Architecture and functional morphology of the skeletal apparatus of ozarkodinid conodonts

MARK A. PURNELL AND PHILIP C. J. DONOGHUE†

Department of Geology, University of Leicester, Leicester LE1 7RH, UK (`map2@le.ac.uk`)

CONTENTS

SUMMARY

Ozarkodinid conodonts were one of the most successful groups of agnathan vertebrates. Only the oropharyngeal feeding apparatus of conodonts was mineralized, and the skeletal elements were generally disarticulated on the death and decay of the body. Occasionally, however, they were preserved in association as 'natural assemblages', fossilized *in situ* after post-mortem collapse of the apparatus. From analysis of element arrangement in natural assemblages of *Idiognathodus* from the Pennsylvanian of Illinois we have produced a precise scale model of the feeding apparatus of ozarkodinid conodonts. At the front lay an axial Sa element, flanked by two groups of four close-set elongate Sb and Sc elements which were inclined obliquely inwards and forwards; above these elements lay a pair of arched and inward pointing M elements. Behind the S–M array lay transversely oriented and bilaterally opposed Pb and Pa elements.

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

1. INTRODUCTION

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

Recent work has established that many conodonts, including some primitive taxa with coniform elements, were macrophagous, probably predatory organisms, and that those conodonts with more complex apparatuses used their phosphatic elements to grasp (Briggs *et al.* 1983), slice and crush their food (Purnell & von Bitter 1992; Purnell 1995). The strongest evidence for these conclusions comes from microwear analyses of surface features on conodont elements (Purnell 1995), but this study, and all rigorous analysis of conodont functional morphology, relies to some extent on a sound understanding of the arrangement of the elements in the conodont apparatus.

---

† Present address: School of Earth Sciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK (`p.c.j.donoghue@bham.ac.uk`).

Phil. Trans. R. Soc. Lond. B (1997) **352**, 1545–1564
Printed in Great Britain

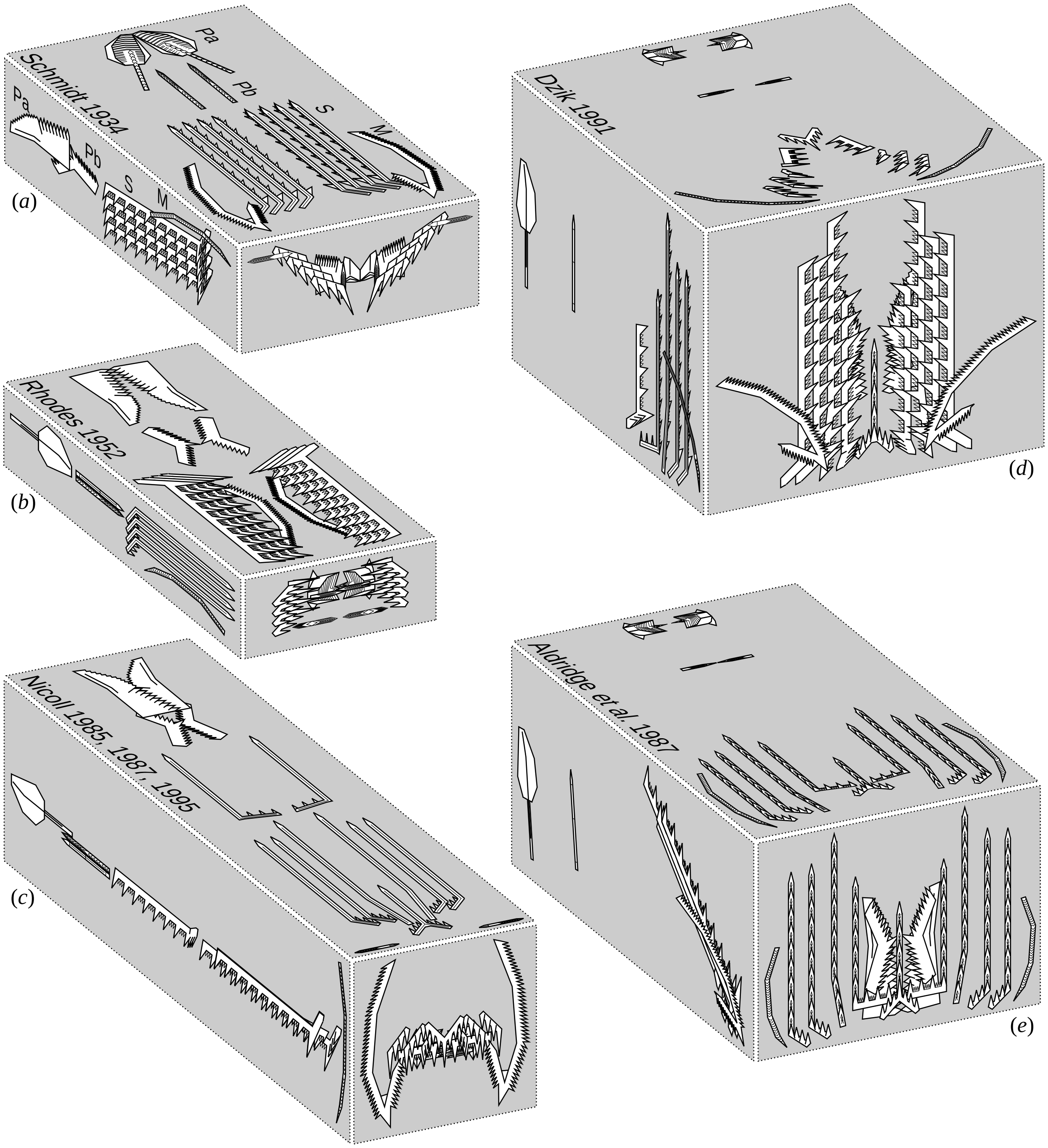

Figure 1. Hypotheses of element arrangement in ozarkodinid conodonts. Front, side and top views of the apparatus are projected onto the sides of each box; element morphology is diagrammatic, but based on *Idiognathodus*; (*a*) also shows P, M, S element notation used in the text. (*a*) Linear arrangement 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 & 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.

The development of ideas about conodont skeletal architecture (see figure 1) has closely paralleled hypotheses of biological affinity and functional morphology (see Aldridge (1987) for a review). Understanding of architecture underpins analysis of function, but many studies (e.g. Schmidt 1934; Lindström 1964, 1973, 1974; Nicoll 1995) have confused the two by using scenarios of function to construct and constrain models of element arrangement. This lack of methodological rigour has contributed to the diversity of alternative models of skeletal arrangement that have been proposed, some of which are little more than pure speculation (see § 2 below). Part of the blame, however, also lies in a paucity of good fossil material and a consequent lack of morphological constraint. Until the fossilized remains of the conodont body were found it was not possible to determine anterior–posterior and dorso–ventral axes with certainty, but the fossils that provide the means to unravelling the primary, *in vivo* spatial arrangement of conodont elements were first described more than 60 years ago (Schmidt 1934; Scott 1934).

These fossils preserve together numbers of different conodont elements, either as associations on bedding planes or as clusters of elements fused together by diagenetic minerals. Some of these element associations are faecal or disarticulated accumulations that preserve little or nothing of primary skeletal architecture, but the remaining 'natural assemblages' represent collapse of the three-dimensional oropharyngeal apparatus onto a two dimensional bedding plane. Different patterns of element arrangement in natural assemblages therefore represent different orientations of apparatus collapse, the limited number of recurring patterns reflecting the attitude of the dead conodont on the sea floor (cf. Dzik 1986). A conodont carcass lying on its belly produced one characteristic pattern (figures 2 and 3), lying on its side another (figures 4 and 5) and lying head down (or up) in the sediment produced yet another (figures 6 and 7). All these orientations of collapse are possible, as are all the intermediate orientations, but they are not all equally likely, and the majority of natural assemblages reflect collapses in which the conodont carcass lay in an orientation somewhere between those illustrated (see Purnell & Donoghue (1998) for a more detailed discussion of natural assemblage collapse orientations).

Compared to normal collections of disjunct conodont elements, natural assemblages are extremely rare, but despite this they are of paramount importance in conodont palaeontology. They serve as references in the development of conodont taxonomy and anatomical notation, and provide templates for reconstructing the apparatuses of the vast majority of taxa that are known only from dissociated remains. They are also fundamental in the recognition of homologies between taxa and in the interpretation of evolutionary pathways (Purnell & Donoghue 1998). Conodonts have no close living relatives, and without homologous structures in extant organisms to aid interpretation, analysis of natural assemblages is the only rigorous method of reconstructing the original spatial arrangement of conodont elements in the feeding apparatus.

2. ARCHITECTURAL RECONSTRUCTIONS OF THE CONODONT APPARATUS

Recent classifications of conodonts recognize up to seven orders (Sweet 1988; Dzik 1991; Aldridge & Smith 1993). Four have apparatuses composed of morphologically simple elements, and the architecture of some of these, including taxa assigned by Sweet (1988) to the orders Bellodellida and Panderodontida, has recently been reviewed by Sansom *et al.* (1994). Of the three orders characterized by more complex element morphology, the architecture of prioniodontids was addressed by Aldridge *et al.* (1995) and an analysis of prioniodinid apparatuses is in preparation (Purnell & von Bitter 1996). The third order, the Ozarkodinida (*sensu* Sweet 1988), is the focus of this paper. Representatives of this group dominate conodont faunas through most of the Palaeozoic, in terms of both abundance and diversity, and most bedding plane assemblages and clusters are ozarkodinids. Almost all attempts at reconstructing the conodont apparatus have therefore dealt primarily with ozarkodinid taxa.

With few exceptions (e.g. Lindström 1964, 1973, 1974; Nicoll 1995), most analyses of conodont apparatus arrangement have been based on bedding plane assemblages and clusters which are thought to retain something of the original spatial relationships of the elements. These analyses have conformed to two distinct methodologies. Both recognize that the extremely rare natural assemblages with bilaterally symmetrical arrangements of elements (e.g. figures 2 and 3) record primary architectural information, but they differ in the way they treat asymmetric assemblages (e.g. figures 4–9). Most analyses (e.g. figure 1*a*–*c*) have assumed that deviations from symmetry reflect post-mortem movement of the elements with recurrent asymmetric patterns produced by rotations and translations of elements by compression and decomposition or by systematic muscle relaxation–contraction effects (see Aldridge (1987) and Purnell & Donoghue (1998) for a review).

This need to invoke ad hoc post-mortem effects represents a significant weakness in this approach but several authors realized that different apparatus patterns reflected different orientations of collapse of the original three-dimensional structure. For example, based on an interpretation that their collections contained only a few more laterally than dorsoventrally collapsed apparatuses, Schmidt & 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 he 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*).

Observations such as these paved the way for a more rigorous approach to reconstructing apparatus architecture. This methodology differs from that outlined above in that its aim is to produce a single model of apparatus architecture that can account for a variety of natural assemblage patterns without recourse to ad hoc hypotheses of post-mortem muscle relaxation and contraction. Norby (1976, 1979), for example, realized the difficulties of producing asymmetric assemblage patterns from a linear model of element arrangement, and suggested that the elements

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

in the apparatus may have been oriented side by side, with their long axes vertical. Dzik (1976) noted that the natural assemblages illustrated by Rhodes (1952, plate 126, figure 11; figures 2 and 3 herein) and Mashkova (1972, plate 1) were dorso-ventrally and laterally flattened, respectively, and proposed a similar arrangement of elements with their long axes vertical and cusps opposed across the midline of the apparatus as the only one that could account for both assemblage patterns. Dzik's later hypothesis of skeletal architecture (1986, 1991, also discussed in Dzik 1994) modified his earlier arrangement a little in order to account better for observed natural assemblage patterns; his 1991 model is illustrated in figure 1*d* and is discussed in more detail below (§ 3).

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

3. PROBLEMS, MATERIALS AND METHODS

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

Aldridge *et al.* (1987), and later Dzik (1991), identified many of the important general features of ozarkodinid architecture, such as the orientation of the P elements, and the anterior–posterior spatial differentiation within the apparatus. The overall pattern of element arrangement and orientation in the model of Aldridge *et al.* (1987) corresponds well with natural assemblage patterns, but these authors were also aware of a number of limitations. They noted that, in the model, the elements were more widely spaced than in nature, and that 'details of the model, especially the relative positions of the ramiform elements, remain to be refined. In particular, the M elements [in natural assemblages] commonly display an independence from the S elements, suggesting that

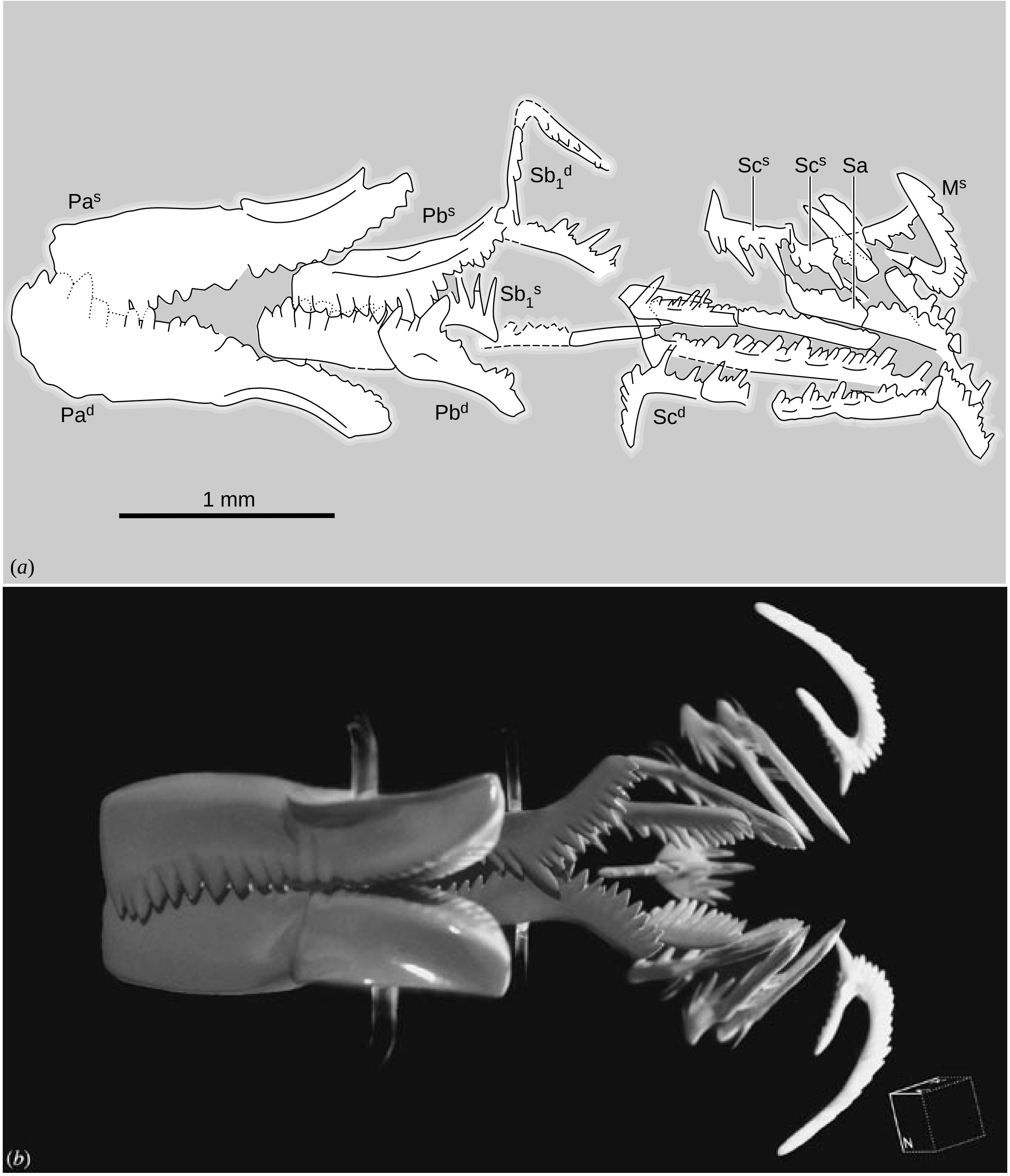

Figure 3. (*a*) Composite camera lucida drawing of specimen UI X-1480, counterpart and part (counterpart on bottom). (*b*) Photograph of model taken from above, behind and slightly to the left to simulate collapse pattern of UI X-1480; small cube indicates orientation of principal axes of apparatus relative to sea floor at time of collapse, $x = 59°$, $y = 30°$, $z = 8°$. Du Bois (1943, plate 25, fig. 4) figured another *Idiognathodus* assemblage exhibiting a similar pattern of element arrangement, but reflecting a slightly more posterior angle of collapse ($x = 71°$, $y = 17°$, $z = 9°$).

they may have been operated by different muscles' (p. 74). Dzik (1991, p. 274) also pointed out that the orientation of the S elements in this model, with their cusps directed anteriorly, was 'a poor fit with natural assemblages'; in particular, it is difficult to account for the consistent inward inclination of S element denticles in assemblages approaching dorso-ventral collapse orientations (e.g. figures 2 and 3*a*). Dzik's own model (figure 1*d*), however, is not without its problems: the vertical orientation of the S elements is not matched by lateral or oblique lateral collapse patterns (e.g. figures 4, 5*a*, 8 and 9*a*), and his hypoth-

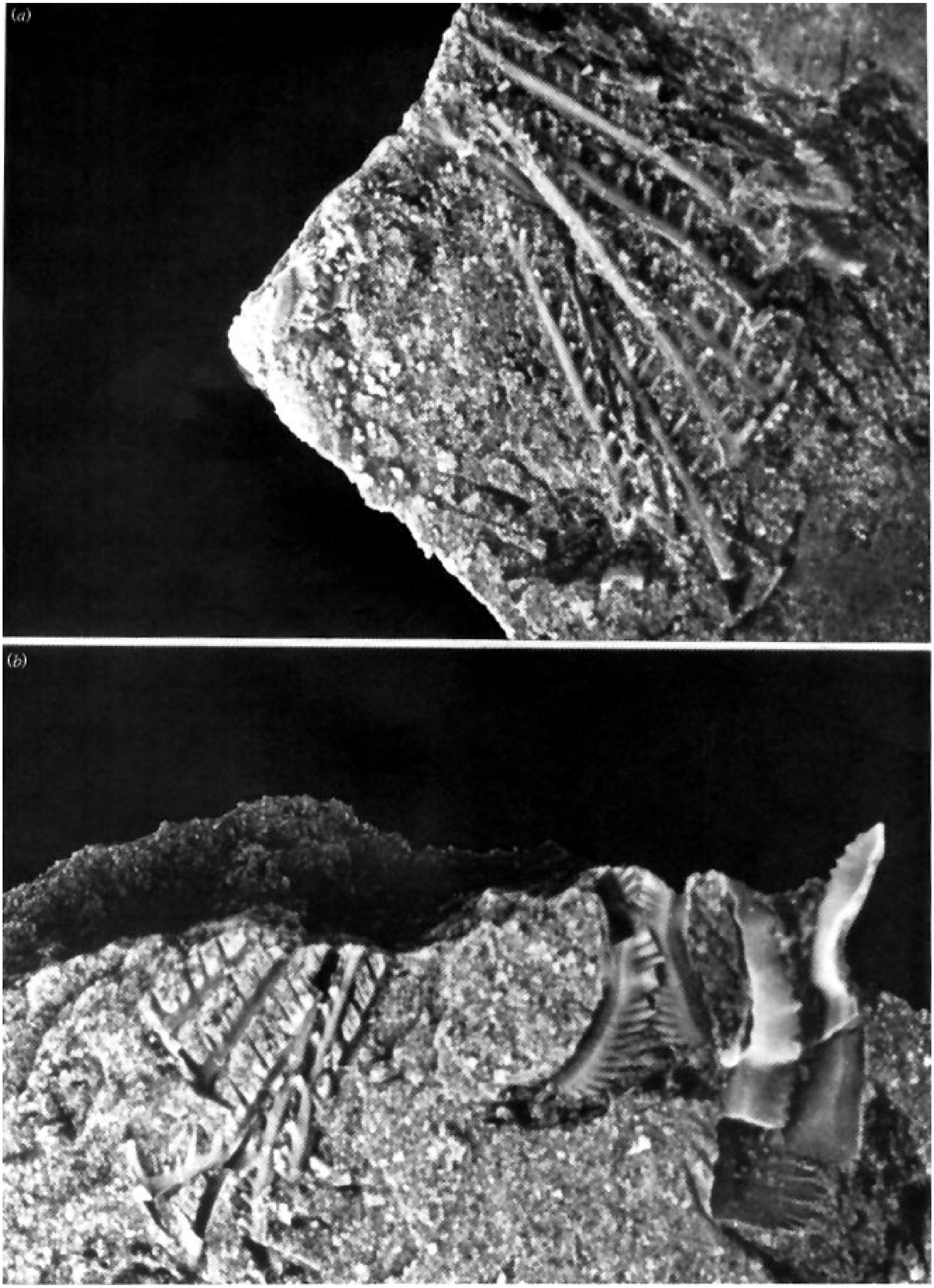

Figure 4. Natural assemblage of *Idiognathodus* from the Pennsylvanian Modesto Formation, Bailey Falls, Illinois, USA; Natural History Museum specimen PM X 2217. (*a*) Part; (*b*) counterpart; see figure 5*a* for scale.

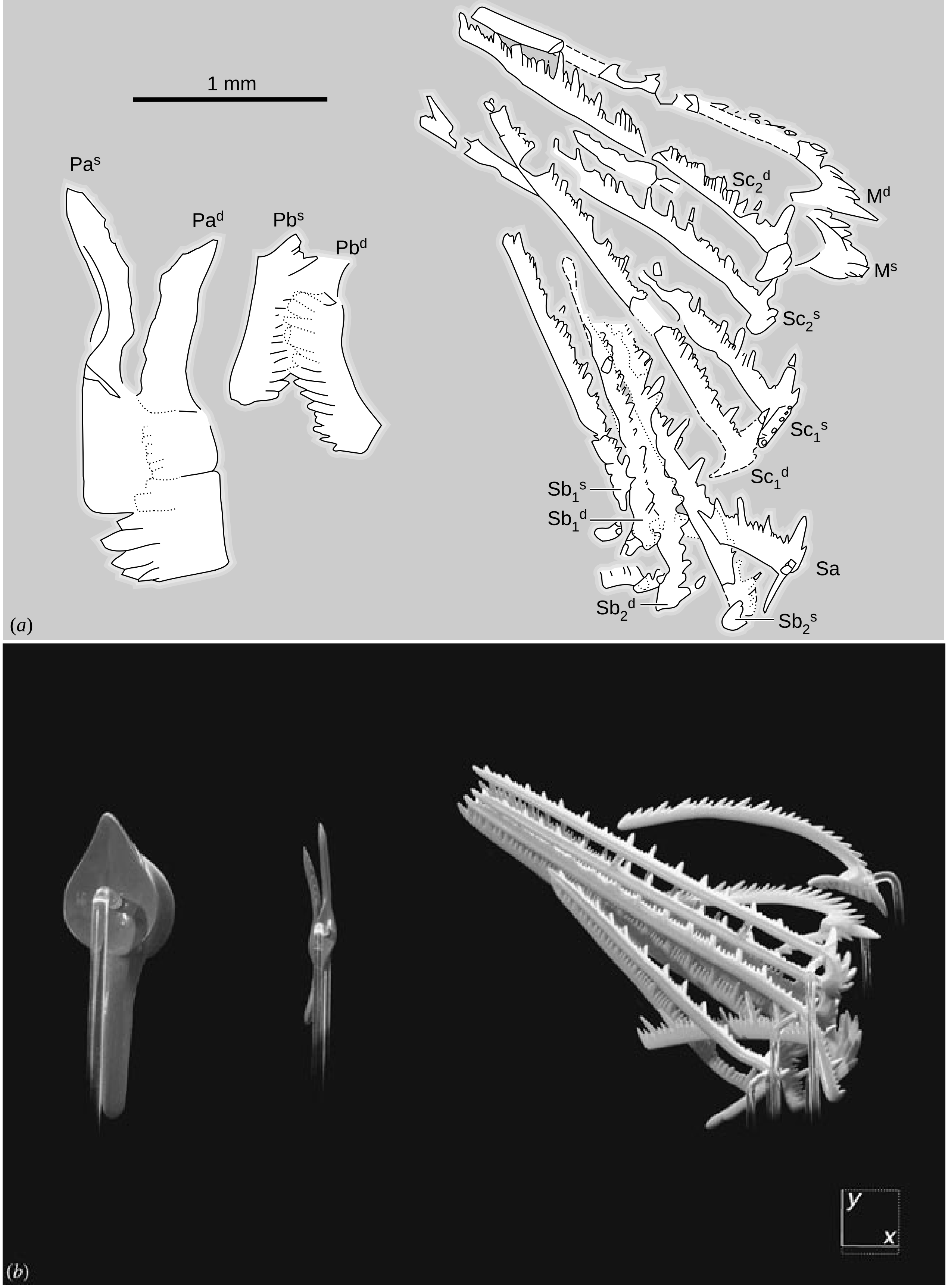

Figure 5. (*a*) Composite camera lucida drawing of specimen PM X 2217, counterpart and part (counterpart on bottom). (*b*) Photograph of model taken from the right side and slightly below to simulate collapse pattern of PM X 2217; small cube indicates orientation of principal axes of apparatus relative to sea floor at time of collapse, $x = 0^\circ$, $y = 8^\circ$, $z = 82^\circ$. *Idiognathodus* assemblages with a similar pattern of element arrangement, reflecting similar collapse orientation, have been figured by Du Bois (1943, plate 25, fig. 17; plate 25, fig. 3 and 11, a slightly more posterior collapse, $x = 29^\circ$, $y = 3^\circ$, $z = 61^\circ$) and Avcin (1974, plate 2, fig. 12).

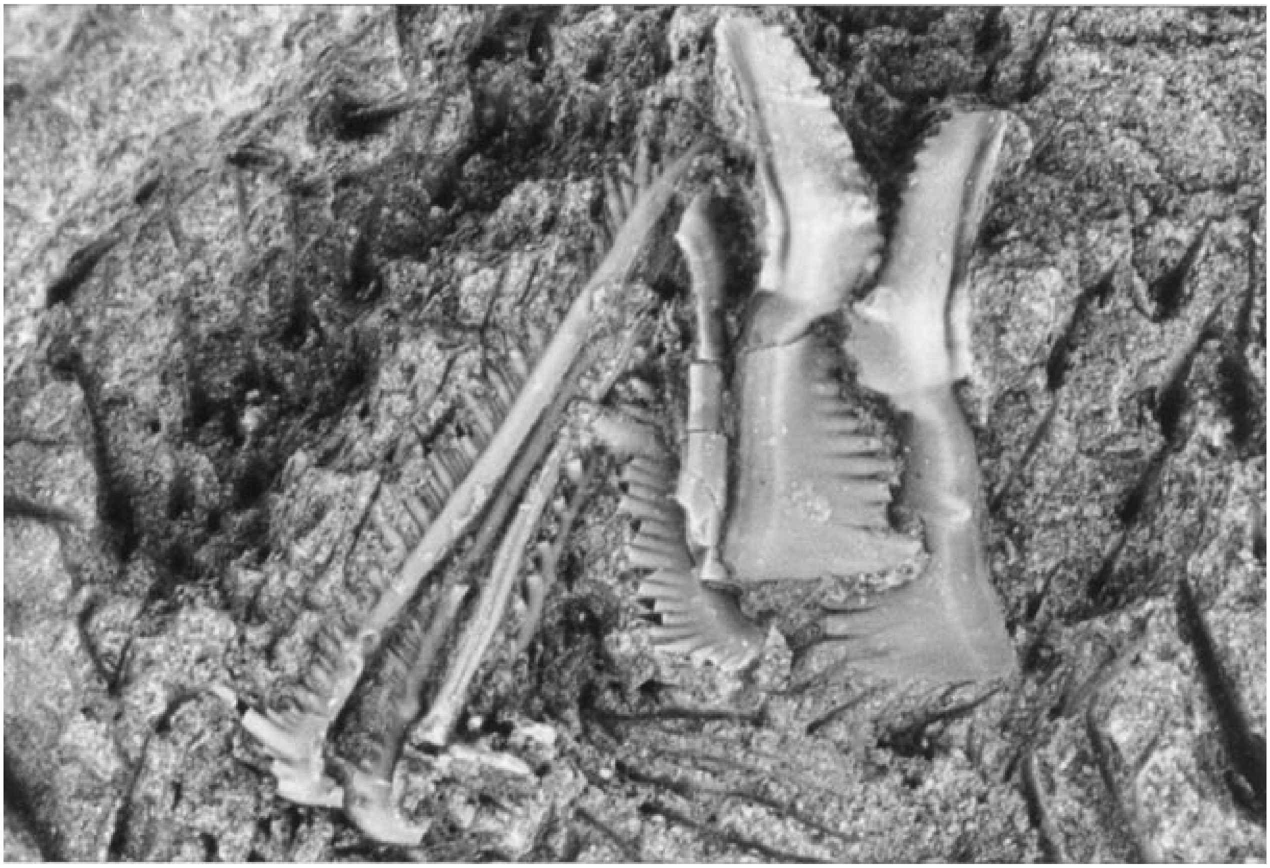

Figure 6. Natural assemblage of *Idiognathodus* from the Pennsylvanian Modesto Formation, Bailey Falls, Illinois, USA; Natural History Museum specimen PM X 2218. P elements and four S elements are preserved on the part; no counterpart. See figure 7*a* for scale.

esis 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.

Natural assemblages of *Idiognathodus* (*sensu* Baeseman 1973; Grayson *et al.* 1991) outnumber those of all other taxa, and the morphology of all the elements of its apparatus is well known (see, for example, Grayson *et al.* 1991). Our architectural reconstruction is, therefore, based on *Idiognathodus.* We have re-examined all significant collections of *Idiognathodus* bedding plane assemblages, including the material of Du Bois (1943), Rhodes (1952), Avcin (1974), Aldridge *et al.* (1987) and Purnell (1993), and new or unpublished material from Bailey Falls and Wolf Covered Bridge in Illinois, USA (see Purnell (1994) for stratigraphic and locality details).

In order to produce the most accurate reconstruction possible, we used regressions derived from measurements of *Idiognathodus* bedding plane assemblages (Purnell 1993, 1994) to calculate the size of elements in an apparatus with Pa elements 2 mm long, and produced 1:50 scale models of all of the elements. The configuration of the elements in the model was determined using a combination of physical modelling and photographic techniques (Briggs & Williams 1981; Aldridge *et al.* 1987, 1995), with final testing achieved by using photographs of the model to simulate patterns of element collapse in natural assemblages. The results of this testing are reproduced here as figures 3, 5, 7 and 9. Due to the limitations of page space, the assemblages and simulated collapse patterns illustrated are just examples which demonstrate the range of patterns observed in *Idiognathodus.* We also include a stereo pair (figure 10) and an anterior view (figure 11) of our model to illustrate details of the apparatus not evident in other photographs.

4. THE ARCHITECTURE OF *IDIOGNATHODUS*

The basic constraints on apparatus orientation are derived from the Scottish Carboniferous animal fossils. These indicate unequivocally that the S and M elements were at the front of the apparatus and that the posterior P elements were oriented with their long axes normal to the long axis of the conodont body (Aldridge *et al.* 1987). Dorsal and ventral have been difficult to determine with certainty (Aldridge *et al.* 1987), but recognition of cartilaginous eye capsules, possible otic structures, and an equivocal dorsal nerve cord (Aldridge *et al.* 1993) all

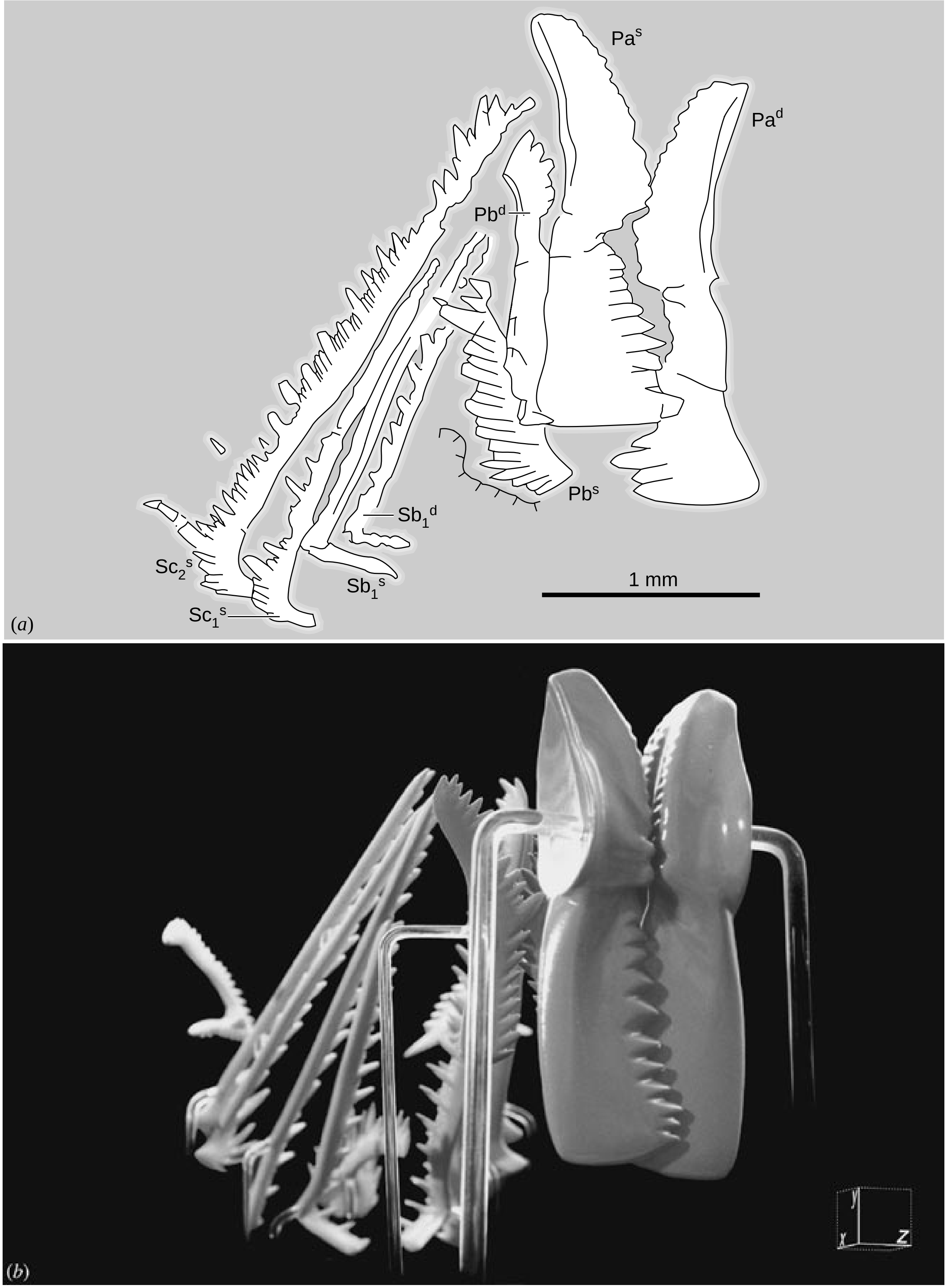

Figure 7. (*a*) Camera lucida drawing of specimen PM X 2218. (*b*) Photograph of model taken from behind, left and slightly below to simulate collapse pattern of PM X 2218; small cube indicates orientation of principal axes of apparatus relative to sea floor at time of collapse, $x = 67°$, $y = 14°$, $z = 18°$. Similar *Idiognathodus* assemblages have been figured by Du Bois (1943, plate 25, fig. 5, $x = 67°$, $y = 10°$, $z = 21°$; fig. 13, $x = 64°$, $y = 5°$, $z = 26°$) and Avcin (1974, plate 2, fig. 19, $x = 71°$, $y = 9°$, $z = 17°$, re-illustrated by Aldridge *et al.* (1987), fig. 4.4).

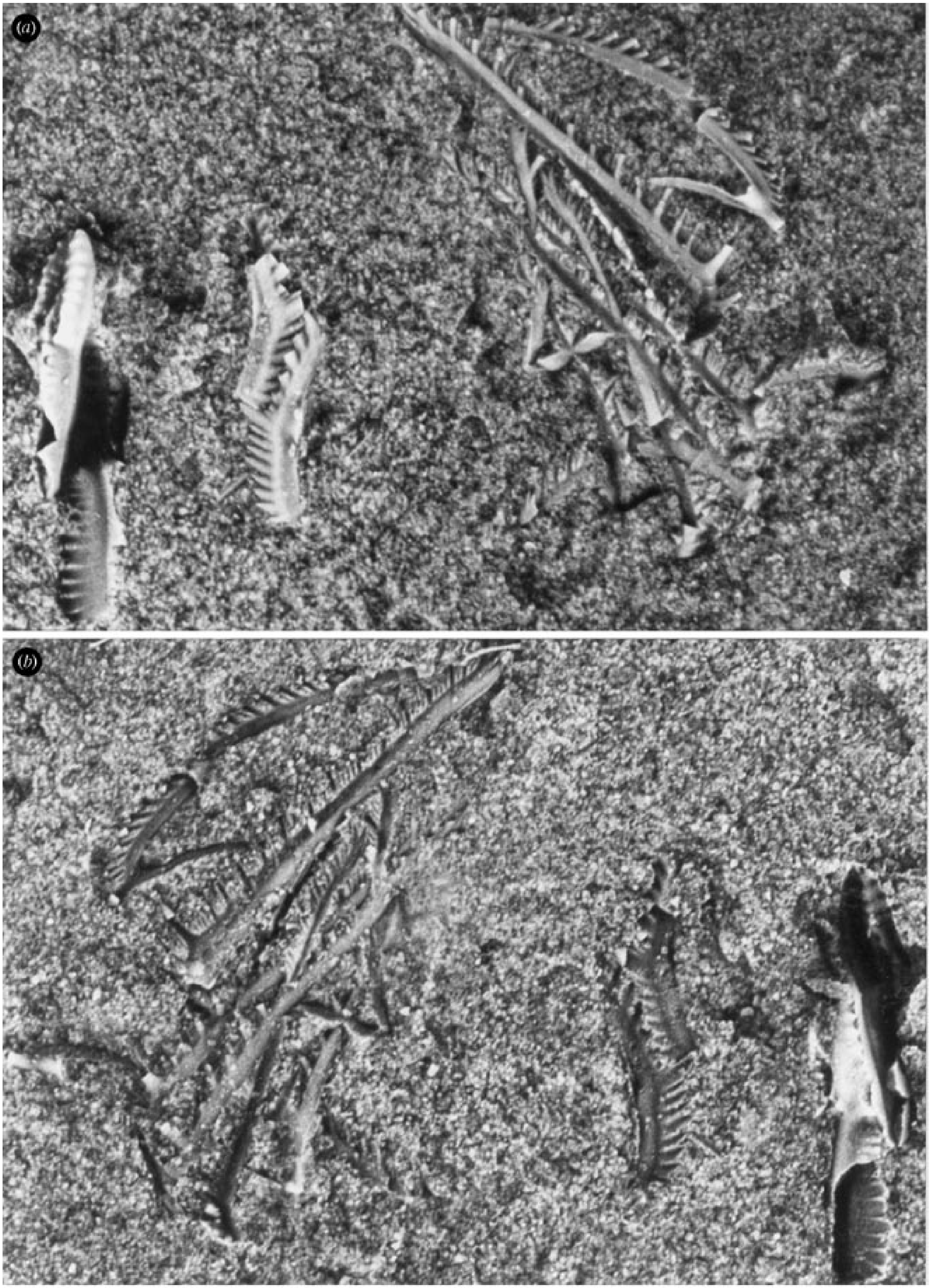

Figure 8. Natural assemblage of *Idiognathodus* from the Pennsylvanian Modesto Formation, Bailey Falls, Illinois, USA; Natural History Museum specimen PM X 2219. (*a*) Part; (*b*) counterpart; see figure 9*a* for scale.

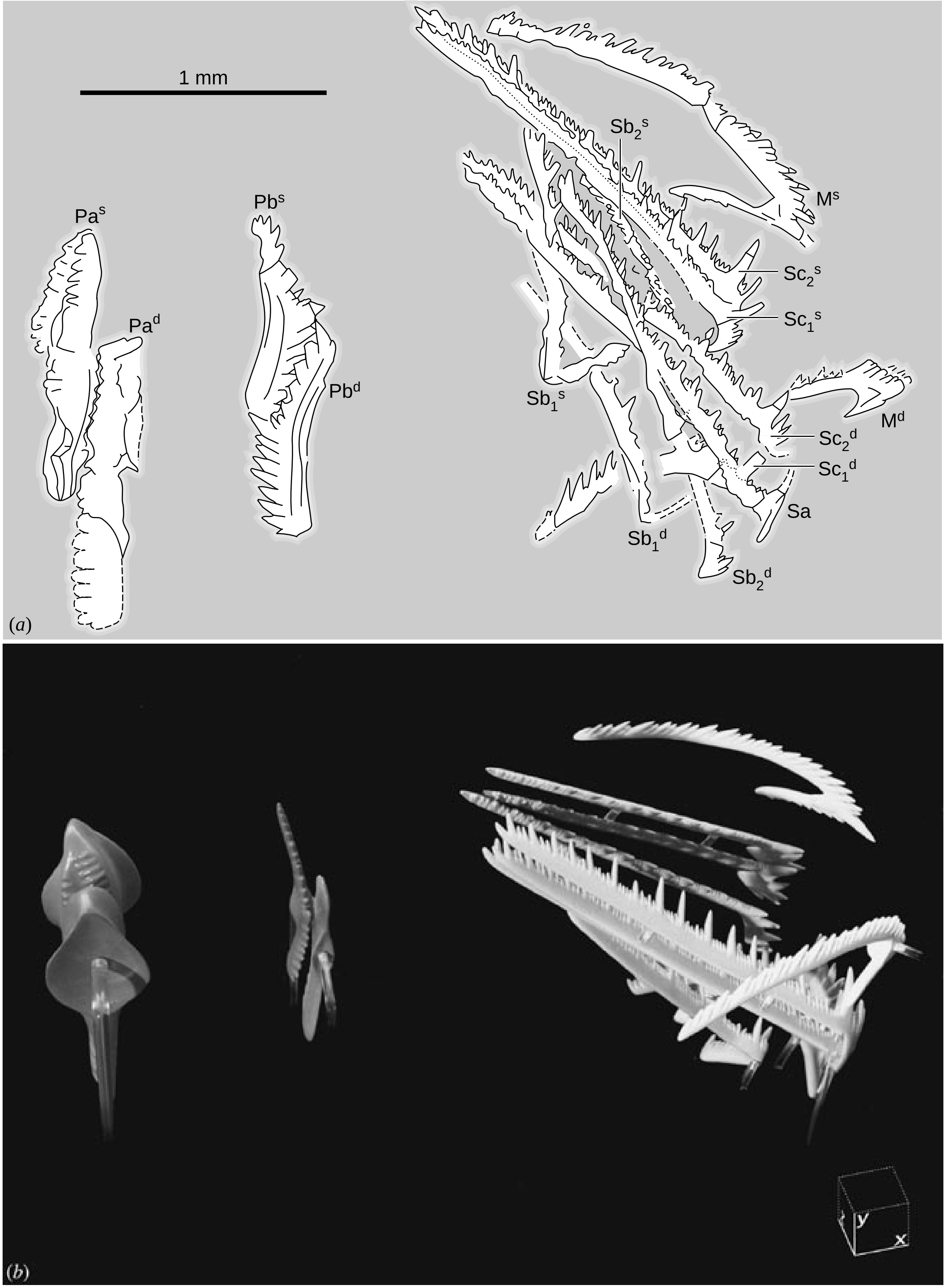

Figure 9. (*a*) Composite camera lucida drawing of specimen PM X 2219, part and counterpart (part on bottom). (*b*) Photograph of model taken from above, right, and slightly behind to simulate collapse pattern of PM X 2219; small cube indicates orientation of principal axes of apparatus relative to sea floor at time of collapse, $x = 12°$, $y = 43°$, $z = 44°$. A similar orientation of collapse is recorded by the specimen figured by Avcin (1974, plate 1, fig. 8, plate 2, fig. 1, $x = 1°$, $y = 40°$, $z = 50°$; refigured by Aldridge *et al.* (1987), fig. 4.8A).

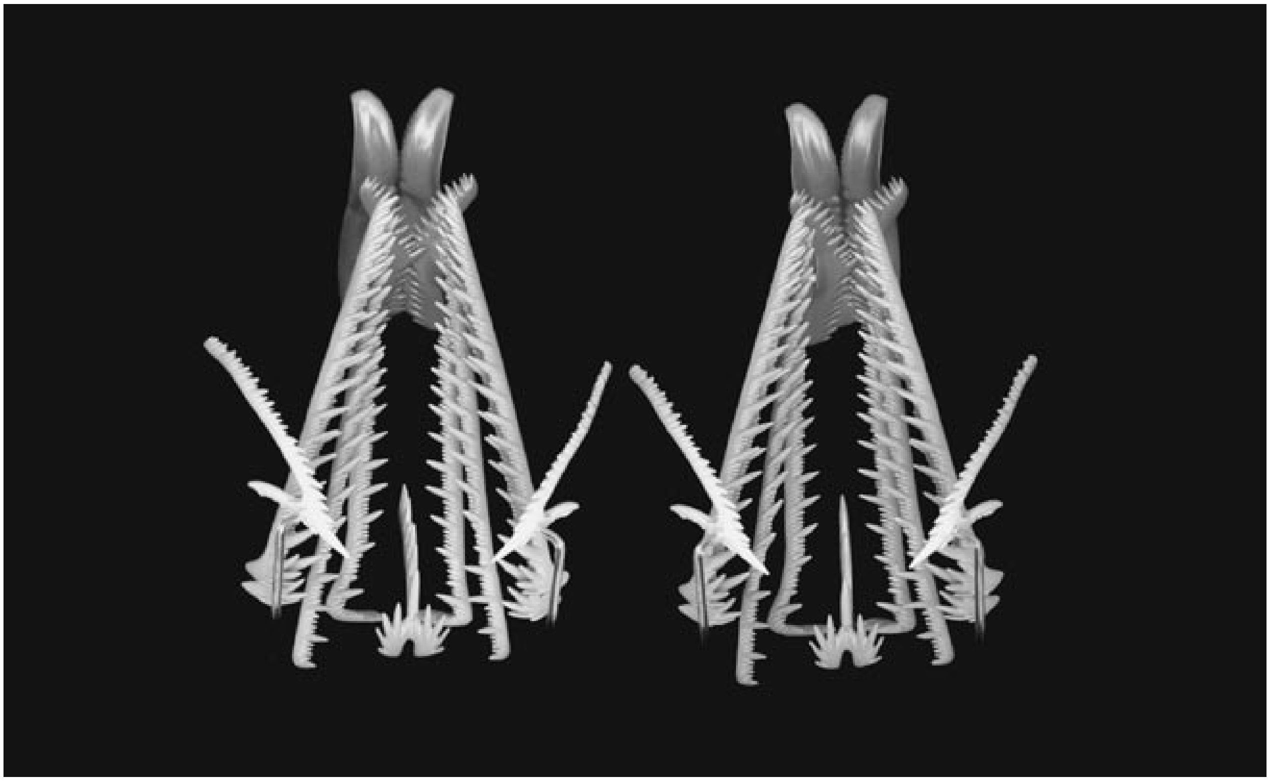

Figure 10. Stereo pair of the *Idiognathodus* apparatus model, viewed from above front.

indicate that the apparatus was oriented such that the 'posterior' of the P elements (according to conventional designation) was directed dorsally.

A full description of the apparatus architecture of *Idiognathodus* appears in Appendix 1. It is important to note here, however, that our reconstruction (figures 3, 5, 7 and 9–11) differs from those proposed previously in two important respects. First, the Pa elements in our model are arranged with the left element behind the right. This may appear a rather subtle difference, but it has far reaching implications for functional studies and the detection of conodont microwear patterns (Purnell 1995). Secondly, and more obviously, our model differs from that proposed by Aldridge *et al.* (1987; figure 1*e*) in the arrangement of the S and M elements at the anterior of the apparatus. Their reconstruction placed the S elements in parallel, with approximately equal forward inclination, with no vertical displacement from one element to the next, and with no inward inclination. The M elements flanked the S array, and had a similar general orientation, the long axis parallel to those of the S elements. In our reconstruction, the long axes of the S elements diverge anteriorly; the axis of the Sa element is horizontal, and the angle of forward inclination of the other S elements decreases away from the sagittal plane; the inward inclination of the S elements increases away from the vertically oriented Sa. The M elements are located above, and oriented obliquely to the S elements. These differences are not trivial; they represent a significant improvement in our understanding of the skeletal anatomy of conodonts, and are fundamental to analysis of functional morphology and the problem of food acquisition in conodonts (see § 6).

The orientations of the S and M elements in our reconstruction also differ from Dzik's hypothesis of architecture (1991; figure 1*d*). He considered the S elements to be vertical, their long axes parallel, and their cusp directed inwards at 90° to the sagittal plane; he also placed the M elements at the front of the apparatus.

5. SIMULATIONS OF *IDIOGNATHODUS* COLLAPSE PATTERNS

The model of apparatus architecture described above stands or falls according to how closely it can simulate the patterns of element distribution in natural assemblages of *Idiognathodus*. The specimen in figures 2 and 3*a* is the most widely illustrated natural assemblage (originally figured by Du Bois (1943), plate 25, figure 14), primarily because of its clear bilateral symmetry. Previous attempts to simulate the collapse of this assemblage (e.g. Aldridge *et al.* 1987, figure 4.12; Purnell *et al.* 1995, figure 6) have, however, incorrectly identified the left and right sides of the apparatus, and have therefore produced incorrect simulations. As preserved on the specimen part (figure 2) the apparatus has collapsed obliquely, from below and in front towards top and behind. This orientation cannot be simulated photographically (it would require the base-board of the model to be completely transparent), so our simulation is of the whole apparatus as drawn in the camera lucida (figure 3*a*) with the counterpart on the bottom. Details such as the overlap between the Pa and Pb

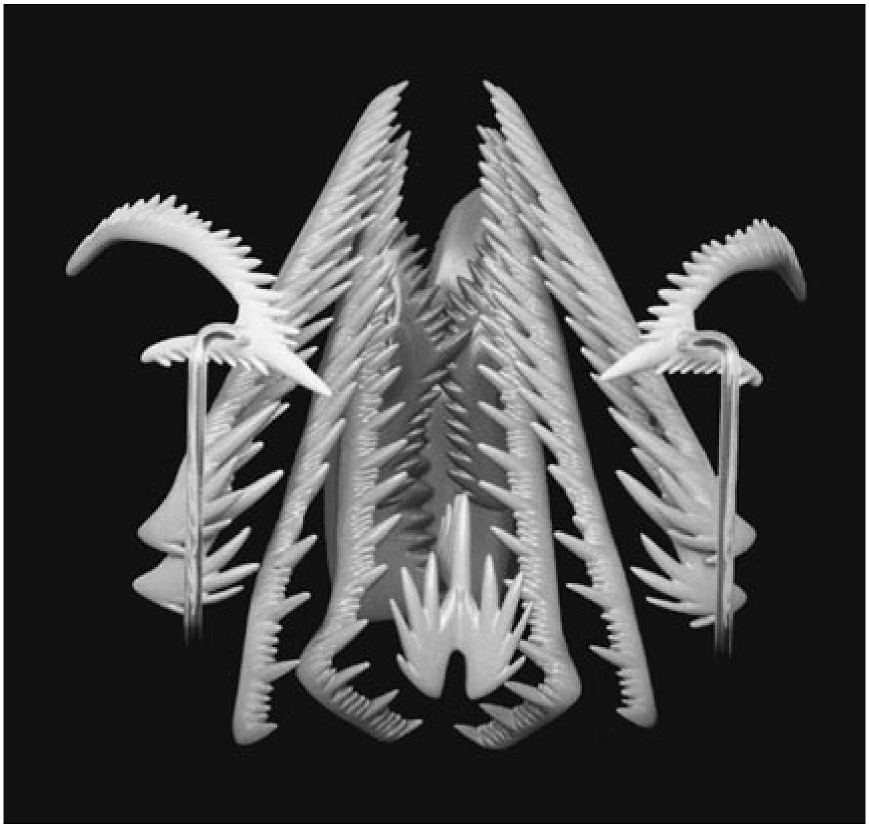

Figure 11. Anterior view of the *Idiognathodus* apparatus model.

elements, the orientation of the S element denticles inwards and towards the anterior, the location of the Sc element cusps, and the position of the preserved sinistral M element are all accurately matched in the simulation (figure 3*b*). The main visual differences between the simulation and the specimen arise from the foreshortening of elements caused by the oblique angle of photography; in reality, the long axes of elements all came to lie in the same plane during collapse, but this cannot be simulated photographically.

Figures 4 and 5*a* illustrate a lateral collapse. In this orientation, the P elements could probably have fallen either way, but they have come to rest with the more anterior dextral element in front of the sinistral elements. The simulation of this assemblage (figure 5*b*) accurately reproduces the relative juxtapositions and orientations of the S and M elements, as shown clearly by the Sa, Sb and M elements. The slightly steeper forward inclination of the S elements in the assemblage probably reflects the reorientation of element long axes as they came to lie on the bedding plane.

Although the lack of a counterpart and probable burial of some elements beneath others means that only eight elements of the apparatus are evident in the assemblage shown in figures 6 and 7*a*, the pattern of element arrangement exhibited by the specimen is accurately simulated by photographing the model from behind, to the left and slightly below (figure 7*b*).

The pattern of element position and orientation preserved in the specimen shown in figures 8 and 9*a* is matched almost exactly by simulating oblique collapse from above, right, and slightly behind (figure 9*b*). The unusual arrangement of the M elements, at first sight anomalous in having the sinistral M parallel to the S elements, but the dextral M lying across them, is faithfully reproduced in the simulation. The locations of the S elements, those on the sinistral side lying above and behind their dextral counterparts, is reproduced accurately, with the sinistral Sb_2 element, for example, located in the space between the sinistral Sc_1 and the dextral Sc_2 in both the fossil and the simulation. The P elements are lying with the sinistral member of each pair offset above and behind the other.

These illustrations serve only as examples, but they clearly demonstrate that our apparatus model passes the test of being able to simulate the range of different element arrangements in natural assemblages of *Idiognathodus* (see Purnell & Donoghue (1998) for more examples). The fidelity with which these photographs reproduce fossil patterns reflecting different orientations of collapse provides compelling evidence that our model is accurate, and given the number of variables involved and the complexity of the apparatus, it is inconceivable that a significantly different apparatus architecture could produce equally accurate simulations. Our model must therefore be close to the *in vivo* skeletal architecture of *Idiognathodus*. Analysis of collapse patterns in natural assemblages of other taxa (Purnell & Donoghue 1998) indicates that the model also reflects the architecture of ozarkodinid conodonts as a whole.

6. THE FUNCTION OF THE APPARATUS

Prior to the discovery of the first conodont animal (Briggs *et al.* 1983), a general lack of biological constraint rendered rigorous functional analysis of conodonts effectively impossible (Bengtson 1980). Since then, however, a number of studies have considered the function of elements as components of an integrated feeding structure in the head of an eel-like marine animal. Some have suggested that the apparatus was a tissue covered filter-feeding device (Nicoll 1985, 1987, 1995; Nicoll & Rexroad 1987), but this hypothesis is refuted by analysis of apparatus growth rates (Purnell 1993, 1994) and by the demonstration of shearing microwear on the surfaces of some conodont elements (Purnell 1995). The available evidence indicates that the conodont apparatus had a toothlike function, and that in ozarkodinids the posterior P elements processed food by crushing and/or slicing (Briggs *et al.* 1983; Aldridge & Briggs 1986; Aldridge *et al.* 1987; Purnell & von Bitter 1992; Purnell 1993, 1994, 1995). The question of food acquisition and the function of the anterior S and M elements is more problematic. Apparatus location, architecture, ontogeny, element morphology and wear patterns on P elements accord with a general hypothesis that the S and M elements performed a grasping function, but the means by which this was achieved is unknown. Most detailed analyses of function have focused on the Pa elements, and although Briggs *et al.* (1983) and subsequent authors have speculated that S and M elements may have operated in a manner broadly analogous to the lingual apparatus of hagfish, statements concerning S and M function are generally vague. In part, this is because it is difficult to envisage how elements arranged in the parallel array proposed by Aldridge *et al.* (1987) actually grasped. If the anterior S and M array was a grasping device it could not have been static, and movement of elements during function has been postulated several times (e.g. Jeppsson 1971). Aldridge *et al.* (1987) suggested that a 90° rotation of each side of the ramiform array was required in order to bring the cusps of the S and M elements into opposition. Our revised model of apparatus architecture sheds new light on this problem.

Our model provides both firm physical constraints and a foundation upon which to construct hypotheses of the mechanics of element motion. Further, biological constraints are imposed by the phylogenetic position of conodonts. The evidence that conodonts were jawless vertebrates is now compelling (see Aldridge & Purnell (1996) for a recent review), and this has provided a group of living relatives with which conodonts can be compared. Comparisons must, however, be made with care. Conodonts may share a number of important characters with extant agnathans, but they are clearly a distinct and specialized clade. In particular, functional analogies between the conodont apparatus and the lingual apparatus of lampreys and hagfish must be drawn with caution because the synapomorphy that unites the Conodonta is the phosphatic feeding apparatus. It is also possible that new evidence may weaken or refute the hypothesis that conodonts were jawless vertebrates. This would not alter our architectural reconstruction, however, and our hypotheses of function would therefore remain, albeit without the support of analogies with agnathans.

The fact that our model can simulate the range of natural assemblage collapse patterns indicates that the elements generally lay in the same stable configuration in all dead but undecomposed conodonts. The Sb–Sc elements were arranged as two obliquely opposed sets of closely spaced subparallel elements, their functional surfaces were directed obliquely dorsal, and the aboral surfaces of the elements in each set lay in approximately the same plane. Irrespective of phylogenetic relationships, this arrangement is comparable with the eversible lingual apparatus of extant agnathans; in both lampreys and hagfish, the keratin biting elements of the lingual apparatus are arranged as oblique sets attached to the dorsal side of a cartilage plate or plates. We interpret the juxtaposition and orientation of the Sb–Sc elements also to reflect their location on a pair of underlying cartilaginous dental plates. The hypothesis that conodont elements sat on supporting structures is not new (e.g. Kirk 1929; Smith *et al.* 1987, and references therein), but it has not been previously suggested that opposable dental plates united the Sb-Sc elements as integrated functional units. Without such aboral cartilage support, the control of movement and orientation of each element would have required a separate set of complex musculature. This hypothesis is difficult to reconcile with the lack of space between the Sb-Sc elements; also, it is not supported by analogies with any other agnathans. The orientation and the position of the Sa element suggest that it did not sit on the same cartilage plate as the Sb–Sc elements, but on a separate medial ridge or plate of cartilage. For this reason we propose separate plates for the sinistral and dextral side of the apparatus, similar to the situation in lampreys, rather than the single flexible dental plate of hagfish (Yalden 1985). The position and orientation of the M elements, and the inclination of their denticles, are markedly different to S elements and suggest that their motion was also somewhat different. They may have sat on lateral projections of the Sb–Sc plates, capable of a degree of independent articulation, or on separate basal plates. Note that we do not equate cartilage support structures with the conodont basal body.

The process of grasping clearly required both opening and closing of the apparatus, and the first step in understanding the operation of the apparatus is to assess the point of the cycle represented by the configuration of elements in the architectural model. The location of the apparatuses in the Granton conodont animal specimens indicates that unless the mouth was in an unusually posterior position, the S and M elements must have moved forward in order to have grasped food. This suggests that our model represents an apparatus near to closure. The orientation of the Sb–Sc element cusps and denticles, in oblique opposition, and the position and orientation of the

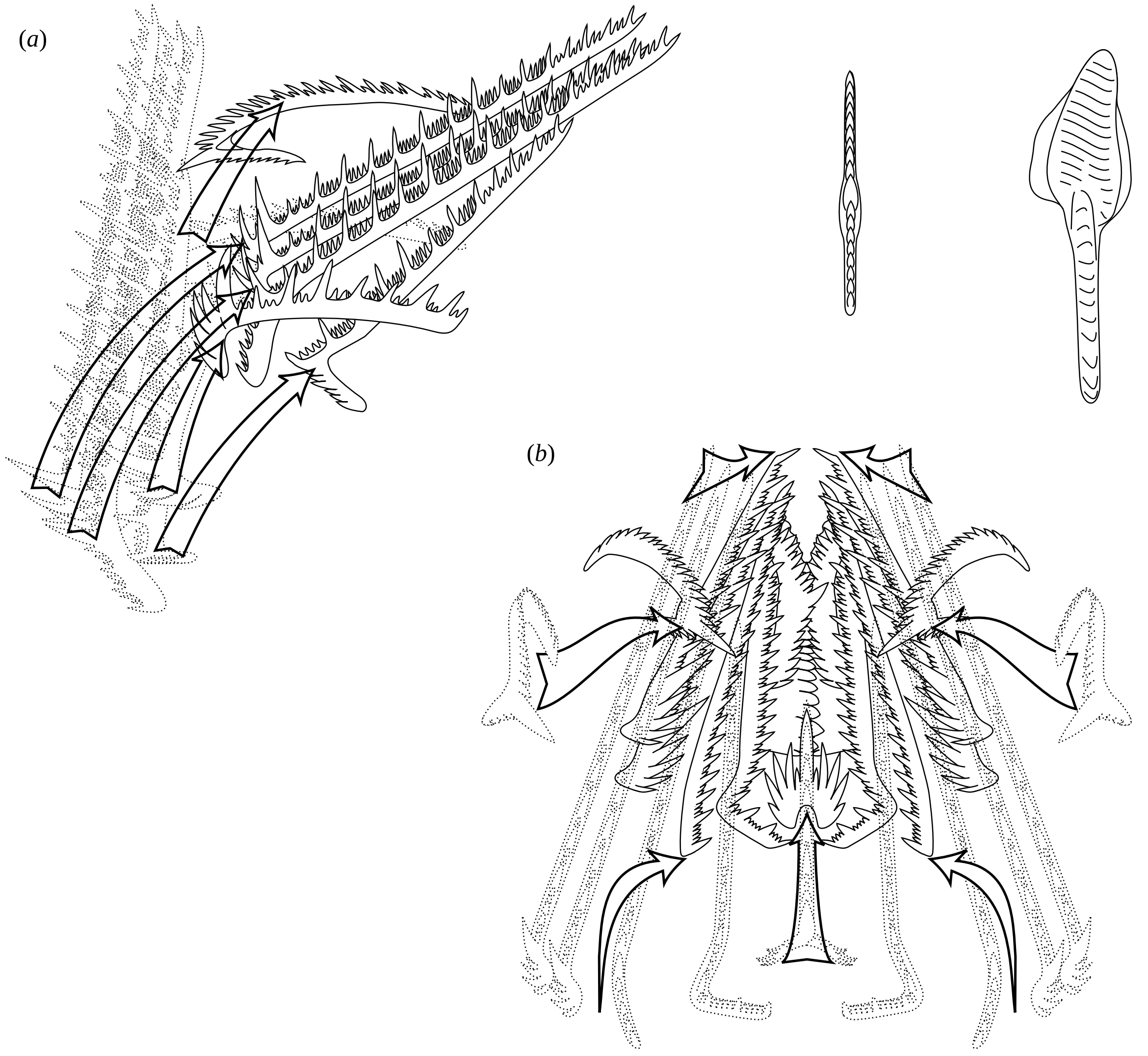

Figure 12. Operation of the anterior array of the ozarkodinid apparatus illustrated by *Idiognathodus*. Elements drawn with dotted lines indicate their position when the apparatus is everted and open; elements drawn with solid lines are in the retracted, closed position. (*a*) Lateral view of the dextral side of the apparatus; arrows indicate net movement of Sa, Sb_1, Sb_2, Sc_2 and M elements during retraction and closure of the anterior array. (*b*) Anterior view of the whole apparatus; arrows indicate net movement of S and M elements.

M elements, curving round above and in front of the S elements, support this interpretation, as does the fact that the position of the P elements would have prevented significant posterior movement of the S elements. It is pertinent to note that the lingual apparatus of extant agnathans comes to rest in a closed position in dead animals. The Granton fossils also preserve evidence of paired eyes and otic capsules (Aldridge *et al.* 1993), and conodonts must have had a true head and a differentiated brain. This, and the oblique dorsal orientation of the S elements indicate that a significant component of ventral movement was required in order to open the conodont apparatus.

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

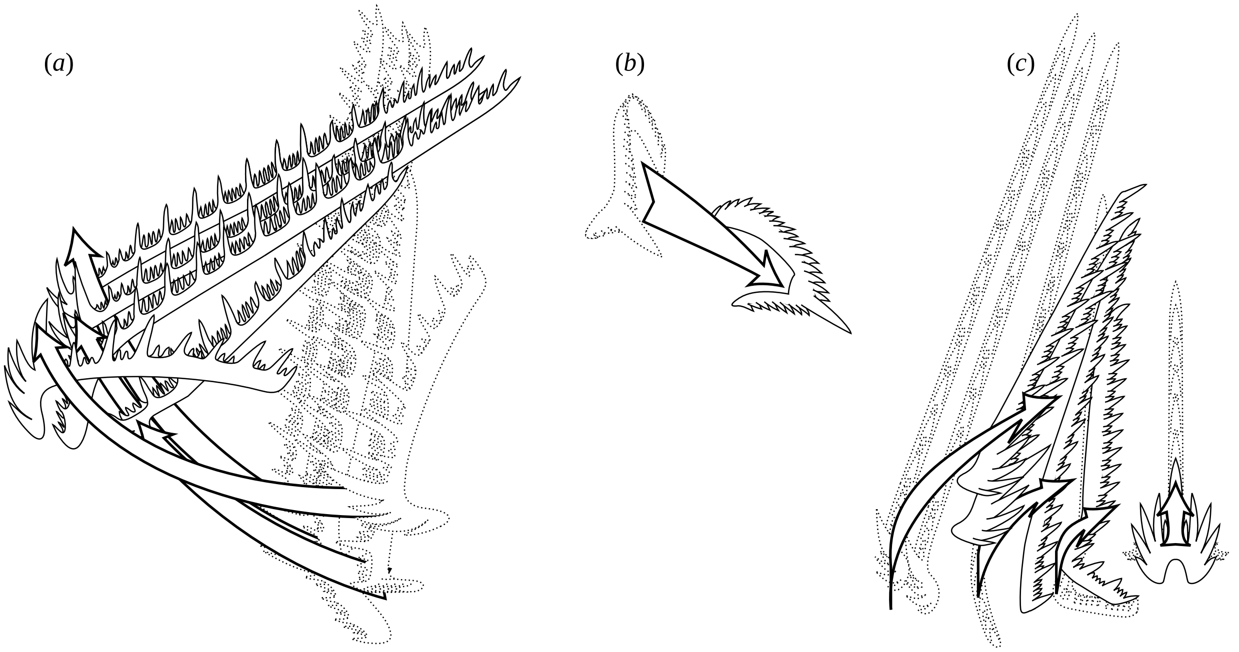

Figure 13. Relative motion of S and M elements during closure of the anterior array. Elements drawn with dotted lines indicate their position when the apparatus is everted and open; elements drawn with solid lines are in the retracted position. (*a*) Lateral view of dextral S elements and Sa element; arrows indicate motion of Sa, Sb_1, Sb_2, and Sc_2 elements relative to a fixed point at the distal end of the posterior process of the Sb_1 element. (*b*) Anterior view of dextral M element; arrow indicates motion relative to cusp of Sa element. (*c*) Anterior view dextral S elements and Sa element; arrows indicate motion of Sa, Sb_1, Sb_2, and Sc_2 elements relative to a fixed point at the distal end of the anterior process of the Sb_1 element.

grasping). The anterior and ventral motions involved in opening of the conodont apparatus, therefore, resulted from pulling of the dental plates forwards out of the laterally confining U-shape, and pivoting them over the anterior edge of the ventral cartilage into a subvertical position in which the S element denticles were directed anteriorly. The protractor muscles responsible for such motion must have wrapped round the anterior end of the ventral cartilage and inserted somewhere on its ventral side.

This hypothesis of element motion is illustrated in figure 12. Because the apparatus came to rest near to closure, the first stage in the grasping cycle must have been opening of the apparatus, but it is closure that is important for understanding how grasping was achieved, and our illustrations and discussion therefore concentrate on element movements during retraction of the apparatus. The apparatus was, however, opened by reversal of the element movements illustrated. Closure of the apparatus was brought about by the action of retractor muscles inserted onto the dental plate bearing the Sb–Sc and possibly the M elements. This resulted in a net posterior and inward rotation of the elements as indicated by the arrows on figure 12. This motion need not have been a steady, smooth action; as the dental plates pivoted over the anterior edge of the underlying cartilage the apparatus may have snapped back into the closed position, in a manner similar to closure of the hagfish lingual apparatus (Dawson 1963; Krejsa 1990*a*). The retracted, resting position of the Sa element was anterior and more ventral of the adjacent elements; this, and the shape of the medial cartilage on which we suggest it lay, resulted in a different trajectory as the apparatus closed. Relative to the other S elements it moved up and back, passing through the axial space between the Sb_1 elements. The M elements, during closure, moved backwards and swung inwards.

Although the net effect of retraction of the apparatus was to move the S and M elements backwards, upwards and inwards (figure 12), the mechanism by which food was grasped by the elements is more clearly illustrated by considering their relative rather than their absolute motions (figure 13). During closure, the Sb–Sc elements swung upwards through an arc approximately parallel to the curvature of the cusp and denticles (figure 13*a*), a motion comparable to the closure of the lower jaw in mammals (e.g. Crompton & Hiiemae 1970). At the same time they rotated inwards, again along trajectories approximately parallel to the orientation of the cusp and denticles (figure 13*c*). Through the same phase of closure the M elements rotated inwards, downwards, and slightly forwards (figure 13*b*). The combined effect of these movements would have produced a highly effective grasping action, the cusps and denticles of the elements converging to grab and impale any food item that lay anterior of the open array. The posterior component of apparatus retraction would have simultaneously drawn food back into the mouth. It is possible the Sb–Sc elements were retracted a little further than the position illustrated (i.e. the configuration of elements in the model) so that the cusps were brought into more direct opposition. However, we envisage a grasping, rather than a biting function for the S and M elements, and this does not require complete closure of the array. It does seem likely, however, that the Sa element continued its backward arc, the posterior process moving through the horizontal to a position of posterior inclination. Through this cycle of retraction, the cusp and lateral processes of the Sa element would have moved from a position close to the cusp of the Sb_1 element when fully everted, past the cusps of each of the other Sb–Sc elements in turn. Thus, at the earliest stages of closure the Sa element would have performed a grasping function, but as retraction continued, food impaled on the Sb–Sc elements would have been lifted off and moved backwards towards the P elements.

It has been suggested that with the anterior S and M array in retracted position, conodont elements may have been withdrawn into enclosing pockets of epithelium (Aldridge *et al.* 1987; cf. Bengtson 1976). However, the evidence that S elements were closely juxtaposed, our hypothesis that they lay on cartilage dental plates and were still functional when retracted (cf. Bengtson 1983), and recent reinterpretation of element histology (Sansom 1996; Donoghue 1998) together indicate that his hypothesis is no longer tenable.

In ozarkodinid conodonts, food captured by the S and M elements was sliced and crushed by the Pb and Pa elements (e.g. Briggs *et al.* 1983; Purnell & von Bitter 1992; Purnell 1995). Morphology, occlusion and wear patterns indicate that P elements operated by being rotated against each other across the axis (Nicoll 1987; Weddige 1990; Purnell & von Bitter 1992); sharp blade-like elements, for example, functioned like a pair of serrated scissors (Purnell & von Bitter 1992; Purnell 1995). The relative movement of these elements is understood, but how motion was produced is not. It is possible that rotation was produced by mechanisms of retraction similar to those proposed for the S and M elements, but the precision with which elements were brought into repeated contact argues against this (Purnell 1995). Rather, it seems more likely that the P elements were located at the entrance to the pharynx (Aldridge *et al.* 1995), and movement was controlled by antagonistic muscles located above and below the elements in the dorsal and ventral walls of the pharynx. Janvier's speculative suggestion that the P elements were 'attached to a transversely moving structure derived from a velum of larval lamprey type' (Janvier 1996, p. 277) is consistent with their pharyngeal location, but is difficult to test. However, the velum in larval lampreys pushes water into the pharynx, and its primary motion is anterior–posterior (Mallatt 1996). The musculature of this structure would, therefore, require significant remodelling if it were to bring about the axially directed rotational action of ozarkodinid P elements. Furthermore, faint transverse traces preserved immediately behind the eyes of one conodont specimen (IGSE 13821; Briggs *et al.* 1983, figures 2C and 3A) have been interpreted as possible branchial structures (Aldridge *et al.* 1993). If correct, this would suggest that the velum in conodonts (if they possessed one) was located anterior of the P elements.

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

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

For loans and access to material we thank Professor Richard Aldridge, University of Leicester, Dr Rod Norby, Illinois Geological Survey, and Professor Peter von Bitter, Royal Ontario Museum. Dr Rod Norby, Professor Peter von Bitter and Dr C. Pius Wiebel assisted in collecting material from Bailey Falls. We thank Professor Richard Aldridge for discussion, and Professor Derek Briggs and an anonymous reviewer for critical comments on this and earlier versions of the manuscript. Photographic assistance was provided by Mr Ian Paterson and Mr Colin Brooks. Mr David York assisted in rod bending and drilling. This work was funded by NERC Fellowship GT5/F/GS/95/6 (M.A.P.), and a University of Leicester postgraduate studentship (P.C.J.D.).

APPENDIX 1. DESCRIPTION OF THE APPARATUS OF *IDIOGNATHODUS*

In this description, a plane parallel to the long axis of the animal and orthogonal to the sagittal plane is taken as horizontal. The whole model (1:50 scale), measured from the tip of the cusp of the Sa element to the blade of the Pa element, is 25 cm long, and an animal with 2 mm long Pa elements would, therefore, have had an apparatus 5 mm long. The elements of the apparatus of *Idiognathodus* grew isometrically (Purnell 1993, 1994), and assuming the same to be true of the whole apparatus, dimensions expressed as proportions are applicable to *Idiognathodus* apparatuses of any size. We therefore give dimensions as proportions of total apparatus length. At its widest (between the distal tips of the M elements), the apparatus is 60% of length, and its full dorso-ventral depth (between ventral ends of anterior processes of Sb_1 elements and distal tips of Sc_2 elements) is 50% of length. Note that our usage of element notation and the problems of element orientation are discussed elsewhere (Purnell & Donoghue 1998).

Detailed description of the elements of *Idiognathodus* is beyond the scope of this paper, but brief clarification of the morphology of the elements occupying S positions is necessary. Sa element: shortest of S elements, posterior process approximately half length of that of Sc. Sb_1 elements: bipennate, lack pronounced cusp, have fairly long anterior process that curves sharply inwards through approximately 90°; posterior process about three-quarters the length of that of the Sb_2 and Sc elements. Sb_2 elements: bipennate, lack pronounced cusp, have fairly long anterior process that curves gently inwards and downwards. Sc elements: bipennate, with pronounced cusp and short incurved and downcurved anterior process bearing recurved elongate denticles; anterior process of Sc_1 more tightly incurved than Sc_2, in some specimens aboral edge of anterior process of Sc_2 is recurved and more hook-like than Sc_1. Posterior inclination of denticles on the posterior processes of the elements decreases from an angle of approximately 50° (with respect to the posterior process) in Sb_1 elements to approximately 60–65° in Sc elements. The denticles of Sb_1 elements are also more strongly incurved.

The Sa is the most anterior of the S elements; it lies on the sagittal plane with its posterior process approximately horizontal and its cusp vertical (figures 5, 10 and 11). It is flanked by four pairs of symmetrically arranged S elements: Sb_1, Sb_2, Sc_1 and Sc_2 (in sequence, away from the axis). The Sb_1 cusps are set back approximately 10% of apparatus length from the Sa cusp and lie approximately 4% of apparatus length from the sagittal plane. The Sb_2 cusps are approximately 5% behind the Sa, and approximately 5.5% from the sagittal plane. The two Sc elements on each side are tightly grouped, their cusps slightly behind that of the Sa, and the Sc_2 cusp approximately 9% of apparatus length from the sagittal plane. Posteriorly, the posterior processes of the Sb and Sc elements terminate approximately 4–5% of apparatus length from the sagittal plane; the Sb_1 posterior processes are parallel to the sagittal plane, but those of the other elements diverge anteriorly, the Sb_2 elements at approximately 5°, the Sc elements at approximately 15° with respect to the sagittal plane.

The vertical disposition of the elements is relative to a horizontal datum along the base of the posterior process of the Sa. The Sb_1 elements are the most ventral in the apparatus (figures 5, 10 and 11), and the other elements have progressively more dorsal locations away from the axis. Relative to the datum, the basal cavity beneath the cusp of each Sb_1 element is approximately 6% of apparatus length below, that of each Sb_2 element is very slightly above, that of each Sc_1 element approximately 4% above, and that of each Sc_2 element 10% above. The posterior tips of the Sc_2 elements terminate approximately 35% of apparatus length above the datum, and apart from the horizontal Sa element, all the S elements are oriented with their posterior process tilted forwards. Relative to the horizontal, this angle decreases from approximately 45° in the Sb_1 through approximately 35° in the Sb_2 to approximately 30° in the Sc elements. The Sb–Sc elements are also inclined inwards; the plane in which the denticles of the posterior process lie is inclined at approximately 45° to the sagittal plane in Sb_1 elements and increases through to approximately 60° in Sc elements (figures 7, 10 and 11).

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

The Pb elements lie 72% of apparatus length behind the Sa cusp, and the Pa elements at the back of the apparatus, approximately 28% behind the Pb elements. The element on the left side of each pair is the more posterior of the two (figures 3, 6, 7 and 10).

The long axes of the P elements are approximately vertical, and the oral surfaces of the elements are directed inwards at 90° to the sagittal plane. The dorsalmost tips of the elements lie approximately 30% of apparatus length above the Sa datum. The Pb elements extend ventrally to approximately 2% above, and the Pa elements to 10% below the datum.

REFERENCES

Aldridge, R. J. 1987 Conodont palaeobiology: a historical review. In *Palaeobiology of conodonts* (ed. R. J. Aldridge), pp. 11–34. Chichester: Ellis Horwood.

Aldridge, R. J. & Briggs, D. E. G. 1986 Conodonts. In *Problematic fossil taxa* (ed. A. Hoffman & M. H. Nitecki), pp. 227–239. Oxford University Press.

Aldridge, R. J. & Purnell, M. A. 1996 The conodont controversies. *Trends Ecol. Evol.* **11**, 463–468.

Aldridge, R. J. & Smith, M. P. 1993 Conodonta. In *The fossil record 2* (ed. M. J. Benton), pp. 563–572. London: Chapman & Hall.

Aldridge, R. J., Briggs, D. E. G., Sansom, I. J. & Smith, M. P. 1994 The latest vertebrates are the earliest. *Geol. Today* **11**, 141–145.

Aldridge, R. J., Briggs, D. E. G., Smith, M. P., Clarkson, E. N. K. & Clark, N. D. L. 1993 The anatomy of conodonts. *Phil. Trans. R. Soc. Lond.* B **340**, 405–421.

Aldridge, R. J., Purnell, M. A., Gabbott, S. E. & Theron, J. N. 1995 The apparatus architecture and function of *Promissum pulchrum* Kovács-Endrödy (Conodonta, Upper Ordovician), and the prioniodontid plan. *Phil. Trans. R. Soc. Lond.* B **347**, 275–291.

Aldridge, R. J., Smith, M. P., Norby, R. D. & Briggs, D. E. G. 1987 The architecture and function of Carboniferous polygnathacean conodont apparatuses. In *Palaeobiology of conodonts* (ed. R. J. Aldridge), pp. 63–76. Chichester: Ellis Horwood.

Avcin Jr, M. J. 1974 Des Moinesian conodont assemblages from the Illinois Basin. Ph.D. thesis, University of Illinois at Urbana-Champaign.

Baesemann, J. F. 1973 Missourian (Upper Pennsylvanian) conodonts of northeastern Kansas. *J. Paleont.* **47**, 689–710.

Bengtson, S. 1976 The structure of some Middle Cambrian conodonts, and the early evolution of conodont structure and function. *Lethaia* **9**, 185–206.

Bengtson, S. 1980 Conodonts: the need for a functional model. *Lethaia* **13**, 320.

Bengtson, S. 1983 A functional model for the conodont apparatus. *Lethaia* **16**, 38.

Briggs, D. E. G., Clarkson, E. N. K. & Aldridge, R. J. 1983 The conodont animal. *Lethaia* **16**, 1–14.

Briggs, D. E. G. & Williams, S. H. 1981 The restoration of flattened fossils. *Lethaia* **14**, 157–164.

Crompton, A. W. & Hiiemae, K. 1970 Molar occlusion and mandibular movements during occlusion in the American opossum *Didelphis marsupialis* L. *Zool. J. Linn. Soc.* **49**, 21–47.

Dawson, J. A. 1963 The oral cavity, the 'jaws' and the horny teeth of *Myxine glutinosa.* In *The biology of myxine* (ed. A. Brodal & R. Fänge), pp. 231–255. Oslo: Universitetsforlaget.

Donoghue, P. C. J. 1998 Growth and patterning in the conodont skeleton. *Phil. Trans. R. Soc. Lond.* B **353**. (In the press.)

Du Bois, E. P. 1943 Evidence on the nature of conodonts. *J. Paleont.* **17**, 155–159.

Dzik, J. 1976 Remarks on the evolution of Ordovician conodonts. *Acta Palaeontol. Pol.* **21**, 395–455.

Dzik, J. 1986 Chordate affinities of the conodonts. In *Problematic fossil taxa* (ed. A. Hoffman & M. H. Nitecki), pp. 240–254. Oxford University Press.

Dzik, J. 1991 Evolution of the oral apparatuses in the conodont chordates. *Acta Palaeontol. Pol.* **36**, 265–323.

Dzik, J. 1994 Conodonts of the Mójcza Limestone. *Palaeontol. Pol.* **53**, 43–128.

Gee, H. 1996 *Before the backbone: views on the origin of the vertebrates.* London: Chapman & Hall.

Grayson, R. C., Merrill, G. K. & Lambert, L. L. 1991 Carboniferous gnathodontid conodont apparatuses: evidence of a dual origin for Pennsylvanian taxa. *Cour. Forsch. Inst. Senckenberg* **118**, 353–396.

Janvier, P. 1981 The phylogeny of the Craniata, with particular reference to the significance of fossil 'agnathans'. *J. Vert. Paleont.* **1**, 121–159.

Janvier, P. 1995 Conodonts join the club. *Nature* **374**, 761–762.

Janvier, P. 1996 The dawn of the vertebrates: characters versus common ascent in the rise of current vertebrate phylogenies. *Palaeontology* **39**, 259–287.

Jeppsson, L. 1971 Element arrangement in conodont apparatuses of *Hindeodella* type and in similar forms. *Lethaia* **4**, 101–123.

Kirk, S. R. 1929 Conodonts associated with the Ordovician fish fauna of Colorado: a preliminary note. *Am. J. Sci.* ser. 5, **18**, 493–496.

Krejsa, R. J., Bringas, P. & Slavkin, H. C. 1990*a* The cyclostome model: an interpretation of conodont element structure and function based on cyclostome tooth morphology, function, and life history. *Cour. Forsch. Inst. Senckenberg* **118**, 473–492.

Krejsa, R. J., Bringas, P. & Slavkin, H. C. 1990*b* A neontological interpretation of conodont elements based on agnathan cyclostome tooth structure, function, and development. *Lethaia* **23**, 359–378.

Lindström, M. 1964 *Conodonts.* Amsterdam: Elsevier.

Lindström, M. 1973 On the affinities of conodonts. In *Conodont paleozoology* (ed. F. H. T. Rhodes), pp. 85–102. Boulder: Geological Society of America.

Lindström, M. 1974 The conodont feeding apparatus as a food-gathering mechanism. *Palaeontology* **17**, 729–744.

Mallatt, J. 1996 Ventilation and the origin of jawed vertebrates: a new mouth. *Zool. J. Linn. Soc.* **117**, 329–404.

Mashkova, T. V. 1972 *Ozarkodina steinhornensis* (Ziegler) apparatus, its conodonts and biozone. *Geol. Palaeontol.* **1**, 81–90.

Nicoll, R. S. 1977 Conodont apparatuses in an Upper Devonian palaeoniscoid fish from the Canning Basin, Western Australia. *BMR J. Aust. Geol. Geophys.* **2**, 217–228.

Nicoll, R. S. 1985 Multi-element composition of the conodont species *Polygnathus xylus xylus* (Stauffer 1940) and *Ozarkodina brevis* (Bischoff & Ziegler 1957) from the Upper Devonian of the Canning Basin, Western Australia. *BMR J. Aust. Geol. Geophys.* **9**, 133–147.

Nicoll, R. S. 1987 Form and function of the Pa element in the conodont animal. In *Palaeobiology of conodonts* (ed. R. J. Aldridge), pp. 77–90. Chichester: Ellis Horwood.

Nicoll, R. S. 1995 Conodont element morphology, apparatus reconstructions and element function: a new interpretation of conodont biology with taxonomic implications. *Cour. Forsch. Inst. Senckenberg* **182**, 247–262.

Nicoll, R. S. & Rexroad, C. B. 1987 Re-examination of Silurian conodont clusters from northern Indiana. In *Palaeobiology of conodonts* (ed. R. J. Aldridge), pp. 49–61. Chichester: Ellis Horwood.

Norby, R. D. 1976 Conodont apparatuses from Chesterian (Mississippian) strata of Montana and Illinois. Ph.D. thesis, University of Illinois at Urbana-Champaign.

Norby, R. D. 1979 Elemental architecture of natural platform conodont apparatuses of Mississippian and Pennsylvanian age. In *IX Int. Congr. Carbonif.*, Abstacts of papers, p. 249.

Purnell, M. A. 1993 Feeding mechanisms in conodonts and the function of the earliest vertebrate hard tissues. *Geology* **21**, 375–377.

Purnell, M. A. 1994 Skeletal ontogeny and feeding mechanisms in conodonts. *Lethaia* **27**, 129–138.

Purnell, M. A. 1995 Microwear on conodont elements and macrophagy in the first vertebrates. *Nature* **374**, 798–800.

Purnell, M. A. & Donoghue, P. C. J. 1998 Architecture, taphonomy and homologies of the skeletal apparatus of ozarkodinid conodonts. *Palaeontology* **41**. (In the press.)

Purnell, M. A. & von Bitter, P. H. 1992 Blade-shaped conodont elements functioned as cutting teeth. *Nature* **359**, 629–631.

Purnell, M. A. & von Bitter, P. H. 1996 Bedding-plane assemblages of *Idioprioniodus*, element locations, and the Bauplan of prioniodinid conodonts. In *Sixth European Conodont Symp., Abstracts* (ed. J. Dzik), pp. 48. Warszawa: Instytut Paleobiologii PAN.

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

Rhodes, F. H. T. 1952 A classification of Pennsylvanian conodont assemblages. *J. Paleont.* **26**, 886–901.

Sansom, I. J. 1996 *Pseudooneotodus*, an important Palaeozoic vertebrate lineage. *Zool. J. Linn. Soc.* **118**, 47–57.

Sansom, I. J., Smith, M. P., Armstrong, H. A. & Smith, M. M. 1992 Presence of the earliest vertebrate hard tissues in conodonts. *Science* **256**, 1308–1311.

Sansom, I. J., Armstrong, H. A. & Smith, M. P. 1994 The apparatus architecture of *Panderodus* and its implications for coniform conodont classification. *Palaeontology* **37**, 781–799.

Schmidt, H. 1934 Conodonten-funde in ursprünglichem zusammenhang. *Paläontol. Z.* **16**, 76–85.

Schmidt, H. & Müller, K. J. 1964 Weitere Funde von Conodonten-Gruppen aus dem oberen Karbon des Sauerlandes. *Paläontol. Z.* **38**, 105–135.

Scott, H. W. 1934 The zoological relationships of the conodonts. *J. Paleont.* **8**, 448–455.

Smith, M. P., Briggs, D. E. G. & Aldridge, R. J. 1987 A conodont animal from the lower Silurian of Wisconsin, USA, and the apparatus architecture of panderodontid conodonts. In *Palaeobiology of conodonts* (ed. R. J. Aldridge), pp. 91–104. Chichester: Ellis Horwood.

Sweet, W. C. 1988 *The Conodonta: morphology, taxonomy, paleoecology, and evolutionary history of a long-extinct animal phylum.* Oxford Monographs on Geology and Geophysics. Oxford: Clarendon.

Walliser, O. H. 1994 Architecture of the polygnathid conodont apparatus. *Cour. Forsch. Inst. Senckenberg* **168**, 31–36.

Weddige, K. 1990 Pathological conodonts. *Cour. Forsch. Inst. Senckenberg* **118**, 563–589.

Yalden, D. W. 1985 Feeding mechanisms as evidence of cyclostome monophyly. *Zool. J. Linn. Soc.* **84**, 291–300.

Received 20 November 1996; accepted 3 January 1997