrate the fidelity with which our model can reproduce the range of patterns of element arrangement seen in natural assemblages of *Idiognathodus* (for more examples, see Purnell and Donoghue 1997 and Appendix).

During the course of this work, we have also developed a method for calculating the orientation of the principal axes of the conodont apparatus and the conodont head prior to collapse ( $x$  = rostro-caudal axis,  $y$  = dorso-ventral axis,  $z$  = medio-lateral axis; see Text-fig. 17). Photographs of the model simulate collapse of the apparatus, the focal plane of the camera simulating the bedding-plane of the fossil. The angular relationships between the model and the focal plane therefore reproduce the angular relationships between the conodont head and the sea floor at the time of apparatus collapse. In order to calculate the original orientation of the principal axes of the

conodont head, the model is arbitrarily fixed with the sagittal plane vertical and oriented north-south (i.e. with principal axes at  $x = 0^\circ$ ,  $y = 90^\circ$ ,  $z = 90^\circ$ ); the attitude of the focal plane of the camera is then measured while simulating collapse. Stereographic rotation of these data to restore 'bedding' (i.e. the focal plane) to horizontal thus yields the original orientation of the principal axes.

Independent repetition of some measurements indicates 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. However, the orientations of the  $x$  and  $y$  axes indicate the pitch and roll of the head. The orientation of the  $z$  axis reflects the angle of yaw and has no effect on collapse patterns. Furthermore, because our method involves arbitrarily orienting the sagittal plane of the model north-south, the calculated angle of  $z$  (i.e. the yaw of the head) has no real meaning.

#### APPARATUS ARCHITECTURE AND SIMULATIONS OF COLLAPSE PATTERNS

A full description of our reconstruction is published elsewhere (Purnell and Donoghue 1997), but the various oblique and lateral views of our model shown here (Text-figs 3B, 5B, 6B, 8B, 10B, 11B, 13B, 14B, 16B) and the three-dimensional view (Text-fig. 18) provide sufficient detail for our purposes with this paper. The model differs from that proposed by Aldridge *et al.* (1987; Text-fig. 1E) primarily in the arrangement of the S and M elements, which they placed in parallel, with approximately equal forward inclination, with no vertical displacement from one element to the next, and with no inward inclination. It is also in the orientations of the S and M elements that our reconstruction differs from Dzik's (1991) hypothesis (Text-fig. 1D). He considered the S elements to be vertical, their long axes parallel, and their cusp directed inwards at  $90^\circ$ , with the M elements at the front of the apparatus.

#### *Collapse patterns*

*Idiognathodus*. The specimen in Text-figures 2 and 3A is the most widely illustrated natural assemblage (originally figured by Du Bois 1943, pl. 25, fig. 14; see Appendix for subsequent illustrations). Our simulation is of the apparatus as drawn in Text-figure 3A, with the counterpart on the bottom, replicating oblique collapse from above and behind with the principal axes of the apparatus oriented at  $x = 59^\circ$ ,  $y = 30^\circ$ ,  $z = 8^\circ$  with respect to horizontal (Text-fig. 3B). 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 parallel to bedding during collapse, but this cannot be simulated photographically. Du Bois (1943, pl. 25, fig. 4) figured another *Idiognathodus* assemblage exhibiting a similar pattern of element arrangement, but reflecting a slightly more posterior angle of collapse ( $x = 71^\circ$ ,  $y = 17^\circ$ ,  $z = 9^\circ$ ).

The assemblage illustrated in Text-figures 4 and 5A is accurately simulated by photographing the model from behind and to the right, the principal axes of the apparatus oriented at  $x = 43^\circ$ ,  $y = 4^\circ$ ,  $z = 47^\circ$  (Text-fig. 5B). 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 at almost  $90^\circ$  to the sea floor, has broken part way down the process, the two parts coming to lie parallel to bedding in the orientations that one would predict from their orientations in the model. In the simulation, there is a space between the Pa and Pb elements, and another between the dextral Pb and the sinistral M element; in reality these spaces 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  $Sb_1$  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 (pl. 25, figs 3, 11,  $x = 29^\circ$ ,  $y = 3^\circ$ ,  $z = 61^\circ$ ; fig. 12,  $x = 62^\circ$ ,  $y = 5^\circ$ ,  $z = 28^\circ$ ).

A photograph of the model from front, left and below, with principal axes at  $x = 33^\circ$ ,  $y = 19^\circ$ ,  $z = 49^\circ$  relative to sea floor at the time of collapse (Text-fig. 6B) simulates the pattern seen in Plate 1 and Text-figure 6A. 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  $Sb_2$  and  $Sc$  elements. Identification of the  $Sb_2$ ,  $Sc_1$  and  $Sc_2$  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, fig. 5) exhibits a similar pattern of apparatus collapse ( $x = 36^\circ$ ,  $y = 8^\circ$ ,  $z = 53^\circ$ ).

*Other ozarkodinid taxa.* Our primary aim with this paper is to evaluate the model as a general hypothesis of the skeletal architecture of ozarkodinid conodonts, and we have therefore attempted to simulate the collapse patterns observed in as many ozarkodinid taxa as possible (Pls 2–3; Text-figs 7–16; see also notes in Appendix). Schmidt (1934) was the first to illustrate complete natural assemblages of conodonts, and although the specimen illustrated in Text-figures 7 and 8A 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 principal axes of the apparatus at  $x = 30^\circ$ ,  $y = 60^\circ$ ,  $z = 4^\circ$  relative to the sea floor, accurately simulates the assemblage (Text-fig. 8B). Text-figures 9 and 10A also illustrate an assemblage of *G. bilineatus*, and this pattern of element arrangement, similar to that shown by the specimen of *Idiognathodus* in Plate 1 and Text-figure 6, is accurately reproduced by a photograph taken from front, left and below, simulating collapse with principal 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, fig. 3, pl. 6 fig. 3) is similar to that simulated in Text-figure 16B (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, pl. 8, fig. 5) is similar to that in Text-figure 14B ( $x = 37^\circ$ ,  $y = 38^\circ$ ,  $z = 31^\circ$ ); another of his assemblages (Norby 1976, pl. 8, fig. 2; also figured by Sweet 1988, p. 2) is similar to that simulated in Text-figure 3B, but with a slight offset and a higher angle of collapse ( $x = 65^\circ$ ,  $y = 18^\circ$ ,  $z = 17^\circ$ ; approaching the orientation shown in Purnell and Donoghue 1997, fig. 7b). Two specimens (Norby 1976, pl. 8, figs 1, 7), although partially disrupted, are comparable to one of the arrangements simulated in Purnell and Donoghue (1997, figure 7b), as is a specimen figured by Varker (1994, pl. 1, fig. 7;  $x = 74^\circ$ ,  $y = 16^\circ$ ,  $z = 3^\circ$ ). Varker (1994, pl. 1, fig. 4) also figured a specimen with a collapse orientation between that of Text-figures 3B and 16B ( $x = 56^\circ$ ,  $y = 21^\circ$ ,  $z = 25^\circ$ ). Figure 6 of Schmidt and Müller (1964;  $x = 37^\circ$ ,  $y = 1^\circ$ ,  $z = 53^\circ$ ) is similar to the arrangement simulated in Text-figure 5B, and Purnell (1994, fig. 2B) figured one of Norby's (1976) specimens, the arrangement of which is very close to that simulated in Text-figure 16B (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 strong 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 those of *Idiognathodus* or *Gnathodus*. *Lochriea* is a more distant relative of *Idiognathodus*, but the model can match collapse patterns observed in *Lochriea* assemblages. The specimen illustrated in Plate 2 and Text-figure 11A, for example, is reproduced by photographing the model from the side and very slightly in front, simulating collapse with principal axes at  $x = 10^\circ$ ,  $y = 3^\circ$ ,  $z = 80^\circ$ . An interesting feature of this

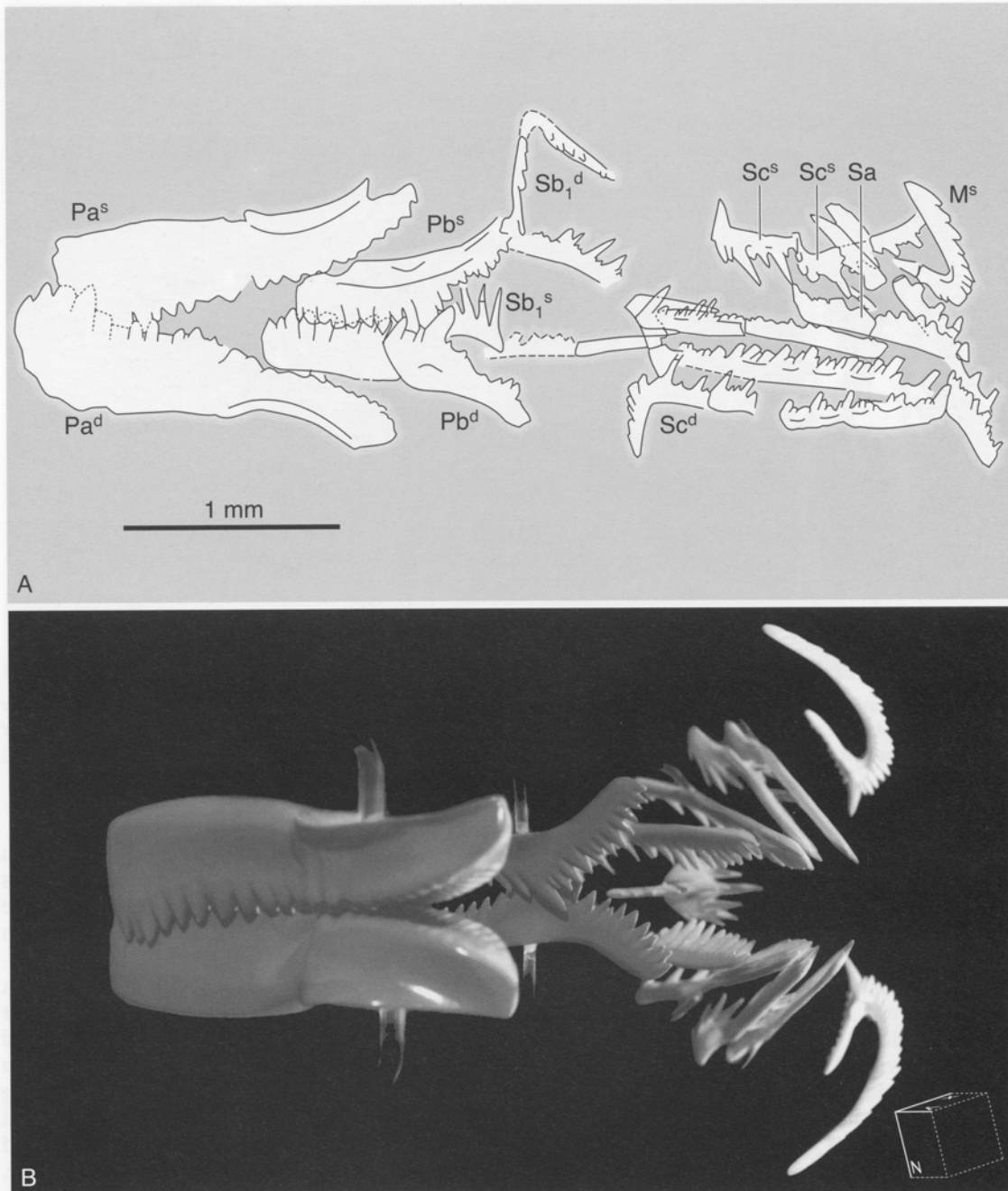


TEXT-FIG. 2. Natural assemblage of *Idiognathodus*; UI X-1480; Pennsylvanian Modesto Formation, Bailey Falls, Illinois, USA; originally figured by Du Bois (1943; see Appendix for subsequent illustrations). All four P elements, the remains of at least six S elements, and one M element are preserved in the part; counterpart not illustrated;  $\times 32$ .

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, pl. 14, figs 8–9) are very similar to the collapse patterns simulated in Text-figures 13B and 16B respectively (see Appendix).

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 distinct from that of *Idiognathodus*, and the 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 (Text-figs 12–13) 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 recognized, 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 (Text-fig. 13A) 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 (Text-fig. 13B),



TEXT-FIG. 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 principal axes of apparatus relative to sea floor at time of collapse,  $x = 59^\circ$ ,  $y = 30^\circ$ ,  $z = 8^\circ$ . Note that as preserved on the specimen part (Text-fig. 2) the apparatus has collapsed obliquely, from below and in front towards top and behind, but without a transparent base to the model this orientation cannot be simulated photographically. Therefore, our simulation is of the whole apparatus as shown in the camera lucida drawing with the counterpart on the bottom.



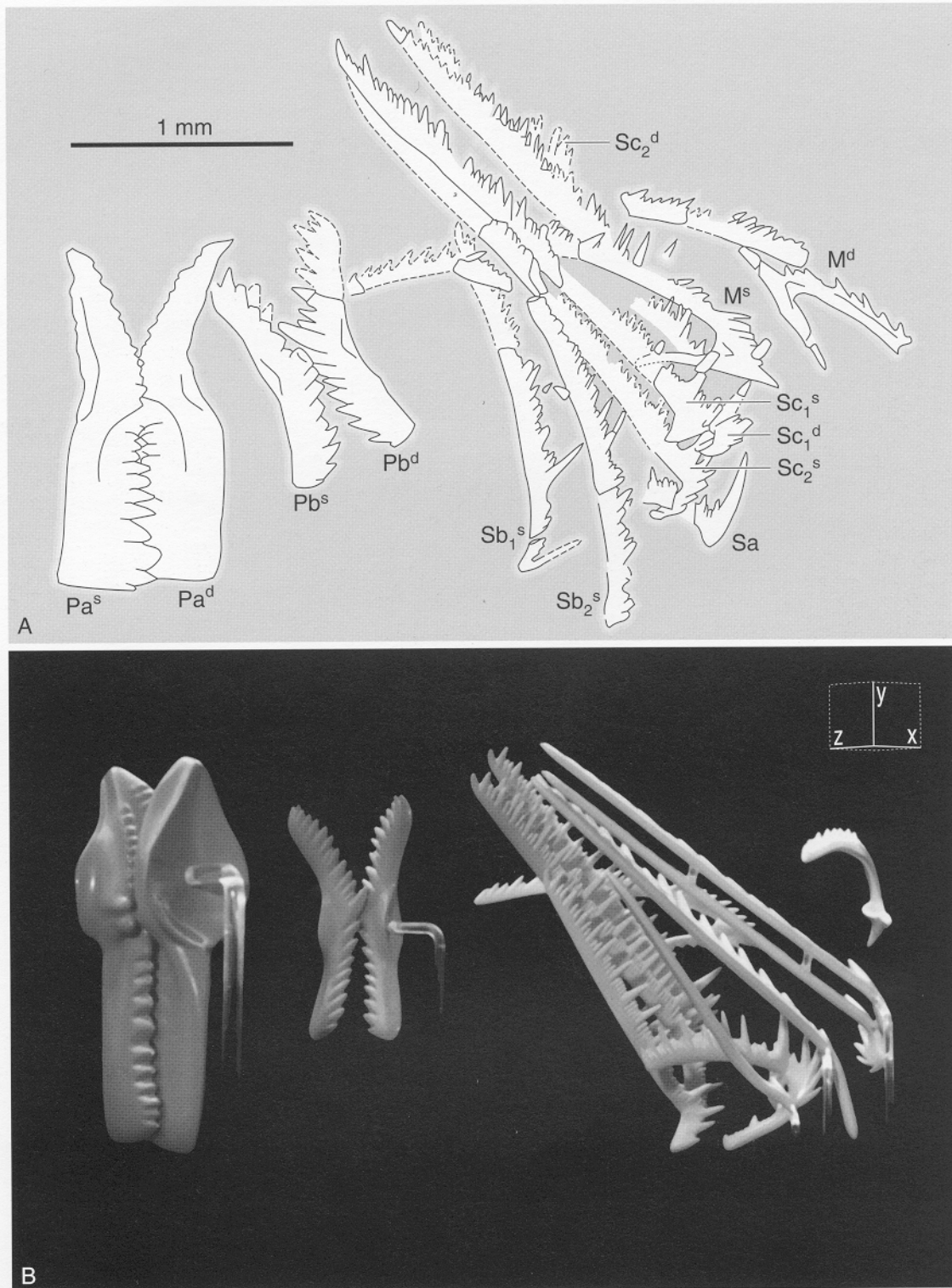


TEXT-FIG. 4. Natural assemblage of *Idiognathodus*; UI X-6377; Pennsylvanian Modesto Formation, Bailey Falls, Illinois, USA; originally figured by Du Bois (1943; see Appendix for subsequent illustrations). All four P elements, the remains of seven S elements, and both M elements are preserved on the part; no counterpart;  $\times 35$ .

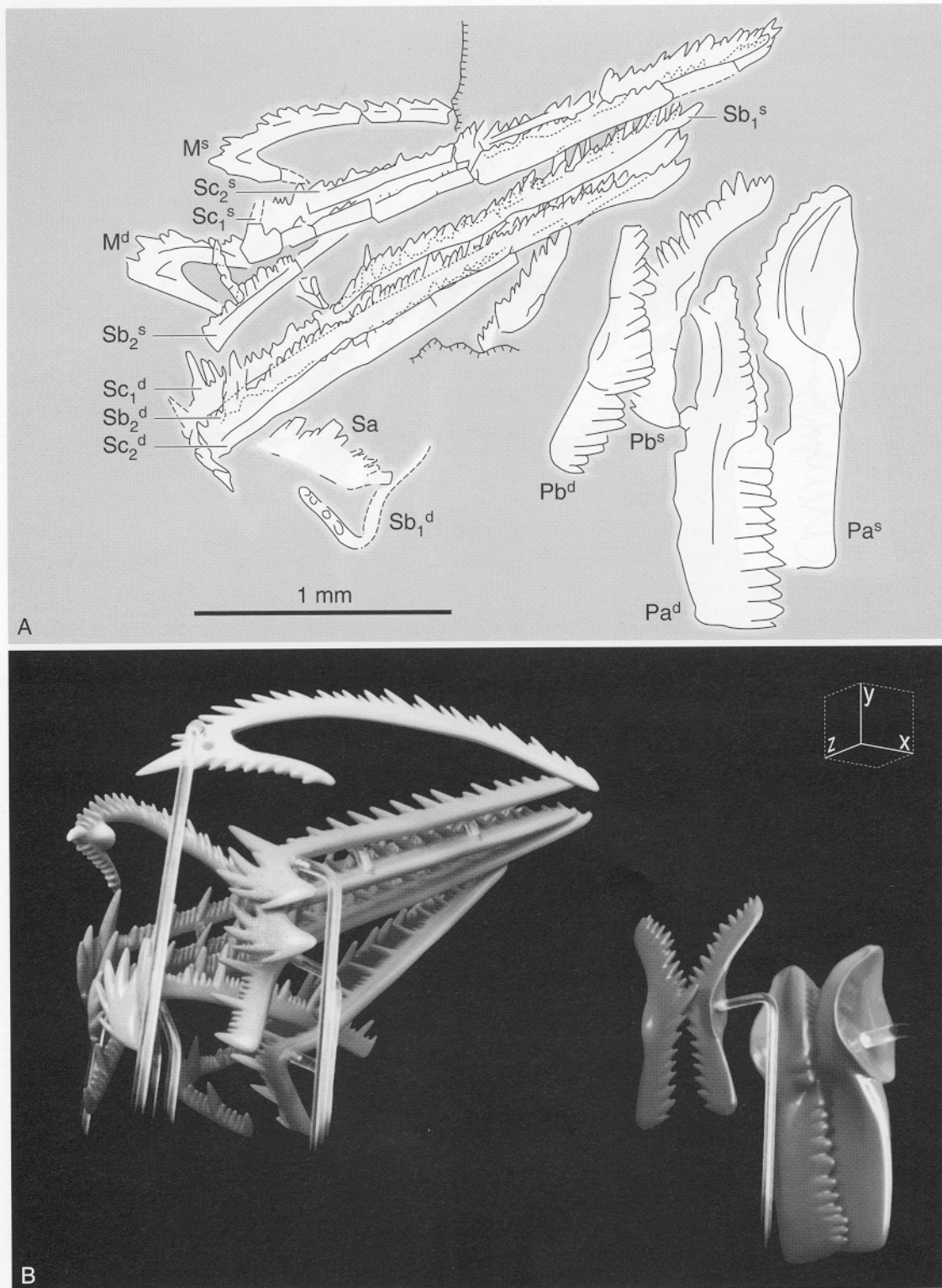
simulating collapse with principal axes at  $x = 50^\circ$ ,  $y = 20^\circ$ ,  $z = 33^\circ$  relative to the sea floor (an orientation similar to that shown in Text-fig. 6B). Clearly the architecture of the apparatus was extremely similar to that of *Idiognathodus*, although the orientation of the 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 from 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, pl. 111, figs 3–5, 16; Nicoll and Rexroad 1987, pl. 3.4, figs 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, pl. 111, figs 3–5) can be simulated closely by the model (Purnell and Donoghue 1997, fig. 7b); another of Pollock's

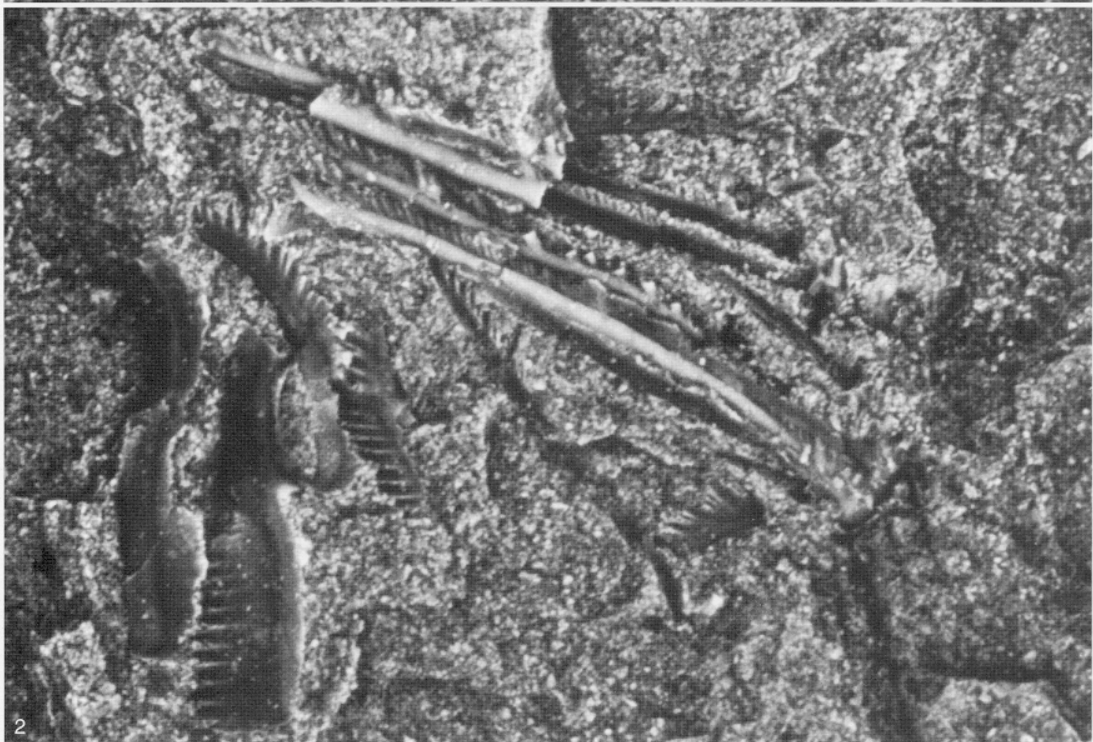
TEXT-FIG. 5. A, camera lucida drawing of specimen UI X-6377. B, photograph of model taken from behind, right to simulate collapse pattern of UI X-6377; small cube indicates orientation of principal axes of apparatus relative to sea floor at time of collapse,  $x = 43^\circ$ ,  $y = 4^\circ$ ,  $z = 47^\circ$ .



TEXT-FIG. 5. For caption see opposite.

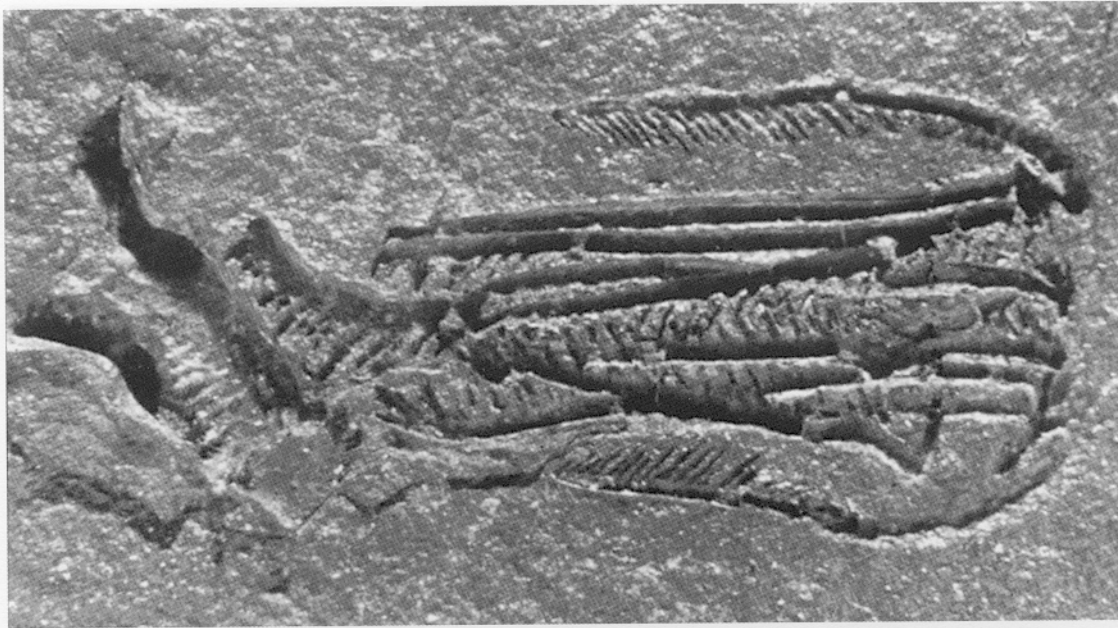


TEXT-FIG. 6. For caption see p. 72.



PURNELL and DONOGHUE, *Idiognathodus* (for explanation see p. 72)





TEXT-FIG. 7. Natural assemblage of *Gnathodus* from the lower Namurian, Hemer, Nordrhein-Westfalen, Germany; specimen lost during World War II, originally figured by Schmidt (1934; see Appendix for subsequent illustrations). Moulds of all 15 elements of the apparatus are preserved on the part; counterpart not illustrated. Photograph reproduced, with permission, from Schmidt 1934, pl. 6, fig. 1;  $\times 21$ .

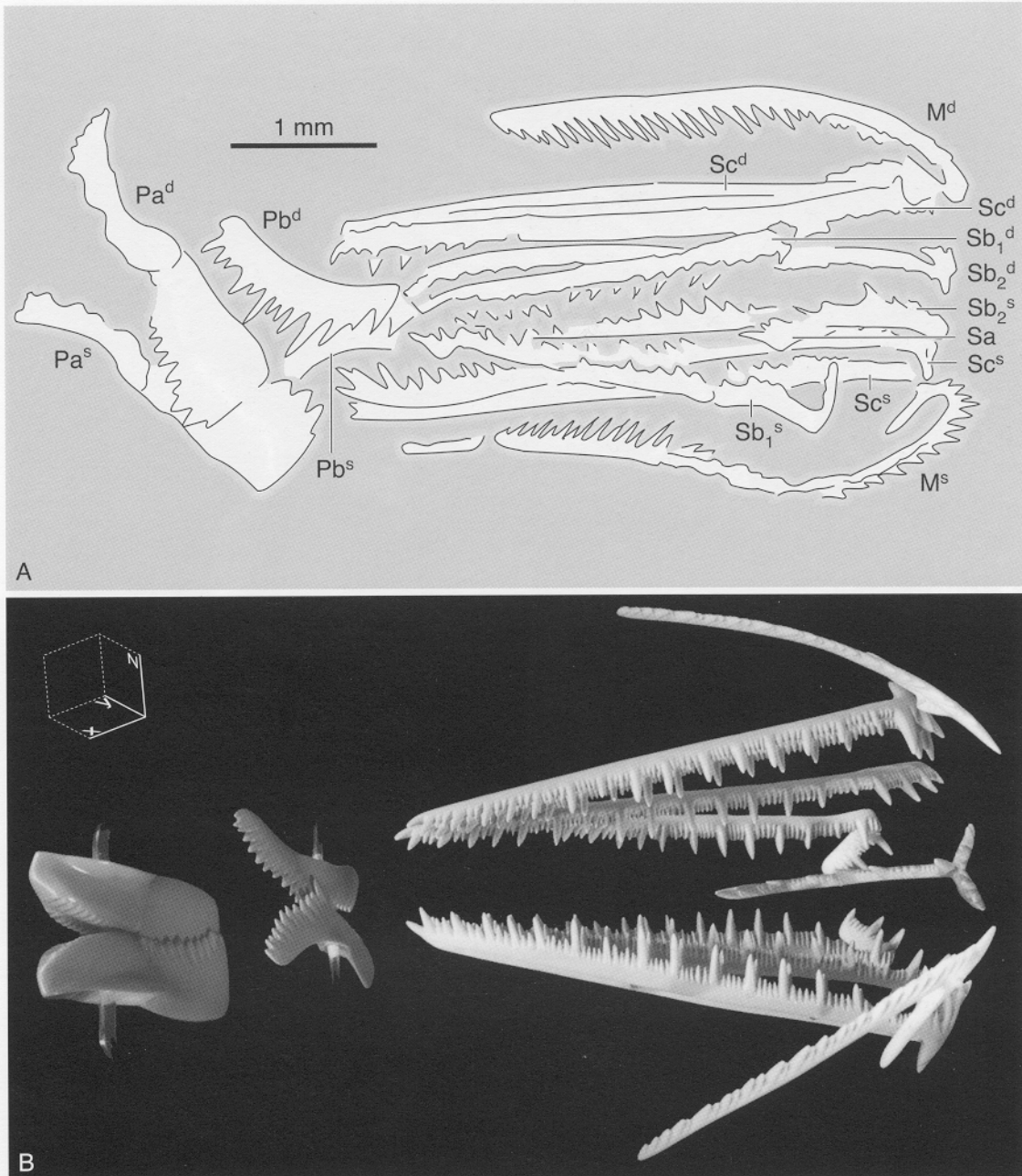
specimens (pl. 111, fig. 16) exhibits a similar pattern, but reflects collapse from behind-right rather than left. One of the specimens figured by Nicoll and Rexroad (1987, pl. 3.4, figs 1, 3, 5) reflects lateral collapse in an orientation very close to that simulated in Purnell and Donoghue (1997, figure 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 (Pl. 3; Text-fig. 14A) lies within, and was eaten by a shark (*Cladoselache*) but it is clearly a good natural assemblage with minimal post-mortem disruption of the apparatus. A photograph of the model from above and in front (Text-fig. 14B), simulating collapse with principal 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 side of the apparatus suggests that collapse was on to the right side; among

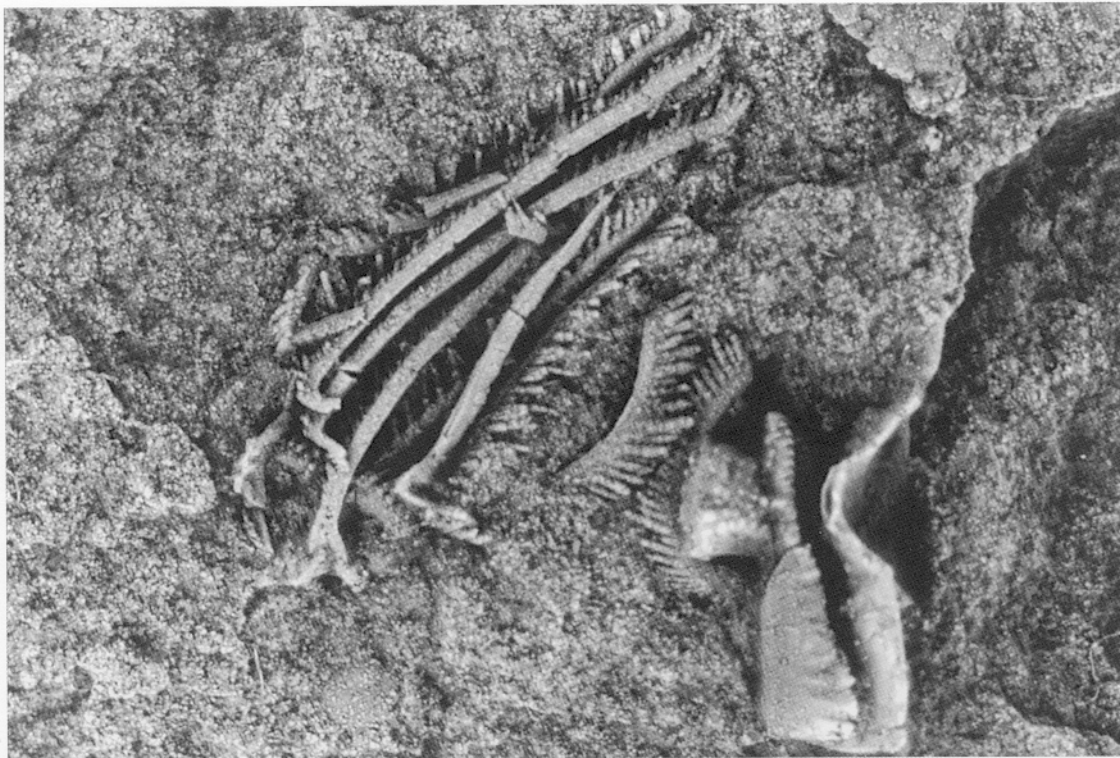
TEXT-FIG. 6. A, composite camera lucida drawing of specimen PM X 2220, part and counterpart (part on bottom). B, photograph of model taken from front, left and below to simulate collapse pattern of PM X 2220; small cube indicates orientation of principal axes of apparatus relative to sea floor at time of collapse,  $x = 33^\circ$ ,  $y = 19^\circ$ ,  $z = 49^\circ$ .

#### EXPLANATION OF PLATE I

Figs 1–2. Natural assemblage of *Idiognathodus*; PM X 2220; Pennsylvanian Modesto Formation, Bailey Falls, Illinois, USA. 1, part; 2, counterpart;  $\times 40$ .



TEXT-FIG. 8. A, tracing of 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 principal axes of apparatus relative to 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.



TEXT-FIG. 9. Natural assemblage of *Gnathodus*; IMGP Gö 600-44; lower Namurian, Hemer, Nordrhein-Westfalen, Germany; originally illustrated by Schmidt and Müller (1964; see Appendix for subsequent illustrations). Silicon rubber cast of part preserving moulds of all elements except dextral M; counterpart not illustrated. Cast coated with ammonium chloride;  $\times 23$ .

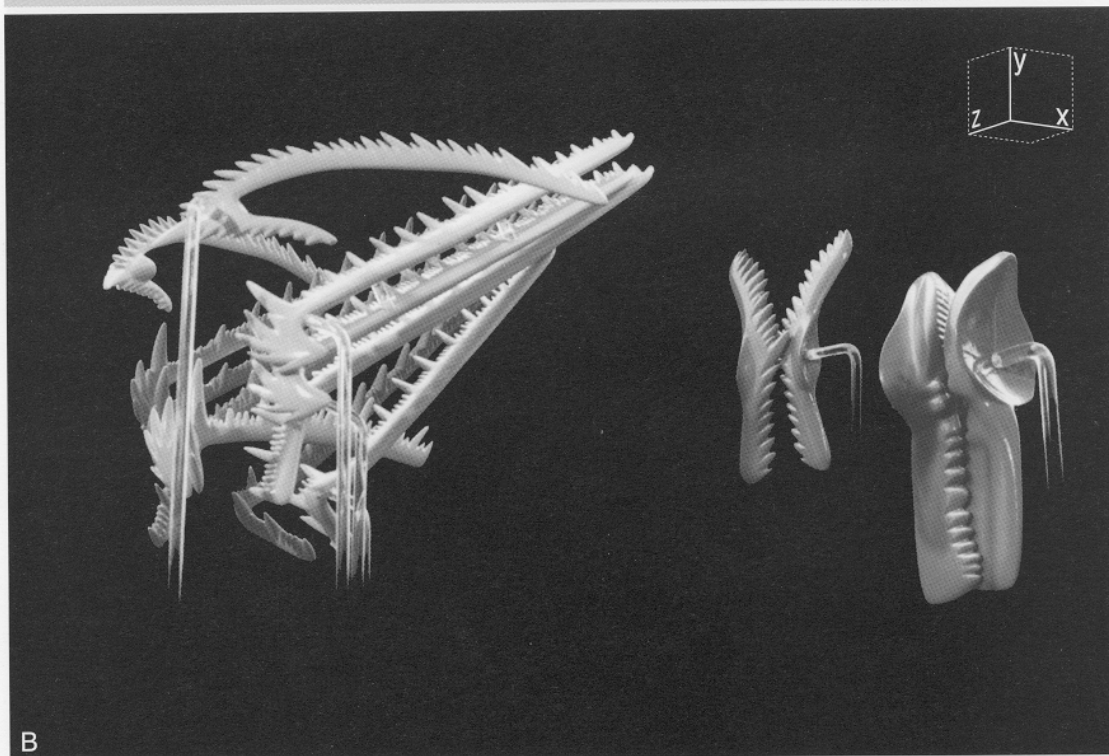
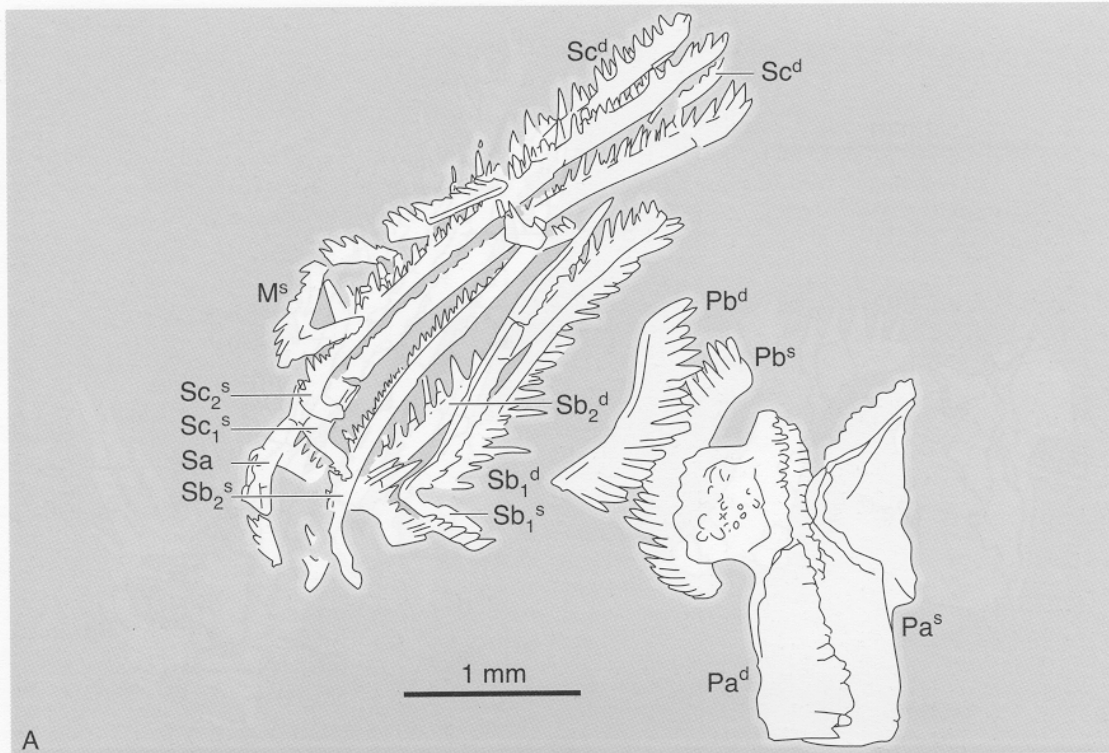
the dextral S elements the only disruption evident has affected the  $Sb_1$  element, the incurved anterior process of which has caused the element to rotate so that its denticles face those of the other dextral S elements. The vertical stacking of the sinistral S elements produced in this orientation of collapse (see Text-fig. 14B) 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, pl. 8, fig. 5).

*Adetognathus* has never been reported as a natural assemblage and the specimen illustrated here (Text-figs 15, 16A) 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 (Text-fig. 16B) simulating collapse with the principal 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*.

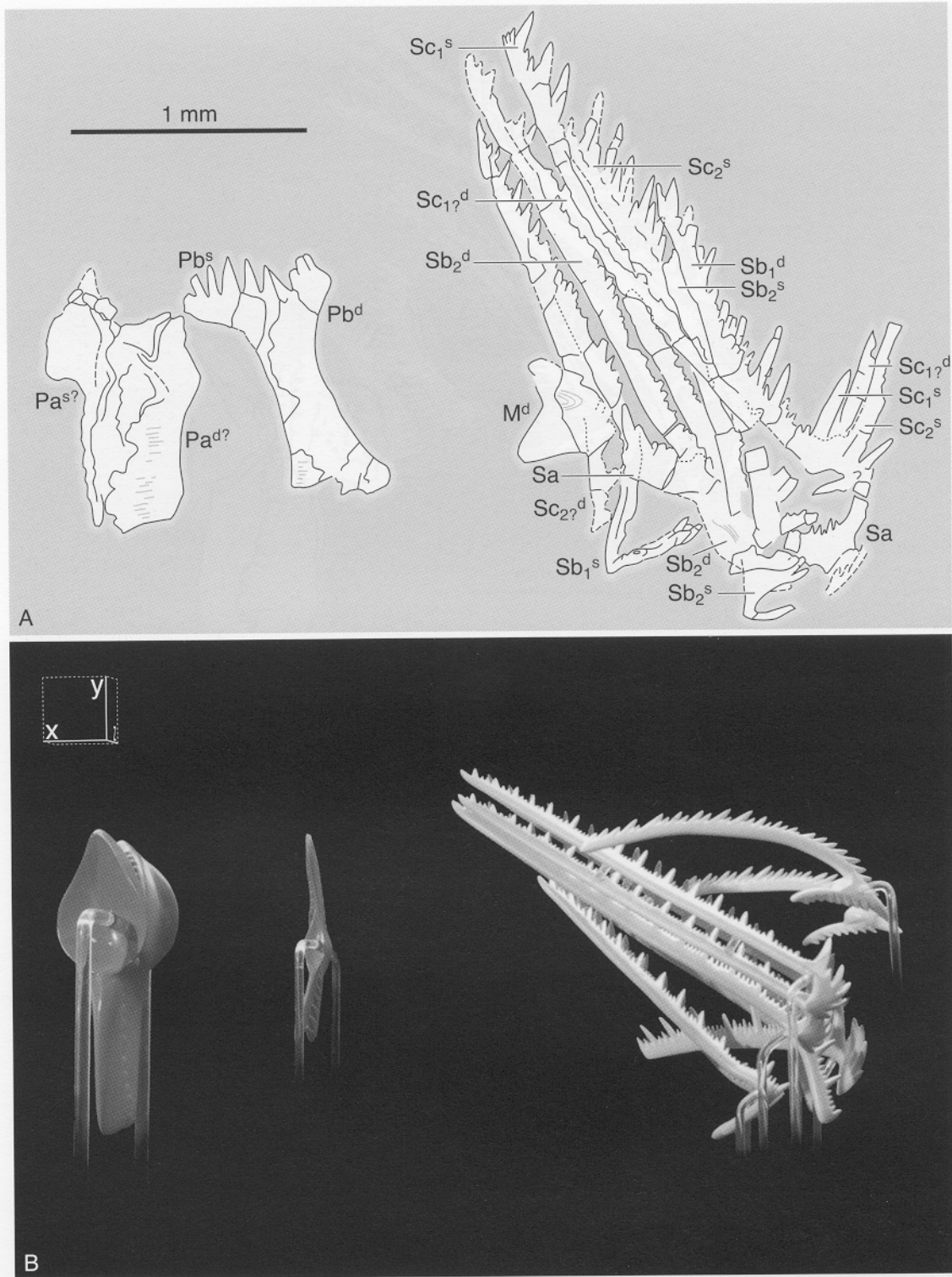
Natural assemblages of a number of other ozarkodinid taxa have previously been figured by several authors, and, although we do not reillustrate them, their patterns of apparatus collapse can

TEXT-FIG. 10. A, camera lucida drawing of *Gnathodus* specimen IMGP Gö 600-44. B, photograph of model taken from front, left and below to simulate collapse pattern of IMGP Gö 600-44; small cube indicates orientation of principal axes of apparatus relative to sea floor at time of collapse,  $x = 33^\circ$ ,  $y = 14^\circ$ ,  $z = 54^\circ$ .

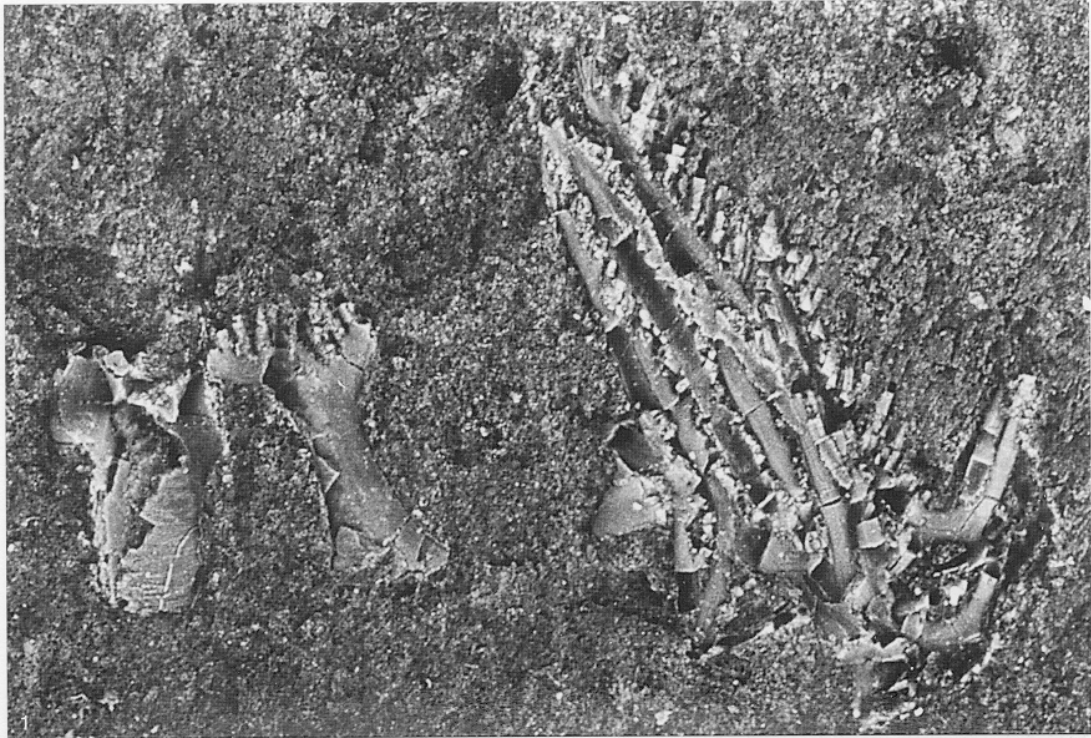




TEXT-FIG. 10. For caption see opposite.

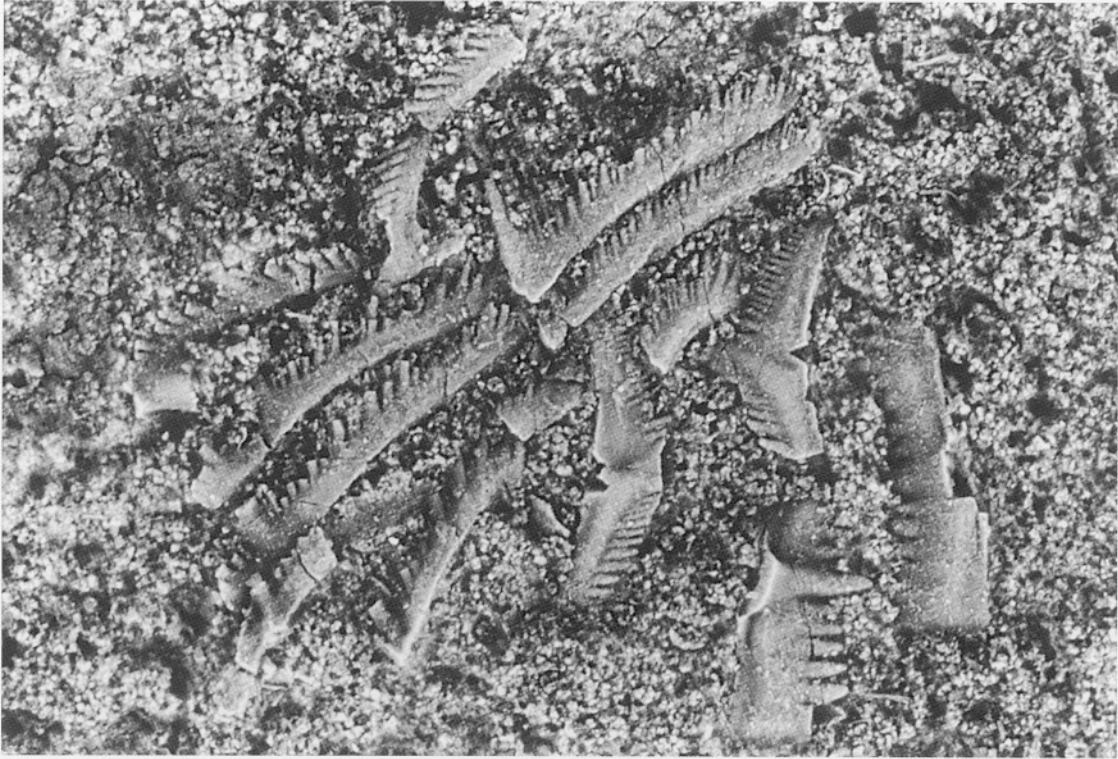


TEXT-FIG. 11. For caption see p. 78.



PURNELL and DONOGHUE, *Lochriea* (for explanation see p. 78)





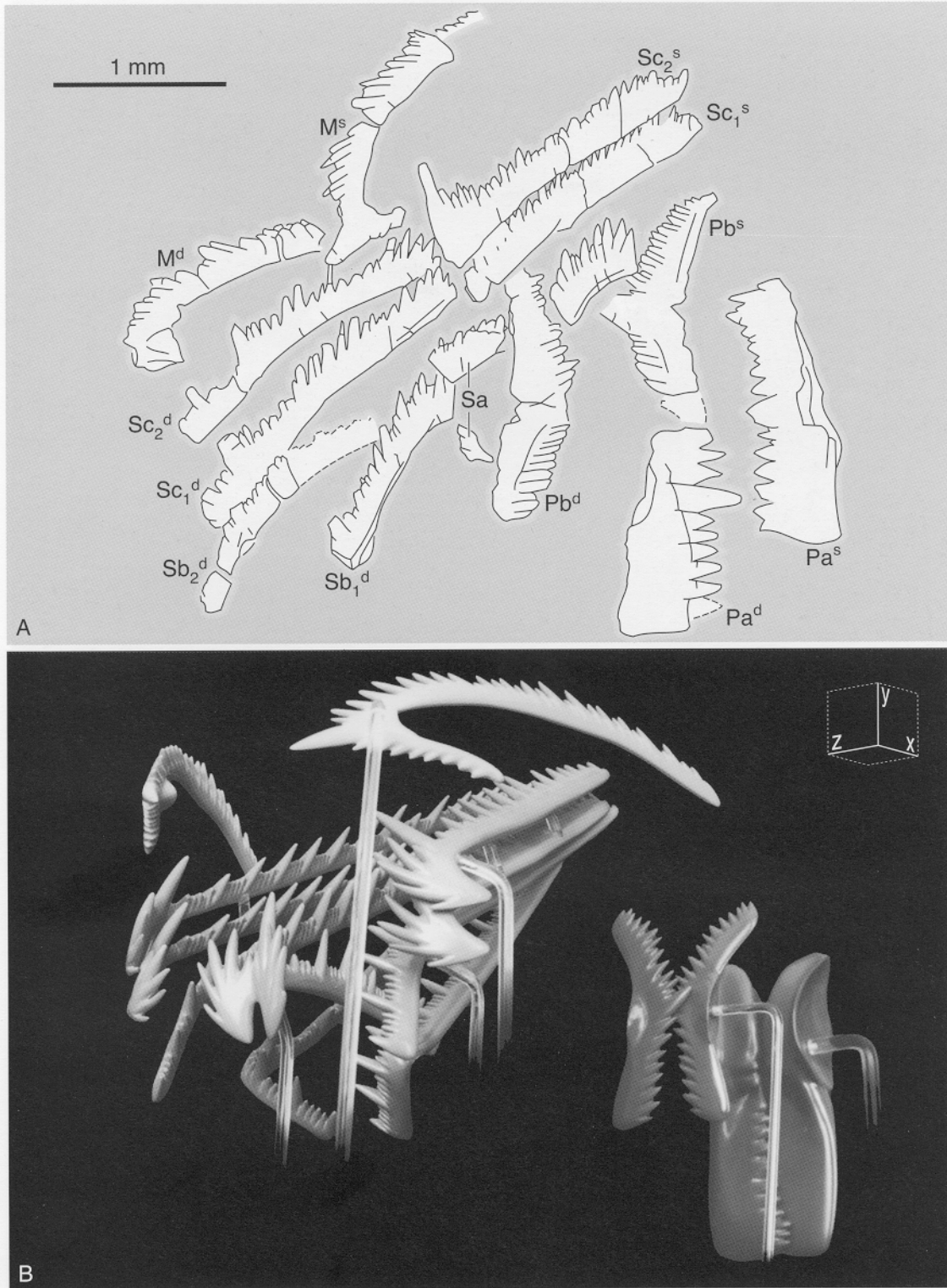
TEXT-FIG. 12. Natural assemblage of *Ozarkodina*; CGM 1/10499; Lower Devonian, Turkparida Valley, Tadjikistan; originally figured by Mashkova (1972; see Appendix for subsequent illustrations). All P and M elements and seven S elements are preserved on the part; no counterpart;  $\times 27$ .

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, fig. 72) and Dzik (1991, fig. 1), although partially disrupted, exhibits a similar collapse pattern to that shown in Text-figure 16B, 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, fig. 3A–B) are incomplete, but reflect a lateral collapse orientation similar to that simulated in Text-figure 11B. Of particular significance, because of their palaeobiological importance, are the apparatuses of the conodont animal specimens assigned to *Clydagnathus windsorensis* (Globensky). The apparatus in

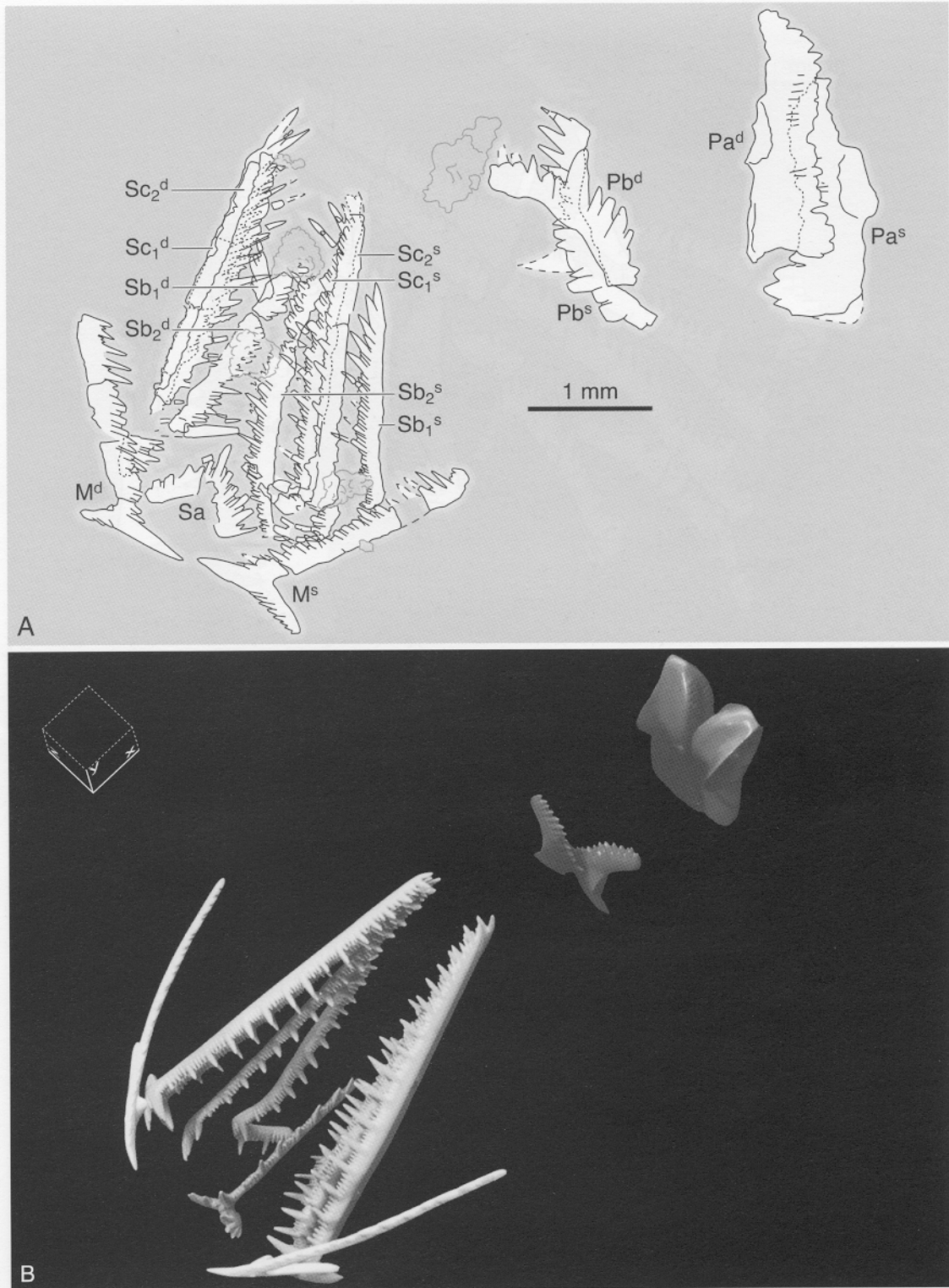
TEXT-FIG. 11. A, composite camera lucida drawing of *Lochriea* specimen IMGP Gö 600–36, counterpart and part (counterpart on bottom). B, photograph of model taken from right side and slightly in front to simulate collapse pattern of IMGP Gö 600–36; small cube indicates orientation of principal axes of apparatus relative to sea floor at time of collapse,  $x = 10^\circ$ ,  $y = 3^\circ$ ,  $z = 80^\circ$ .

#### EXPLANATION OF PLATE 2

Figs 1–2. Natural assemblage of *Lochriea*; IMGP Gö 600-36 from collection of Schmidt and Müller (1964); Namurian, Hemer, Nordrhein-Westfalen, Germany. 1, counterpart; 2, part;  $\times 32$ .



TEXT-FIG. 13. For caption see p. 82.



TEXT-FIG. 14. For caption see p. 82.





PURNELL and DONOGHUE, *Bispathodus* (for explanation see p. 82)





TEXT-FIG. 15. Natural assemblage of *Adetognathus*; ROM 49956; Namurian Bear Gulch Member, Heath Formation, Montana, USA. The assemblage preserves remains of all fifteen elements of the apparatus; it is one of five assemblages on a small slab, no counterpart;  $\times 34$ .

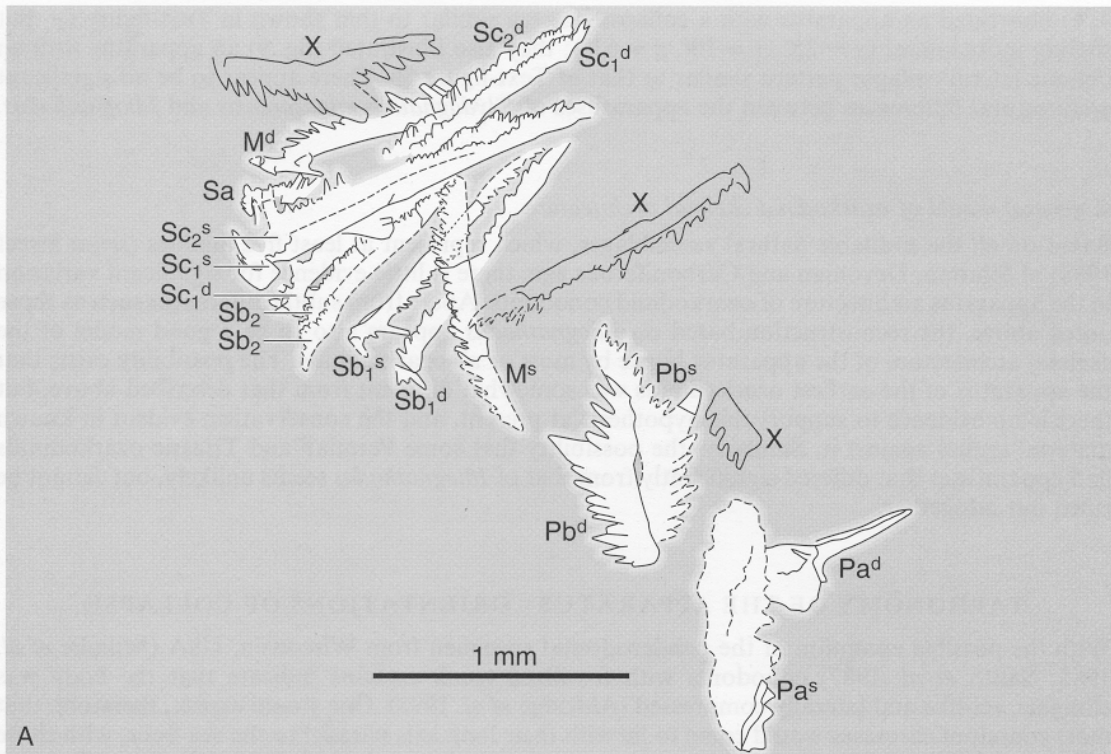
the first conodont animal, illustrated by Briggs *et al.* (1983, figs 1B, 2A–C, 3A–B; refigured many times – see Appendix), exhibits an oblique collapse pattern ( $x = 3^\circ$ ,  $y = 43^\circ$ ,  $z = 47^\circ$ ) similar to the simulation illustrated by Purnell and Donoghue (1997, fig. 9b). These data and the position of the apparatus relative to the eyes indicate that the head of this specimen collapsed neither laterally (*contra* Aldridge *et al.* 1987) nor dorso-ventrally (*contra* Bengtson 1983, and Aldridge *et al.* 1993) but obliquely, as suggested by Briggs *et al.* (1983). The cluster figured by Briggs *et al.* (1983, fig. 6) exhibits a lateral collapse pattern similar to that shown in Text-figure 11B. Aldridge *et al.* (1993, figs

TEXT-FIG. 13. A, camera lucida drawing of *Ozarkodina* specimen 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 principal axes of apparatus relative to sea floor at time of collapse,  $x = 50^\circ$ ,  $y = 20^\circ$ ,  $z = 33^\circ$ .

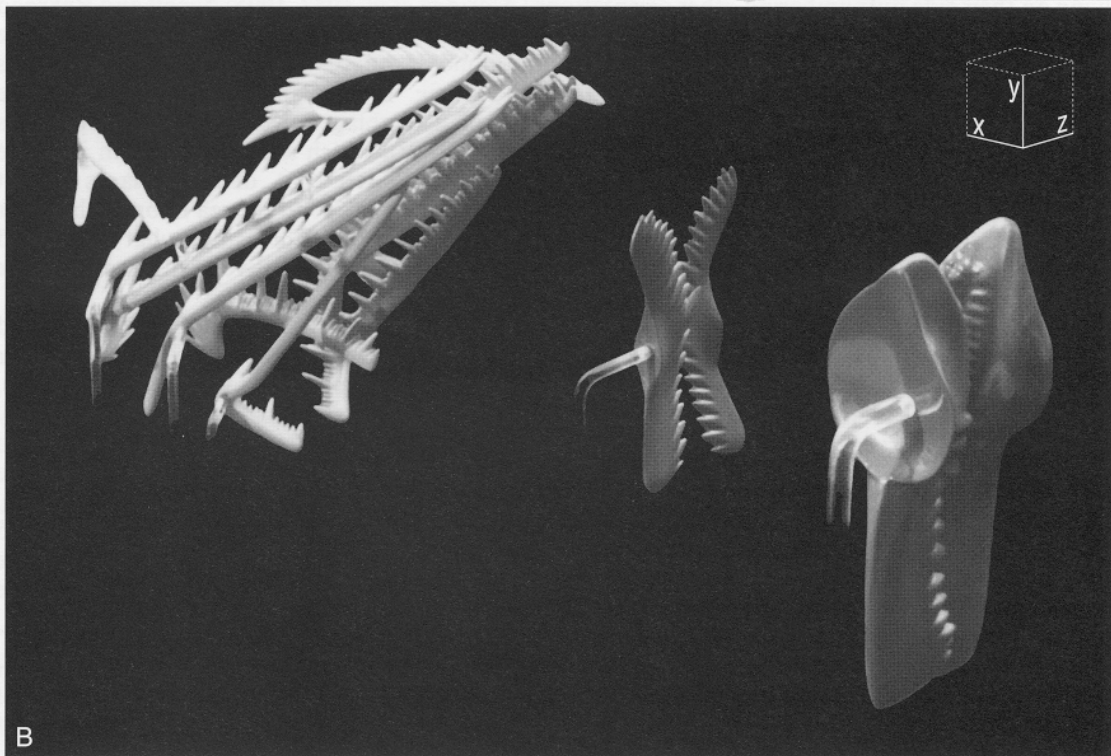
TEXT-FIG. 14. A, composite camera lucida drawing of *Bispathodus* specimen CMNH 9201, counterpart and part (counterpart on bottom). B, photograph of model taken from above, left, and front to simulate collapse pattern of CMNH 9201; small cube indicates orientation of principal axes of apparatus relative to sea floor at time of collapse,  $x = 10^\circ$ ,  $y = 71^\circ$ ,  $z = 16^\circ$ .

#### EXPLANATION OF PLATE 3

Figs 1–2. Natural assemblage of *Bispathodus*; CMNH 9201; Upper Devonian, upper Cleveland Shale, Cleveland, Ohio, USA; 1, part; 2, counterpart;  $\times 19$ . Specimen photographed under water.



A



B

TEXT-FIG. 16. For caption see p. 84.

4, 6) illustrated an apparatus with a collapse pattern similar to that shown in Text-figure 6B, but slightly more lateral ( $x = 25^\circ$ ,  $y = 10^\circ$ ,  $z = 63^\circ$ ); they also illustrated (fig. 9) an apparatus with an oblique lateral collapse pattern similar to that of Text-figure 5B. There appear to be no significant architectural differences between the apparatuses of *Clydagnathus windsorensis* and *Idiognathodus*.

#### *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 from 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.

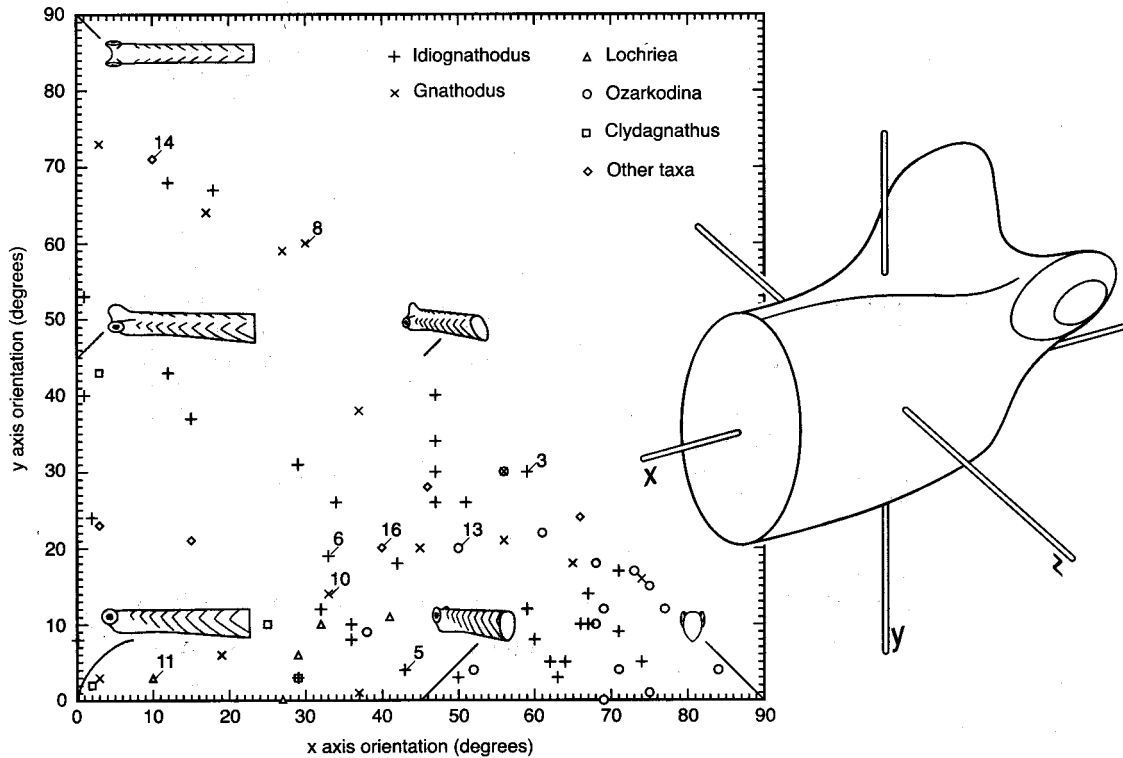
#### TAPHONOMY OF THE APPARATUS – ORIENTATIONS OF COLLAPSE

With the possible exception of the panderodontid specimen from Wisconsin, USA (Mikulic *et al.* 1985; Smith *et al.* 1987) conodonts with fossilized trunk remains 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 (Text-fig. 17) provide some insights into the formation of natural assemblages. Only 8 per cent. of assemblages preserve collapse patterns recording orientations approaching dorso-ventral (i.e.  $y > 45^\circ$ ), which accords well with intuitive assessments of the likelihood of collapse orientations. But 68 per cent. of assemblages exhibit collapse patterns indicating long axis (i.e.  $x$  axis) angles in excess of  $30^\circ$  to the sea floor, with 50 per cent. indicating orientations of collapse in which  $x$  was  $45^\circ$  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 (Text-fig. 17) 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 minimize 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  $Sb_1$  elements (i.e. Nicoll's Sd's) in some of the clusters described by Nicoll (1985) reflects non-overlap resulting from lateral collapse (e.g. Text-figs 10–11, 16), not a more posterior position for the  $Sb_1$  elements (*contra* Nicoll 1985, 1995 and Nicoll and Rexroad 1987). These taphonomic biases involved in cluster formation, however, are not enough to account for the overall distribution of collapse orientations in ozarkodinids because

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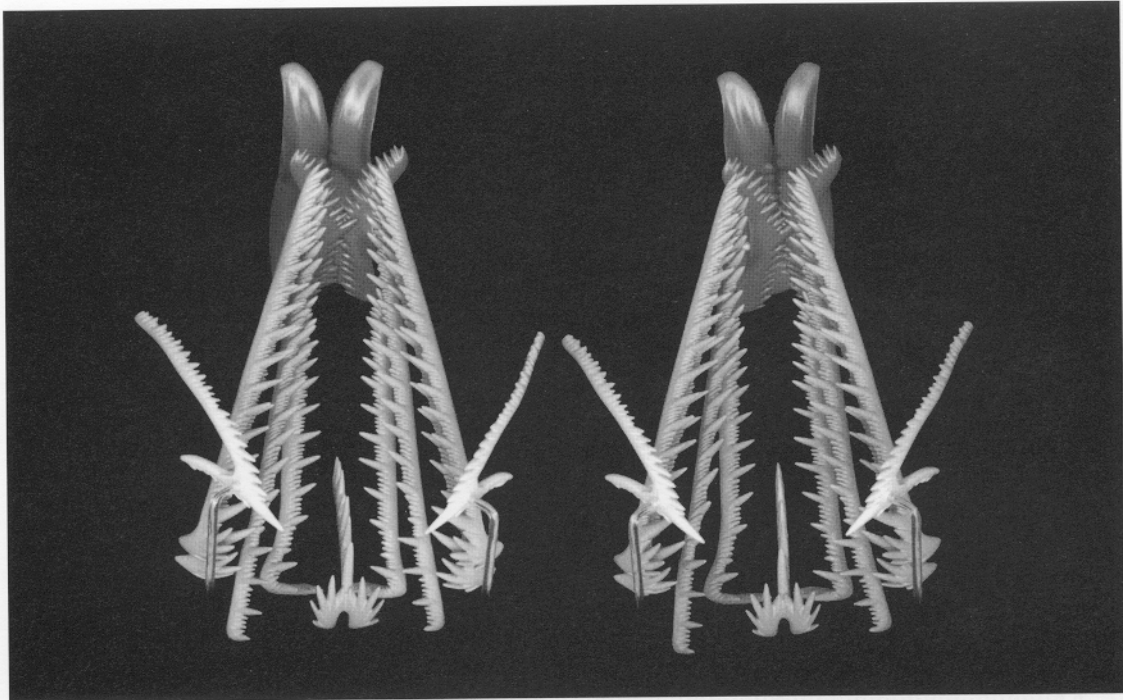
TEXT-FIG. 16. A, camera lucida drawing of *Adetognathus* specimen ROM 49956. Elements labelled X are not part of this apparatus. B, photograph of model taken from behind, left and above to simulate collapse pattern of ROM 49956; small cube indicates orientation of principal axes of apparatus relative to sea floor at time of collapse,  $x = 40^\circ$ ,  $y = 20^\circ$ ,  $z = 43^\circ$ .



TEXT-FIG. 17. Collapse orientations of ozarkodinid apparatuses determined according to the methods outlined in the text; inset at right shows conodont head with principal axes indicated. The orientations of the  $x$  and  $y$  axes indicate the pitch and roll of the apparatus; the orientation of the  $z$  axis (not shown on graph), reflects the angle of yaw and has no effect on collapse patterns. Points with numeric labels are specimens shown in Text-figures. For details of collections from which data are derived see text and Appendix. N. B. The original way up of specimens is generally not known and it is therefore impossible to distinguish between dorsal and ventral, and between left and right. *Idiognathodus* data include unpublished material currently housed at the University of Leicester; *Ozarkodina* data are fused cluster material except for CGM 1/10499 (Text-fig. 13); the 'other' category includes *Adetognathus* (Text-fig. 16), *Bispathodus* (Text-fig. 14), *Hemilistrana* (see Dzik 1991), and three fused clusters of *Polygnathus* (Nicoll 1985).  $n = 79$ .

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 per cent. of *Idiognathodus* assemblages reflect collapse angles in which  $x$  exceeded  $30^\circ$ , and in 51 per cent.  $x$  was more than  $45^\circ$ .

There are a number of possible explanations for  $x$  angles in excess of  $30^\circ$ : 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 conodont 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 1993). 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



TEXT-FIG. 18. Stereo-pair of model viewed from above front. The long axes of the posterior, P elements are vertical; that of the axial, anterior Sa element is horizontal.

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 of low density sediment. It is possible that the commonness of relatively high angles of collapse in *Idiognathodus* is due to the weight of the mineralized conodont apparatus or the action of the tail 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. An alternative hypothesis, that high angles of collapse result from death of conodonts within burrows, is contradicted by the lack of benthic fauna and bioturbation. Indeed, minimal bioturbation is one of the prerequisites for preserving articulated apparatuses.

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* (Text-fig. 17). We have only analysed 14 natural assemblages of *Gnathodus*, but nine of these (64 per cent.) are from early Namurian black shales from Hemer, Germany and they all exhibit collapse in which  $x$  is less than  $45^\circ$ , 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  $x$  axes were inclined at less than  $30^\circ$ , two having  $x$  axis inclinations close to zero. These angles are consistent with carcasses resting on the sea floor with little or no substrate penetration.



THE OZARKODINID SKELETAL PLAN, ELEMENT NOTATION, ORIENTATION,  
AND HOMOLOGIES*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 stabilized. Points of uncertainty and contention remain, however, and our architectural analysis goes some way to resolving these. From the taxonomic and stratigraphical 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 Upper Carboniferous, and it is reasonable to extrapolate from this that the apparatuses of ozarkodinid conodonts remained essentially unchanged throughout their stratigraphical range. One point that is worth addressing specifically is that of 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 are the Sc elements. The two Sb positions are occupied either by bipennate elements or modified digyrate elements; they are morphologically similar, and generally differ from one another only in the form and curvature of the process that in conventional terminology is considered anterior or outer lateral.

*Homologies and element notation*

*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 stabilize fully. 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 quadriramate element and should not be applied to ozarkodinids (Sweet 1988; Over 1992). This problem has arisen because Sweet (1981) recognized 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) realized 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 Sb<sub>1</sub>, Sb<sub>2</sub>, Sc<sub>1</sub>, and Sc<sub>2</sub>, as we have done throughout this paper (see also Aldridge *et al.* 1995, fig. 1). Over (1992) also suggested using the terms Sb<sub>1</sub> and Sb<sub>2</sub>, but we consider his Sb<sub>1</sub> element to be an Sb<sub>2</sub> 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 recognized 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 two Pa positions, two Pb positions, two M positions and nine S positions (from left to right Sc<sub>2</sub>, Sc<sub>1</sub>, Sb<sub>2</sub>, Sb<sub>1</sub>, Sa, Sb<sub>1</sub>, Sb<sub>2</sub>, Sc<sub>1</sub>, Sc<sub>2</sub>). 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 15 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).

*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 Late Devonian Gogo Formation of Western Australia (Nicoll 1977), an incomplete *Idioproniodus* from the lower Namurian of Germany (Schmidt and Müller 1964; Purnell and von Bitter 1996), 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 recognized 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).

*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 recognized 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 Sb<sub>2</sub> element of *Promissum*) anterior away from the axis. Despite the clear homologies between the S elements, Aldridge *et al.* (1995) labelled those of *Promissum* Sb<sub>1</sub>, Sd, Sb<sub>2</sub>, Sc rather than Sb<sub>1</sub>, Sb<sub>2</sub>, Sc<sub>1</sub>, Sc<sub>2</sub>. This was to avoid the terminological confusion of calling quadriramate elements Sb<sub>2</sub>, when they have been widely termed Sd in the literature. This solution reflects the difficulties of separating the locational from the morphological aspects of the P, M, S scheme, but does little to reduce confusion; the Sd element of *Promissum* is homologous with the Sb<sub>2</sub> in ozarkodinids, and the Sb<sub>2</sub> of *Promissum* is homologous with the ozarkodinid Sc<sub>1</sub>. 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 as to 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. comm. 1996; pers. obs.) provides some 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.

*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 realized for decades that the terms of orientation applied to conodont elements are entirely arbitrary and may have no relation to 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 been addressed recently 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.

*Homologies with panderodontids.* Apart from the apparatuses of conodonts characterized 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 locational notation for coniform conodonts, based on the spatial differentiation of the elements in their reconstructed apparatus. They recognized 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 recognized 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 from 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 illustrations of Sansom *et al.* (1994, fig. 6) and Smith *et al.* (1987, fig. 6.10). There are only three or four clusters and bedding plane assemblages from which to interpret 3D architecture, and although the Waukesha specimen is clearly the least distorted, no known assemblages are both complete and free of post-mortem disruption. With such a limited database, the possibility remains that with the discovery of more material, current architectural hypotheses will require some modification. It is interesting to speculate on the collapse pattern that would result from a slightly altered 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 Text-fig. 17). 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. This is clearly a somewhat speculative hypothesis, but it is supported by the evidence that many natural assemblages which preserve bilateral symmetry reflect collapse orientations with high angles of  $x$  (e.g. Text-fig. 2–3, and see Text-fig. 17).

*Architectural conservatism in conodonts and a standardized 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 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 these authors 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 was rather more conservative architecturally than current hypotheses suggest.

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MARK A. PURNELL

Department of Geology  
University of Leicester  
Leicester LE1 7RH, UK  
e-mail map2@le.ac.uk

PHILIP C. J. DONOGHUE

School of Earth Sciences  
University of Birmingham  
Birmingham B15 2TT, UK  
e-mail p.c.j.donoghue@bham.ac.uk

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#### 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 that 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, above and behind' for example, could also be 'oblique lateral collapse from side, below and in front').

*Hinde, 1879.* Devonian, Genesee Shale, New York, USA; specimens BM A-4035, A-4036, actually part and counterpart (Aldridge 1987; pers. obs). Large faecal association, no primary architecture preserved, more than one individual, more than one species. Figured by Huddle (1972).

*Schmidt 1934.* Lower Namurian, Hemer, Nordrhein-Westfalen, Germany; seven assemblages of *Gnathodus* illustrated: fig. 1 disarticulated, ?incomplete; fig. 2 disarticulated; fig. 3 and pl. 6, fig. 3, oblique collapse from above and behind (cf. Pl. 3, Text-fig. 14, but more posterior,  $x = 27^\circ$ ,  $y = 59^\circ$ ,  $z = 14^\circ$ ); fig. 4, partial, articulated S and M array; fig. 5a-b and pl. 6, fig. 1, oblique axial collapse (see Text-figs 7-8; reillustrated by Aldridge *et al.* 1987, fig. 4.6A); fig. 6, disarticulated; fig. 7 and pl. 6, fig. 2, disarticulated, two individuals. All material lost in World War II.

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

*Jones 1935.* Pennsylvanian, Nowata Shale, Oklahoma, USA; unpublished thesis collection of > 50 assemblages, 17 described and illustrated, six of which are ozarkodinid. Plate 5, large faecal assemblage, more than one 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 2-5, 9A, c).

*Kraemer 1940.* Namurian, Arnsberg, Germany; figured partial and/or scattered individual apparatuses and accumulations of more than one individual, little if any trace of primary architecture [Note: some of Schmidt's material was found by Kraemer].

*Scott 1942.* Mississippian, Heath Formation, Montana, USA; collection of c. 180 assemblages, 32 figured; most are incomplete, or disrupted and chaotic; some are remains of more than one individual (e.g. pl. 37, fig. 6), only a few retain traces of primary architecture (e.g. pl. 38, fig. 10). Plate 37, figure 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 and 11 are part and counterpart), mostly *Idiognathodus*, a few *Idioproniodus* (prioniodinid). Plate 25, figures 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 more than one individual; figs 3 and 11, UI X-6363, lateral collapse from side and slightly posterior,  $x = 29^\circ$ ,  $y = 3^\circ$ ,  $z = 61^\circ$  (cf. Text-figs 4-5; a little more posterior than Purnell and Donoghue 1997, figs 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 Text-figs 2-3); fig. 5 (specimen lost), oblique lateral collapse from side and behind,  $x = 67^\circ$ ,  $y = 10^\circ$ ,  $z = 21^\circ$  (cf. Purnell and Donoghue 1997, figs 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. Text-figs 4-5, 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. Purnell and Donoghue 1997, figs 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 Text-figs 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; Purnell and Donoghue 1997, figs 2-3); fig. 17, UI X-6374, lateral collapse from side and slightly behind,  $x = 32^\circ$ ,  $y = 12^\circ$ ,  $z = 55^\circ$  (cf. Purnell and Donoghue 1997 figs 4-5); fig. 21, UI X-6377, lateral collapse from side and slightly behind,  $x = 43^\circ$ ,  $y = 4^\circ$ ,  $z = 47^\circ$  (see Text-figs 4-5; 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 two individuals.
- Rhodes 1952. Pennsylvanian, Illinois and Kentucky, USA; studied > 100 bedding plane assemblages of *Idiognathodus*, *Gondolella* (prioniodinid), and *Idioproniodus* (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. Text-figs 15–16; refigured by Avcin 1974, pl. 1, fig. 10); fig. 11, refigured UI X-1480 (Du Bois 1943, pl. 25, fig. 14). The remains of *Idioproniodus* 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 *Idiognathodus* restudied as part of this investigation.
- Schmidt and Müller 1964. Lower Namurian, Hemer, Nordrhein-Westfalen, Germany; > 50 bedding plane assemblages, seven prepared by acid dissolution of elements followed by rubber casting, and illustrated by line drawings; figured specimens are remains of single *Gnathodus* apparatuses except: fig. 9, IMGP Gö 600–17, disarticulated, faecal, elements from one or two *Gnathodus* apparatuses and an *Idioproniodus* (prioniodinid), fig. 10, IMGP Gö 600–16, partial apparatus of *Idioproniodus*. 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  $Sb_1$  elements backwards); fig. 6, IMGP Gö 600–23, lateral collapse,  $x = 37^\circ$ ,  $y = 1^\circ$ ,  $z = 53^\circ$  (cf. Text-figs 4–5; 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 Text-figs 9–10; 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; two partial fused clusters of *Ozarkodina*, one Pa element pair, one Pb pair.
- Lange 1968. Upper Devonian, Rheinisches Schiefergebirge, Germany; collection of c. 70 clusters, five figured; fig. 1, partial prioniodinid cluster; fig. 2, 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 two 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. Purnell and Donoghue 1997, figs 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. Purnell and Donoghue 1997, figs 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. Purnell and Donoghue 1997, figs 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 Text-figs 12–13; reillustrated by Dzik 1976, fig. 10c; Barskov and Alekseev 1986, p. 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; 1989, fig. 1.6; 1990, figs 25–26; Purnell 1993b, 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 more than one *Adetognathus*, one retaining some primary architecture (also figured by Conway Morris 1985, pl. 2, fig. 2, 1990, figs 16, 18).
- Avcin 1974*. Pennsylvanian, Illinois, USA; unpublished thesis, re-examined Du Bois (1943) and Rhodes (1952) collections, plus c. 300 new assemblages from Bailey Falls locality, c. 200 from other localities. c. 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. Purnell and Donoghue 1997, figs 8–9; 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. Purnell and Donoghue 1997, figs 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. Purnell and Donoghue 1997, figs 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–B, 14A–B, 15A–B, reillustrated UI X-1505, UI X-1506, UI X-1507, UI X-1508, UI X-1503, UI X-1504 (Rhodes 1952, pl. 129, figs 8–13); fig. 16, reillustration of Assemblages 2 of Jones (1938).
- Norby 1976*. Mississippian, Heath and Tyler formations, Montana, USA; unpublished thesis collection of c. 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. Purnell and Donoghue 1997, figs 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. Text-figs 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. Pl. 3, Text-fig. 14); 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. Purnell and Donoghue 1997, figs 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, three or four apparatuses of *L. commutata*, possibly faecal, but some apparatuses retain architectural information (e.g. uppermost apparatus, oblique lateral collapse, only slightly disarticulated,  $x =$



32°,  $y = 10^\circ$ ,  $z = 57^\circ$ ); pl. 14, fig. 4, ISGS 62P-205A, *L. commutata*, faecal, no primary architecture; pl. 14, fig. 5, ISGS 62P-206A, *L. commutata*, faecal, two 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 below,  $x = 29^\circ$ ,  $y = 6^\circ$ ,  $z = 60^\circ$  (cf. Text-figs 12–13); pl. 14, fig. 9, ISGS 62P-210, *L. commutata*, oblique collapse from behind, above and to one side (cf. Text-figs 15–16); pl. 19, fig. 1, ISGS 62P-701A, *Vogelgnathus campbelli*, disarticulated, no primary architecture, ?incomplete (less than nine 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 2–5, 9A, c, refigured assemblage 12 of Burnley (1938), incomplete, disrupted, no primary architecture; figs 6–8, 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).

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

Müller 1978. Fig. 12, reillustrated IMG P Gö 600–12 (Schmidt and Müller 1964, fig. 1).

Ramovš 1978. Middle Triassic, central Slovenia; 92 incomplete fused clusters of *Pseudofurnishius* (prioniodinid), several preserving primary architectural information (some refigured from Ramovš 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 Text-figs 15–16); refigured by Dzik 1991.

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

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

Mietto 1982. Triassic, Trento, north-eastern Italy; partial fused cluster (Pa pair), *Budurovignathus* (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–C, 3A–B, IGSE 13821 and 13822, apparatus of *Clydagnathus windsorensis* in head of conodont animal, preservation of apparatus (particularly position of Sb, probably Sb<sub>2</sub> elements, between Sc elements of sinistral and dextral sides, and position of M element) indicates oblique lateral collapse at c. 45° from axial plane of apparatus,  $x = 3^\circ$ ,  $y = 43^\circ$ ,  $z = 47^\circ$  (cf. Purnell and Donoghue 1997, figs 8–9). 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. Pl. 2, Text-fig. 11; 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 IMG P 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 two 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 two or three S and M elements; figs 4A–I, 9B, CPC25171–CPC25179, CPC25202, are partial clusters of two or three P elements; Fig. 3A, CPC25165, S and M array, lateral collapse from side and very slightly above,  $x = 15^\circ$ ,  $y = 21^\circ$ ,  $z = 64^\circ$  (cf. Pl. 2, Text-fig. 11; P and  $Sb_1$  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. Pl. 2, Text-fig. 11; 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,  $x = 84^\circ$ ,  $y = 4^\circ$ ,  $z = 5^\circ$ ; figs. 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 more than one 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), *Mesogondolella*.

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. Text-figs 15–16; refigured by Aldridge *et al.* 1987, fig. 4.3; Smith 1987, fig. 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, *Clydagnathus windsorensis*, probable oblique lateral collapse.

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

Zhang and Zhang 1986. Upper Permian, central Fujian Province, China; partial cluster of 'neohindeodelliform' S elements.

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 Text-figs 15–16). 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, fig. 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–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, three 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. Purnell and Donoghue 1997, figs 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. Pl. 9.1, figs 1–4, 7, refigured ISGS 62P-603, 62P-605, 62P604, 62P715, 62P16A (Norby 1976, pl. 10, figs 1–5); 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. Fig. 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–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–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 (Conway Morris 1985, pl. 2, fig. 2); 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. 7); 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); fig. 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, fig. 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; four, 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. Pl. 1, Text-fig. 6, 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 Sb<sub>1</sub>, Sc, Sc), lateral collapse from side and slightly behind (cf. Text-figs 4–5).

Purnell 1993a. Fig. 2, BU 2183, bedding plane assemblage of *Idiognathodus* from Pennsylvanian, McLeansboro Group, Bailey Falls, Illinois, USA; oblique lateral collapse from side, behind and above (cf. Text-figs 15–16, 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 Text-figs 2–3 and Text-figs 15–16; 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. Purnell and Donoghue 1997, figs 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 Sb<sub>1</sub>, 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 1993a*, fig. 2); fig. 2B, *Gnathodus bilineatus* (from *Norby 1976*, thesis collection), some post-mortem disruption, oblique lateral collapse from side, above and behind (cf. Text-figs 15–16).

*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, c. 30 thought by authors to preserve primary architecture, none figured, but collapse patterns probably consistent with our model (pers. obs.; cf. *Weddige and Hüsken*).

*Orchard 1996*: Upper Devonian, British Columbia, Canada; fig. 7.4, partial cluster (fused Pa pair) of *Palmatolepis*, partial cluster (fused Pb pair) of ?*Polygnathus*, partial cluster of indeterminate S elements.

*Purnell and Donoghue 1997*. Pennsylvanian, McLeansboro Group, Bailey Falls, Illinois, USA; Natural assemblages of *Idiognathodus*: figs 2, 3a, reillustrated UI X-1480 (*Du Bois 1943*, pl. 25, fig. 14); figs 4, 5a, PM X 2217, lateral collapse from side and slightly below ( $x = 0^\circ$ ,  $y = 8^\circ$ ,  $z = 82^\circ$ ); figs 6, 7a, PM X 2218, collapse from behind, left and slightly below ( $x = 67^\circ$ ,  $y = 14^\circ$ ,  $z = 18^\circ$ ); figs 8, 9A, PM X 2219, collapse from above, right, and slightly behind ( $x = 12^\circ$ ,  $y = 43^\circ$ ,  $z = 44^\circ$ ).