

occur in opposite senses, leading to a crenulated pattern very reminiscent of the observations.

The ridge and convective flow evolution described above are clearly strongly dependant on the initial convective field, whose asymmetry initiates the segmentation. Because of the infinite variety of such initial conditions, the geometry and evolution of the ridge segmentation are very different from one case to another. Some characteristics of the ridge segmentation, however, remain in all cases. For instance, the crenulated ridge observed in the experiment shown in Figs 3 and 4a is obtained whenever the initial orientation of the ridge is perpendicular to the spreading direction. Starting with a ridge oblique to the spreading direction, the convective flow induces a segmentation with offsets in the same sense, preserving the overall initial orientation of the ridge. The latter cases account for the geometry observed in the northern MAR²⁵. In all cases, the drift of the ridge segments in the direction of spreading can explain the asymmetric estimates of crustal thickness on the flanks of the MAR from Bouguer gravity residuals²⁶.

Although the conditions required to produce the ridge segmentation depicted here are simple, they do occur in nature. They result from the elastic rheology of a part of the lithosphere in the valley, allowing the tensile stress maxima induced by the three-dimensional convective flow to form a discontinuous set. These stresses are large enough to create perturbations in the large-scale tectonic stresses responsible for the lithospheric necking, leading to shifts in the spreading axis. Asymptotically, all the model runs lead to segments 100–200 km long, orthogonal to the spreading direction. Any change in spreading direction or the interaction between the ridge and the mantle beneath are likely to lead to a reorganization of the convective flow, generating a new segmentation process. Our approach emphasizes the role played by mantle dynamics in triggering ridge segmentation.

Obviously, lithospheric failure and ridge jumps due to unsteady mantle flow may follow more complex rules than the simple but reasonable one adopted here; future studies should lead to an elucidation of what these rules might be. □

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Microwear on conodont elements and macrophagy in the first vertebrates

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FEEDING mechanisms may hold the key to understanding the selective pressures that led to the evolution of vertebrates^{1–3}. But in the absence of direct evidence, hypotheses of feeding mechanisms in the most primitive extinct vertebrates are somewhat speculative, and scenarios that seek to explain vertebrate origins remain controversial. The recognition that the affinities of conodonts lie among the most primitive vertebrates^{4–6} shifts the balance in this debate. I illustrate here microscopic wear patterns on conodont elements that provide the first unequivocal evidence that they functioned as teeth. These microwear patterns were produced as food was crushed and sheared between opposed conodont elements brought into bilateral occlusion. The presence of teeth and evidence of macrophagy in such primitive and early vertebrates support hypotheses that the first vertebrates were predators.

Although recent hypotheses have highlighted the central roles of feeding mechanisms and mode of life in understanding the origin of vertebrates^{1–3}, there is no direct evidence to indicate how early agnathan fishes fed. This has resulted in a lack of consensus regarding feeding in the first vertebrates. The traditional view contends that they were microphagous pump-suspension feeders (for example, refs 3, 7), a hypothesis based on comparisons with amphioxus and larval lampreys, and fossil

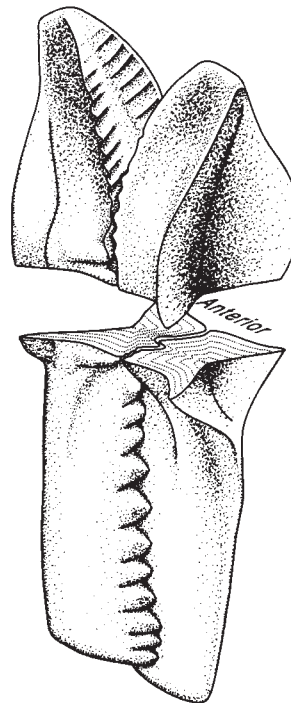


FIG. 1 Bilateral occlusion in ozarkodinid conodonts. The ornamented platform areas of elements were brought into contact by rotation about a hinge point located close to the junction between the platform and the blade. Blade-shaped ozarkodinid elements (not illustrated) also rotated in a similar manner⁹. Illustration is diagrammatic, but based on paired platform (Pa) elements of *Idiogonathodus*.

evidence that early agnathans had heavy dermal armour, lacked adaptations for fast swimming and lacked biting structures. The alternative hypothesis proposes that many of the characters that define vertebrates, such as paired sensory organs and muscular and skeletal adaptations for active life, would not have evolved unless the earliest vertebrates were predatory^{1,2}.

Until recently, conodonts had no relevance to this debate, but it is now recognized that their anatomy and skeletal histology indicate that they were primitive vertebrates^{4,5,8} (although see ref. 4 for a discussion of alternative interpretations). Conodonts first appear in Upper Cambrian strata, 40 million years earlier than other vertebrate remains and, in marked contrast to the paucity of evidence for feeding in early agnathans, the conodont fossil record is made up almost exclusively of their phosphatic mouth parts. However, hypotheses of feeding in conodonts are

controversial. Recent analyses of functional morphology and ontogeny have suggested that conodont elements functioned as teeth^{9,10}, but this hypothesis fails a critical test. The surface of conodont elements is composed of lamellar apatite similar in structure to¹¹, and possibly homologous with, enamel⁵; if they functioned as teeth, therefore, conodont elements should exhibit wear patterns similar to those documented in the teeth of higher vertebrates. The observation that they do not (for example, refs 12–14) is difficult to reconcile with hypotheses of tooth-like function.

Wear has been noted in the teeth of a number of vertebrate groups but systematic study of the microscopic features of dental wear has been restricted to mammals and advanced mammal-like reptiles¹⁵. This 'microwear' is produced *in vivo* by abrasives in food and by the compressive and shearing forces that act on

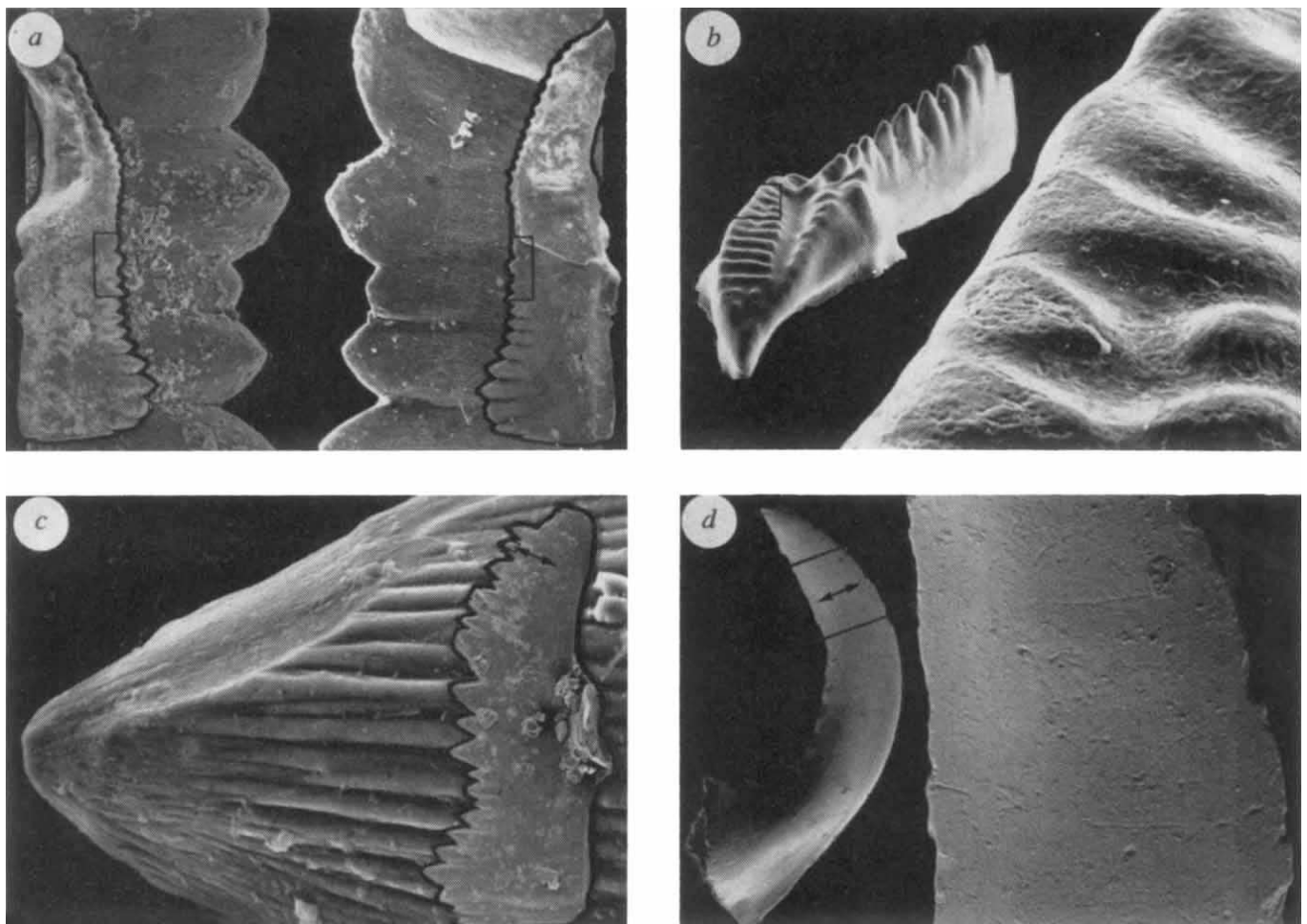


FIG. 2 Microwear in conodont elements. *a*, Pa element of *Gnathodus bilineatus*; the original fibrous surface texture is well preserved on the forward facing surface of the element (shown on left) but has been worn off the backward facing surface (shown on right) where it was in contact with the opposed element. This wear, on one side only, cannot be the result of post-mortem abrasion. The worn areas are smoothly polished with no microfeatures discernible; such smooth polishing or frosting in teeth indicates tooth on tooth contact, either in the absence of food¹⁸ or with non-abrasive food²³. Carboniferous, Stonehead Beck, North Yorkshire; Leicester University specimen LEUIG 114245, whole element $\times 29$, close up $\times 232$. *b*, Pa element of *Idiognathodus*; the crests of the platform ridges in this element are blunted and flattened to form triangular wear facets with pitted microfeatures. Such features are not developed elsewhere on the element and are most unlikely to be post-mortem artefacts. Pitting or chipping of facets is diagnostic of crushing or compression^{16,24}. Upper Carboniferous, Elk County, Kansas,

USA; Royal Ontario Museum specimen ROM 50699, whole element $\sim \times 36$, close up $\sim \times 387$. *c*, Pa element of *Ozarkodina confluens*; a well developed wear facet formed by contact with the opposed element sharply truncates the original fibrous surface texture. The facet is covered with fine, parallel striations which indicate that this element was used for shearing^{17,18,24}; arrows indicate orientation of shearing motion. The distinctive nature of this facet and its location, between denticles, preclude a post-mortem origin. Silurian, Prior's Frome, Hereford and Worcester; Natural History Museum Specimen X-1299, whole element $\times 39$, close up $\times 1,367$. *d*, Element of *Drepanoistodus*, apex tilted a little towards viewer; a number of straight, parallel scratches traverse the slightly convex surface; their parallelism precludes a post-mortem origin. This microwear is characteristic of surfaces used predominantly for shearing^{17,18,24}; arrows indicate orientation of shearing motion. Ordovician, Saudi Arabia, Natural History Museum Specimen X-1300, whole element $\sim \times 36$, close up $\sim \times 194$.

enamel during feeding¹⁵⁻¹⁷. Thus, it records information about the mechanics of food breakdown, the relative motion of teeth, and the nature of food consumed. Analysis of microwear therefore represents a very powerful and direct tool for investigating feeding in fossil animals, but its application to fossil material is complicated by the problem of post-mortem abrasion.

In studies of fossil mammal teeth, post-mortem abrasion can be readily identified because *in vivo* wear forms as distinctive facets at specific locations on functional surfaces¹⁸. In most cases, these functional surfaces were occlusal and, although complex occlusion is generally considered characteristic of mammals¹⁹, a similar condition arose in conodonts^{14,20,21} more than 200 million years earlier. Occlusion in conodonts, however, was bilateral, and in the order Ozarkodinida the left element of a pair fitted behind that on the right (Fig. 1; and manuscript in preparation). This consistent left behind right pairing indicates that rather than being related to asymmetrical feeding behaviour²², morphological asymmetry of ozarkodinid elements represents genetically controlled developmental lateralization to allow occlusion. More importantly, however, recognition of left behind right occlusion enables the identification of functional surfaces of conodont elements. Detailed scanning electron microscopy (SEM) examination of these surfaces has revealed the presence of wear that cannot be post-mortem in origin (Fig. 2) and must have been produced *in vivo*.

Three basic types of microwear occur on mammal teeth: frosting or smooth polishing, fine scratching or striation, and pitting or chipping. The same microwear patterns occur on conodont elements and, in contrast to previous general and sometimes speculative statements of possible 'tooth-like' function, they allow precise characterization of food processing in conodonts. Thus, the polished areas on the blade of *Gnathodus bilineatus* (Fig. 2a) indicate that this part of the element was not in contact with food, or that the species ate food that was not abrasive (compare with refs 18, 23). The pitted microwear on *Idiogonathodus* platforms (Fig. 2b) indicates that food was crushed between opposed elements, but the lack of associated scratches suggests that they did not grind^{16,24}. The parallel scratching on elements of *Ozarkodina confluens* (Fig. 2c) and *Drepanoistodus* (Fig. 2d) is diagnostic of shearing^{17,18,24}. The scratching is related to the abrasiveness of the food consumed¹⁷ and it is probable that *Drepanoistodus* ate food which contained more abrasive particles than that of *O. confluens*. Also, the degree of parallelism of scratches on teeth reflects the tightness of occlusal guidance²⁵; given that conodonts were jawless, the scratching illustrated suggests surprisingly precise control of element contact. This is especially true of *Drepanoistodus* as this genus bore only simple cone-shaped elements and belongs to a primitive order of conodont dating back to the Late Cambrian²⁶.

The presence of wear in conodonts has a number of implications for models of element growth. Wear has been observed on small, immature elements, indicating that conodonts did not grow their teeth to full size before using them. Also, internal discontinuities in conodont growth that have in the past been interpreted as resorption²⁷ may be early phases of surface wear followed by growth. If so, this cycle of alternating growth and use falsifies ontogenetic hypotheses of element shedding and replacement^{28,29}, but makes element histogenesis and growth somewhat problematic. More generally, the interpretation of feeding and mode of life in conodonts and extinct agnathans has been rather speculative, but microwear provides a means of direct analysis and hypothesis testing. For example, some osteostracans³, heterostracans³ and conodonts³⁰ may have been deposit feeders; the feeding elements of such animals should exhibit microwear features that reflect the abrasiveness of their food.

Microwear analysis of conodont function is at a preliminary stage, but the qualitative results presented here, the first application of microwear analysis to non-tetrapods, give an indication of the potential of the methodology. The microwear features

illustrated provide the first unequivocal evidence that conodont elements were teeth and the occurrence of shearing, a method of food breakdown incompatible with microphagy, indicates that conodonts were macrophagous. Conodonts also had good vision³¹ and were probably capable of rapid anguilliform locomotion^{4,30}. The presence of this suite of characters in a group of such antiquity and primitiveness lends strong support to hypotheses that the earliest vertebrates were active predators, their origins linked with an ecological shift from suspension feeding to predation^{1,2}. □

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A giant conodont with preserved muscle tissue from the Upper Ordovician of South Africa

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AN exceptionally preserved new specimen of the giant conodont *Promissum pulchrum* reveals details of the trunk musculature, feeding apparatus and eyes. High-fidelity resolution of ultrastructural features of the trunk myomeres provides the first conclusive evidence of muscle-fibre organization and orientation in an extinct agnathan. The presence of fibrous extrinsic eye muscles confirms the degree of encephalization of the conodonts and is consistent with a cladistic position crownwards of the myxinoids. The soft tissues are uniquely preserved as illite and mixed-layer clay minerals.