Conodonts and the first vertebrates

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

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

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

Since 1981, however, there has been a revolution in our understanding of conodonts. The discovery of fossils preserving not just the conodont elements but also the remains of the soft-bodied animal that bore them [2] has at last enabled reconstruction of conodont anatomy and provided firm ground on which their relationships can be assessed [3]. Parallel research has led to a re-evaluation of the structure and function of the elements [4–7], with important and unexpected implications for hypotheses concerning the origin of vertebrates and their skeletons.

The first vertebrates and the importance of feeding

Some time ago, probably during the early part of the Cambrian Period (~520 million years ago; see Figure 2), a new type of animal appeared. It was small, a few centimetres in length, and elongate; it had no hard skeleton, but a stiffening rod of cartilage along its back and V-shaped blocks of muscle along its sides; it had paired eyes, a brain and tail fins. It was the first vertebrate. Unfortunately, the potential for totally soft-bodied organisms to be fossilized is close to zero; consequently, there is no direct fossil evidence of this evolutionary milestone, and scenarios that seek to explain how and why vertebrates evolved are controversial. Surprisingly, few authorities disagree about the likely anatomy of the earliest forms. Their characteristics must lie somewhere between those of the amphioxus, the closest living invertebrate relative of vertebrates, and the hagfish, the most primitive extant vertebrate. Beyond this, however, agreement fails and issues are hotly debated: how did

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

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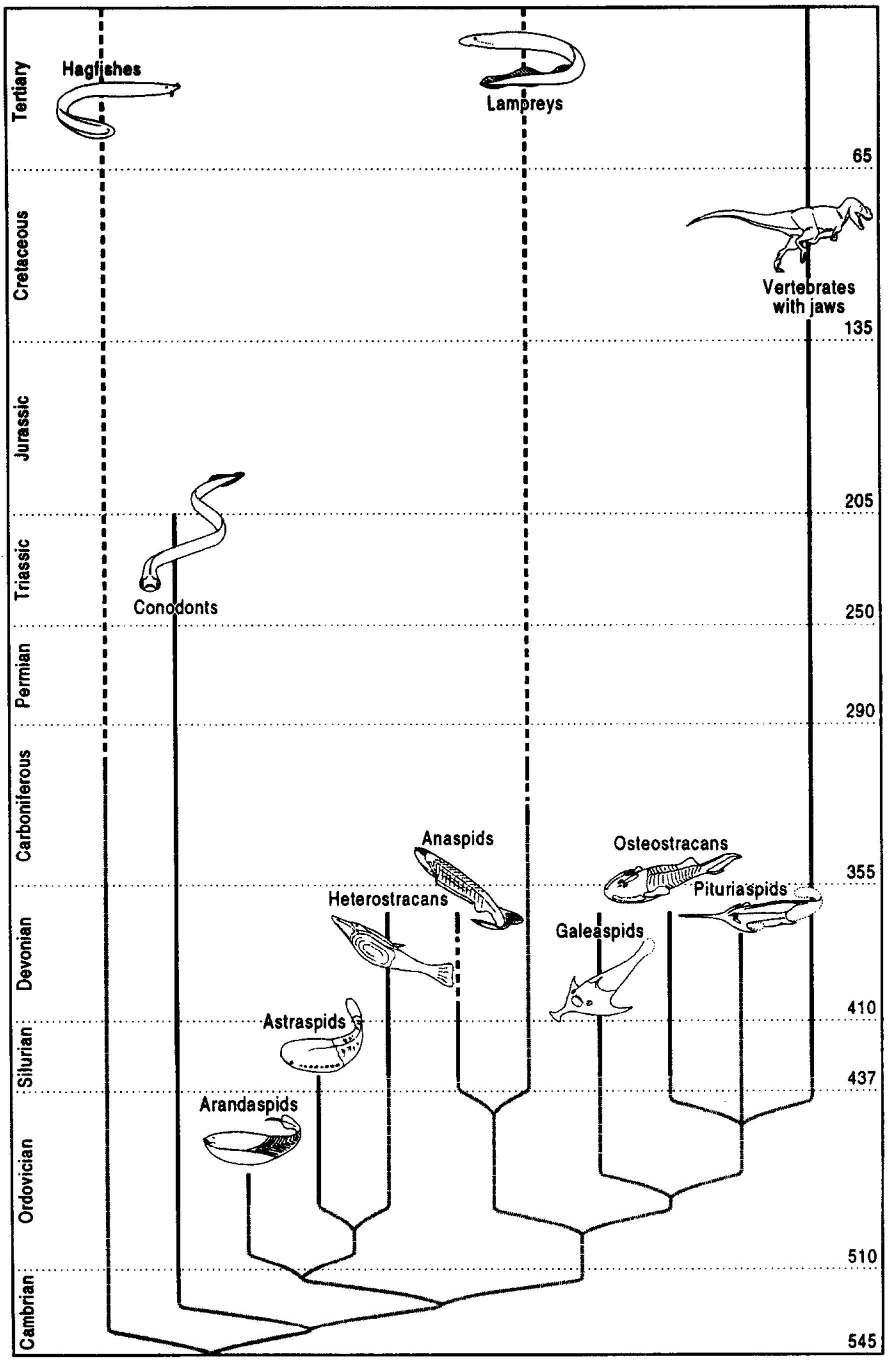

Figure 2 The fossil record of vertebrates, and their evolutionary relationships (modified from [23]). The solid black lines show the known fossil record of each group, the grey lines indicate the relationships between them. Arandaspids, astraspids, heterostracans, anaspids, galeaspids, osteostracans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

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

The question of feeding is particularly contentious. According to the traditional, textbook view, the first vertebrates were relatively inactive, suspension-feeding organisms [10,12], ecologically comparable with the living amphioxus and larval lampreys, which feed by collecting microscopic food particles with a filter. Champions of this view consider that it was only with the evolution of jaws, 100 million years later, that vertebrates were able to become predators. Others have contended that many of the definitive characters of vertebrates, such as the paired eyes and muscular and skeletal adaptations for active life, would not have evolved unless the first vertebrates were predatory [8,9]. According to this theory, the shift from suspension-feeding to predation was one of the most important innovations of the first vertebrates, and provides the key to understanding the evolutionary pressures responsible for their appearance. Evidence for feeding mechanisms in early vertebrates is obviously crucial in the resolution of this debate.

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

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

Conodonts: from enigma to ancestor?

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

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

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

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

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

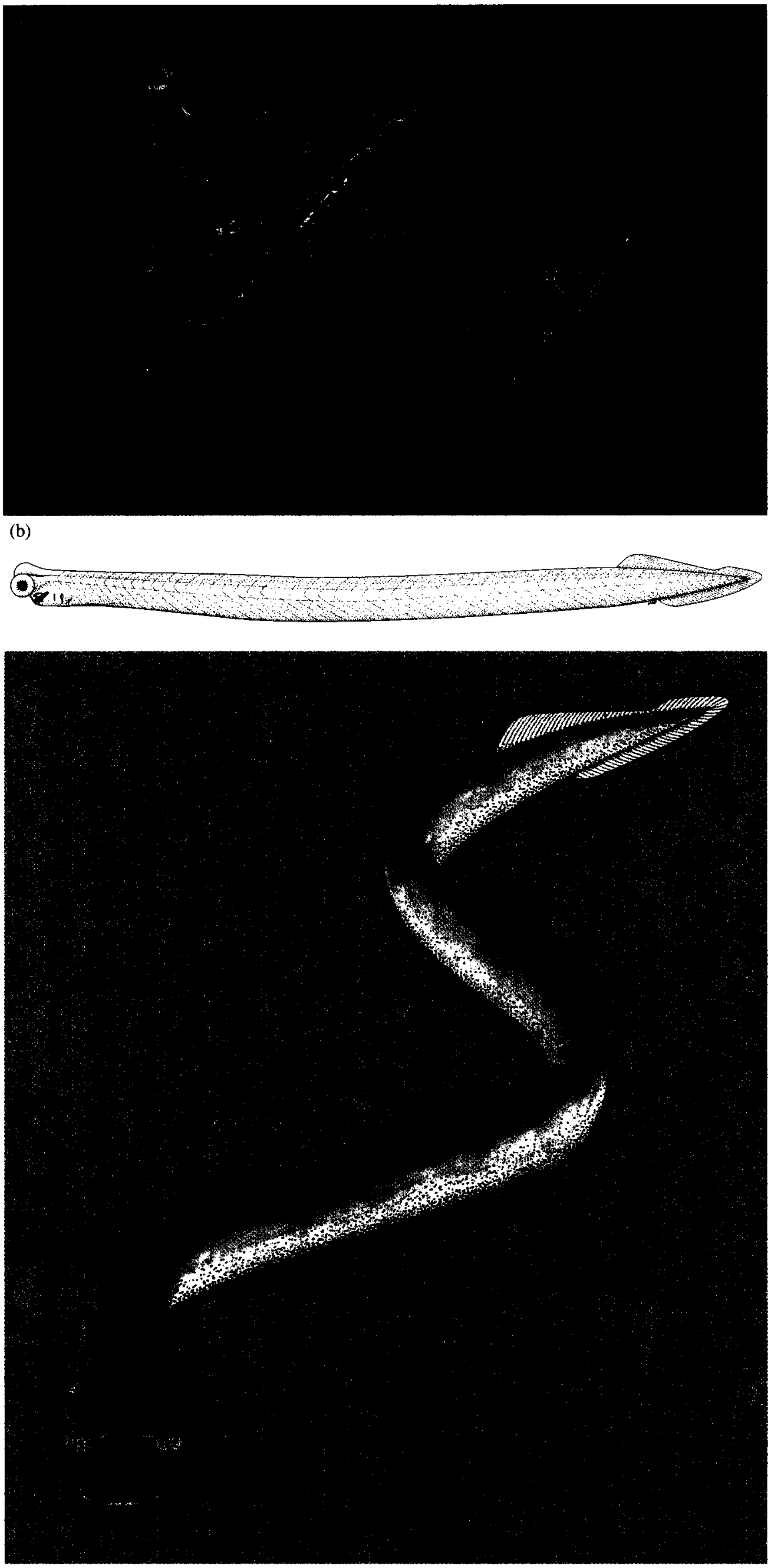

Figure 3 The conodont animal. (a) Fossil from the Carboniferous of Edinburgh (Royal Museum of Scotland specimen 1992.41.1), preserving 38-mm long body; (b) a reconstruction of the conodont animal based primarily on the specimen shown in (a); (c) the animal as it may have looked in life, with its mouth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

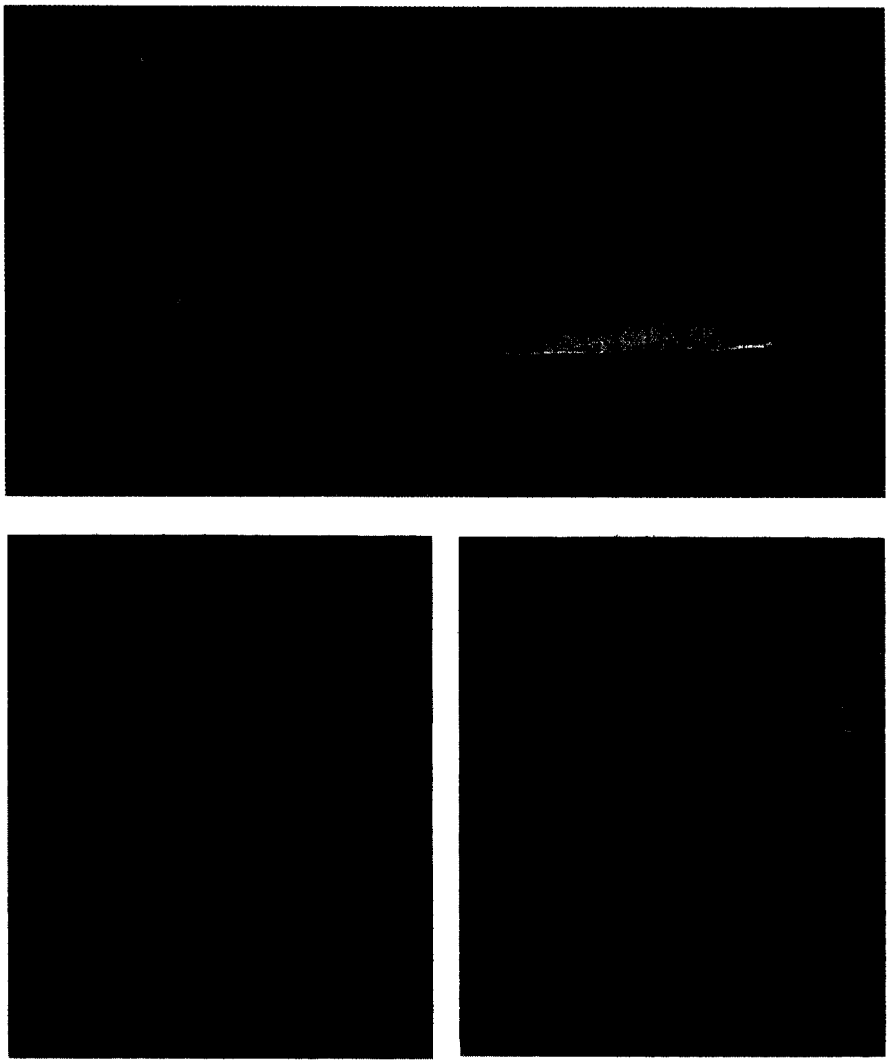

Figure 4 Conodont microstructure. (a) Internal structure of a Pa element of *Ozarkodina*. The structure of the lamellar tissue evident at the left side of the element and shown in (b) is very similar to enamel, and may be homologous. The dark tissue at the core of the element, also shown in (c) contains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

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

Conodont skeletons and functional morphology

The fossil record of conodonts is not only longer than that of other early vertebrates, it is much less patchy. It also contrasts with the record of the ostracoderms, in which there is no direct evidence of feeding mechanisms, by consisting almost entirely of phosphatic elements from the mouth. After the death and decay of a conodont, these elements usually became disarticulated and were scattered over the sea floor by currents and scavengers, and after they were buried in sediment, burrowing organisms often caused even further disruption. Only very rarely did conditions conspire to allow conodont carcasses to be buried without disturbance, preserving the skeletal elements in their original arrangement. As the enclosing sediment turned to rock, the skeletons became flattened onto planes parallel to the original sediment surface. These 'bedding plane assemblages' (Figures 5–7) have been known since the 1930s, but only since the discovery of the complete conodont animals has it been possible to interpret them fully.

The mouth of each conodont contained a number of different elements. Bedding plane assemblages show them to have been arranged in groups, and the animal fossils indicate that an array of elongate comb-like elements lay in front of pairs of shorter, more robust elements. To understand how they operated, however, we need to know the arrangement of the elements in three dimensions, not just the two displayed by the flattened fossils. This information can be deciphered through careful study of the bedding plane assemblages. Each assemblage reflects the collapse of the conodont skeleton onto the sea floor as the supporting soft tissues decayed, and the resulting arrangement of the elements will be affected by the orientation of the conodont carcass on the seabed. Each bedding plane assemblage therefore conforms to one of a small number of recurrent patterns of element arrangement, depending on whether the dead animal was lying on its side, on its back or at an angle. To rebuild the full architecture of the skeletal apparatus we simply need to 'uncollapse' the assemblage out of the rock surface by constructing actual physical models of the skeleton and testing them against the assemblages we find in the rock. If the model can be matched to a variety of different patterns of collapse, then its three-dimensional structure must be correct [14–16].

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

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

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

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

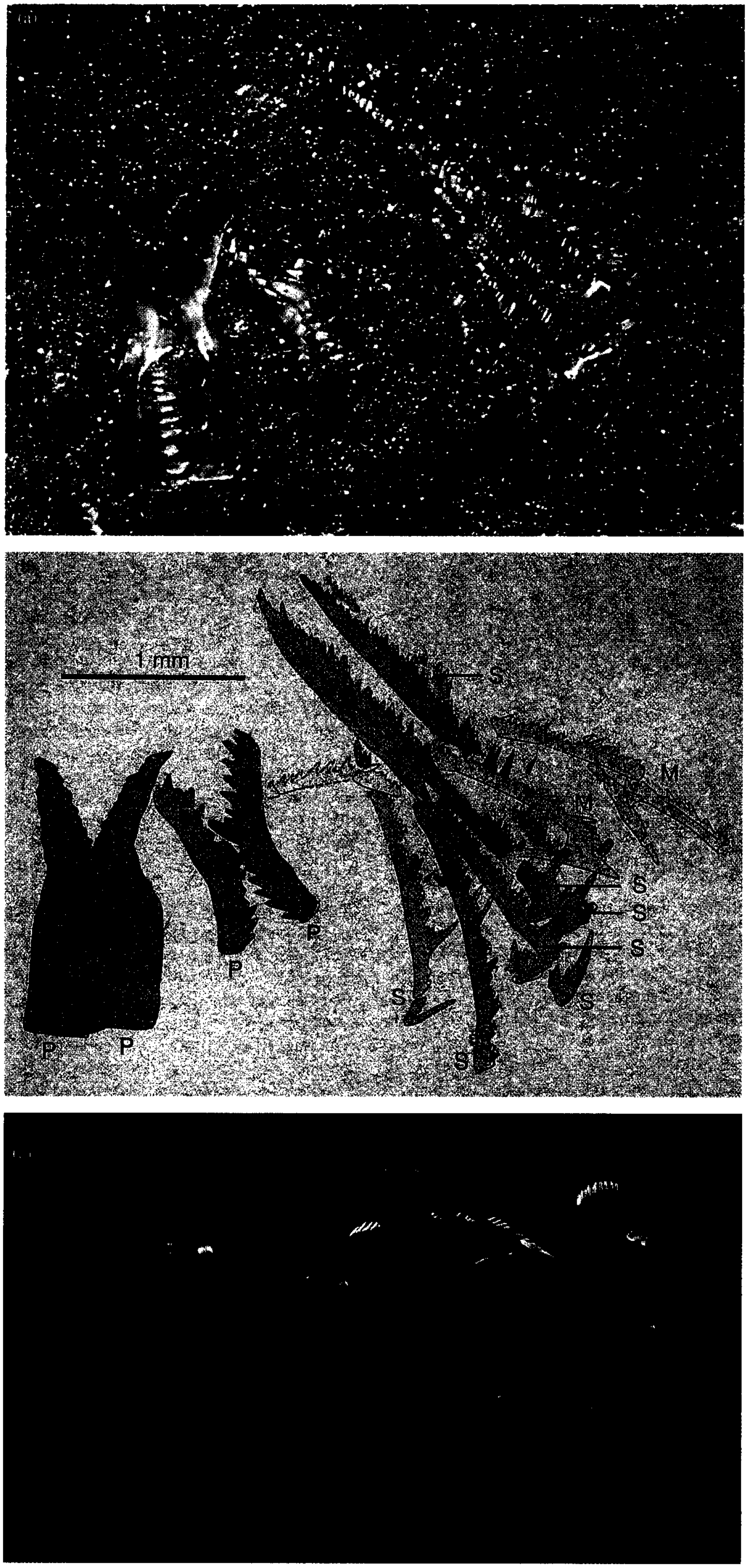

Figure 5

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

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

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

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

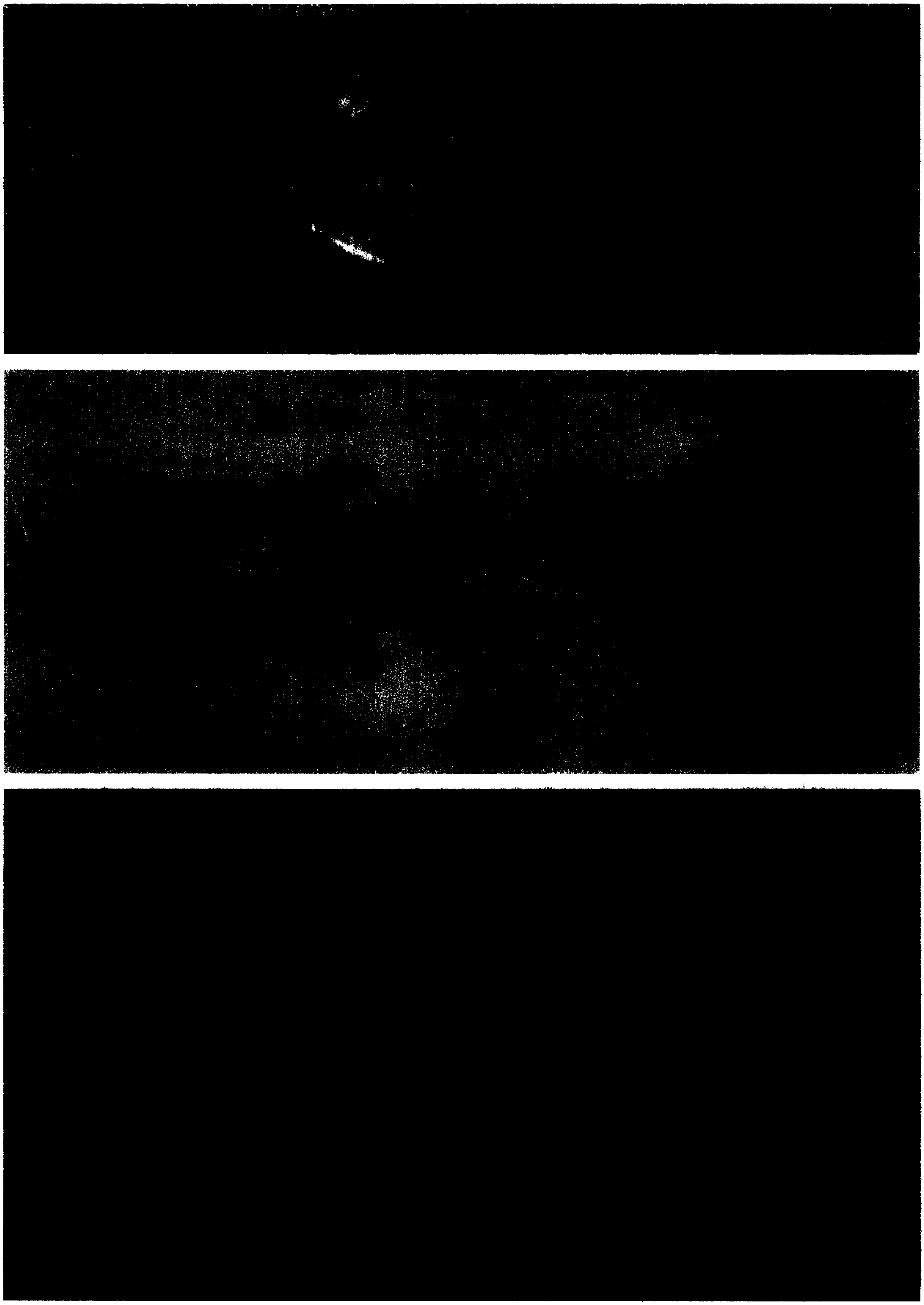

Figure 6

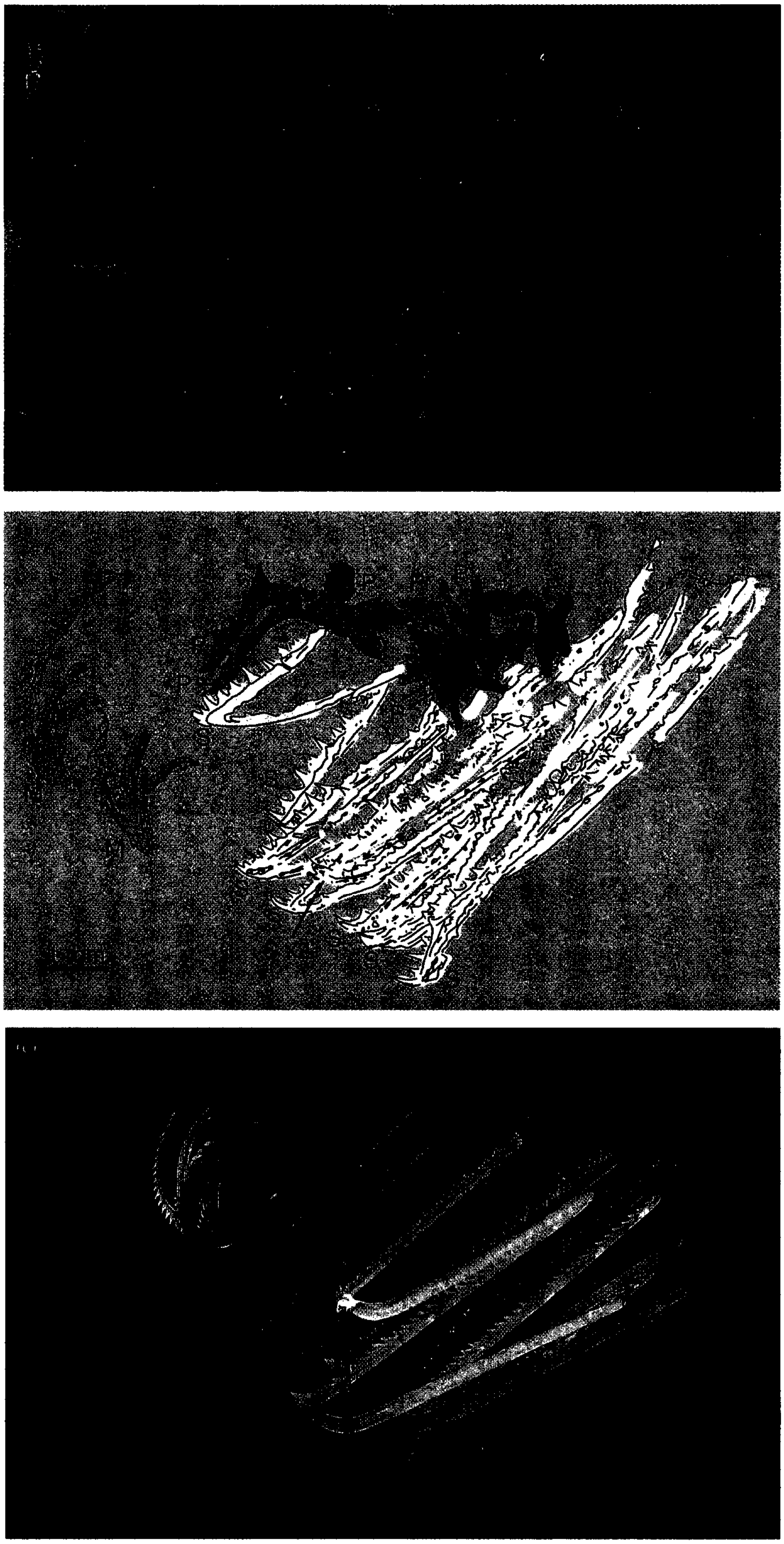

Figure 7 Reconstructing the prioniodontid conodont apparatus. (a) A fossil bedding plane assemblage of the prioniodontid genus *Promissum* from the Ordovician of South Africa. The positions of the different elements of the apparatus are clarified in (b). (c) Our model of the original 3D structure of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

patterns to those found in the teeth of higher vertebrates.

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

Conodonts and the nature of the first vertebrates

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

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

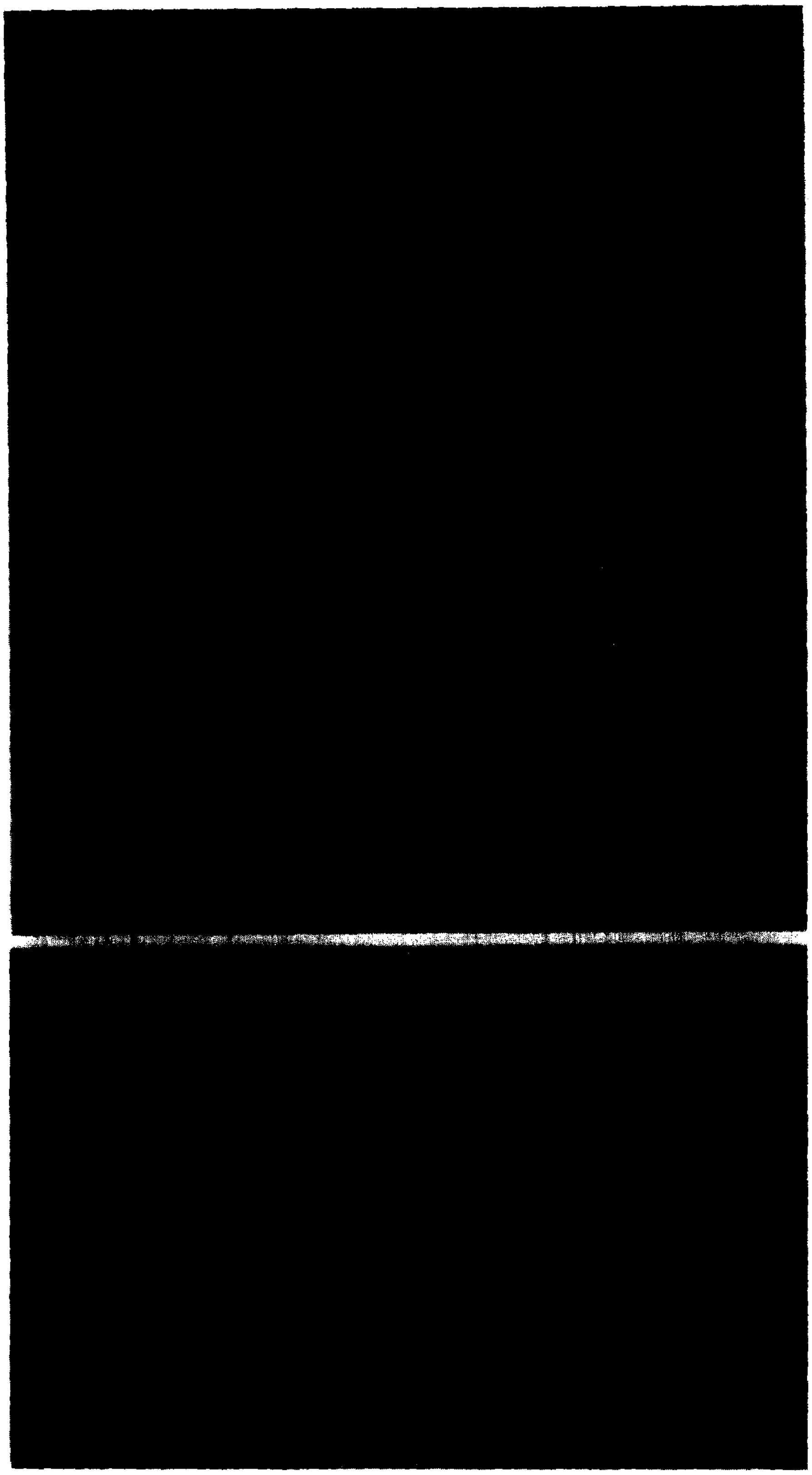

Figure 8 Wear on conodont elements. (a) A well-developed wear facet on a Pa element of *Ozarkodina*; this was formed by repeated contact with another element during feeding; the fine scratching on the surface of the facet indicates that it was caused by shearing movements. The wear illustrated in (b)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

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