

Mammal-like occlusion in conodonts

Philip C. J. Donoghue and Mark A. Purnell

Abstract.—Conodont element function and feeding mechanisms are of considerable paleobiological importance, yet many details remain poorly understood and speculative. Analysis based on morphology, physical juxtaposition, and patterns of surface damage and microwear on pairs of Pa elements from individuals of *Idiognathodus* indicates that these elements crushed food by rotational closure, which brought the oral surfaces into complex interpenetrative occlusion. Other molariform conodont elements also functioned in this manner. Occlusion of this complexity is unique among nonmammalian vertebrates, and is all the more surprising given that conodonts lacked jaws. In addition to enhanced understanding of food processing in conodonts, our analysis suggests that many details of conodont Pa element morphology, which underpin taxonomy and biostratigraphy, can now be interpreted in a paleobiological, functional context.

Philip C. J. Donoghue* and Mark A. Purnell. Department of Geology, University of Leicester, University Road, Leicester LE1 7RH, United Kingdom. E-mail: pcjd2@le.ac.uk and map2@le.ac.uk

*Previous address: School of Earth Sciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, United Kingdom

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Introduction

Once described as little whatzit's (Sweet 1985), conodonts are now generally recognized as vertebrates (see Aldridge and Purnell 1996 for a review), constituting one of the earliest, longest lived, and most diverse clades of jawless fish. This reassignment has left conodonts' biostratigraphic and paleoecological utility undiminished but has dramatically increased their paleobiological significance: the characteristic phosphatic elements of conodonts are among the first remains of vertebrate mineralized tissues in the fossil record (Sansom et al. 1992), and they provide the first direct evidence of macrophagy in early vertebrates (Purnell 1995). Feeding mechanisms are widely held to be of central importance in understanding the evolution and diversification of aquatic vertebrates (e.g., Pough et al. 1996), so conodont element function, once considered esoteric, now has an important role to play in understanding early vertebrate diversity and in analyses of conodont evolutionary history. But many aspects of element function remain poorly constrained and speculative; if the study of conodonts is to realize its paleobiological potential we need to understand food acquisition and processing in detail.

In terms of species and individuals, the ozarkodinid conodonts were the most diverse and abundant. We also know more about ozarkodinids than any other group: almost all of the few known examples of fossilized conodont soft tissues are from taxa assigned to the Ozarkodinida, and from modeling and analysis of natural-assemblages preserving complete element arrays, the architecture of the apparatus is known in detail (Fig. 1) (Aldridge et al. 1987; Purnell and Donoghue 1997). In the ozarkodinid apparatus, the anterior S and M elements (see Fig. 1) grasped food (Aldridge et al. 1987; Purnell and Donoghue 1997) and the P elements, particularly the Pa elements at the posterior of the apparatus sheared and crushed (Purnell 1995). Unlike teeth in more familiar groups of vertebrates, conodont Pa elements were bilaterally opposed across the sagittal plane, and natural assemblages and clusters of diagenetically fused elements indicate that in ozarkodinids the left (sinistral) element of the Pa pair lay behind the right (dextral) (Purnell 1995; Purnell and Donoghue 1997).

Whereas M and S elements are exclusively comblike in shape, many ozarkodinid conodonts developed P elements with complex molar-like morphology, and several authors have suggested that they also developed in-

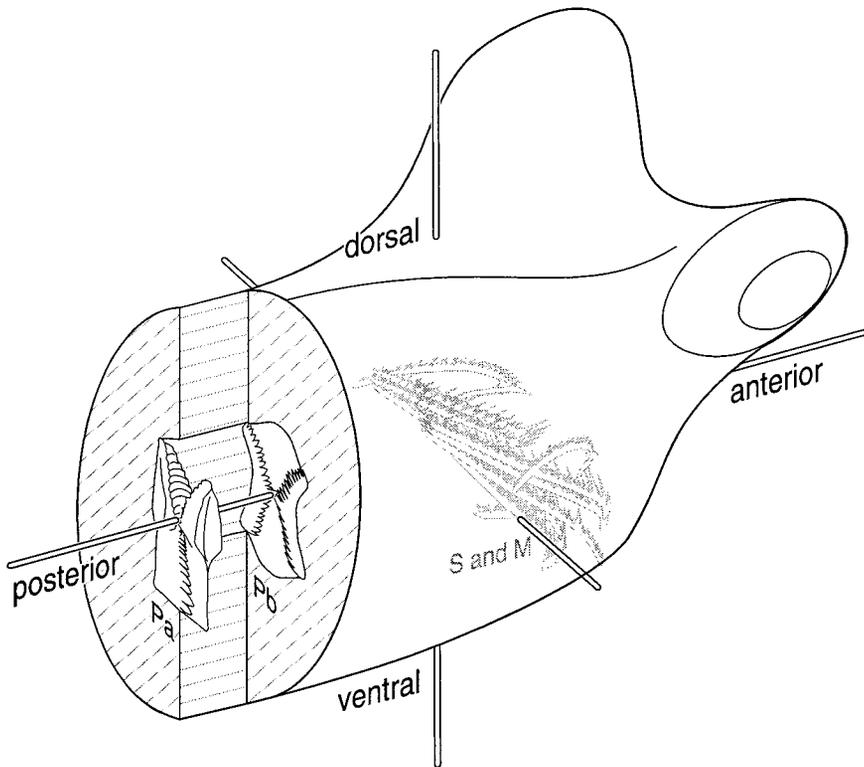


FIGURE 1. Position and orientation of the apparatus in ozarkodinid conodonts. The head is cut away to show the Pa and Pb elements. The principal axes and the terms for orientation used in the text are also shown. Apparatus architecture after Purnell and Donoghue (1997).

terlocking occlusion (Jeppsson 1971; Nicoll 1987; Weddige 1990; Purnell 1995). This hypothesis is supported by microwear patterns indicating that Pa elements were repeatedly brought together with a degree of occlusal guidance that is difficult to reconcile with the fact that conodonts were jawless (Purnell 1995). Occlusion is very uncommon among vertebrates and has rarely been recorded outside mammals. There are exceptions (e.g., two Cretaceous crocodyliforms [Clark et al. 1989; Wu et al. 1995], a Paleocene mammal-like reptile [Fox et al. 1992], two Triassic reptiles [DeMar and Bolt 1981; Carroll and Lindsay 1985], a sauropod [Robinson 1956], a pterosaur [Wild 1978], and lungfish, with complex dental plates that occlude [e.g., Kemp 1977]). In all these examples occlusion is much simpler than in mammal molars, and some authors have gone as far as suggesting that complex occlusal dentition is unique to mammals (Janis 1990; Smith 1993). Improvements in oc-

clusion during the early evolution of mammals were linked to changes in jaw structure, articulation, associated musculature, and brain programs (Young 1978). The possession of jaws at least is usually considered a prerequisite for occlusion, and the hypothesis of complex interlocking occlusion in ozarkodinid conodonts is thus extremely surprising and counterintuitive.

Were conodonts capable of mammal-like occlusion? If so, how was element motion constrained in the absence of jaws? Here, we address these questions through functional analysis of morphology and patterns of surface wear and damage on molariform Pa elements dissected from conodont natural assemblages.

Previous Work on Occlusion in Conodonts.— Direct observation of the occlusal process in conodonts is obviously not possible, and examination of occlusal surfaces on opposed elements is not a simple matter. Natural assemblages preserve together the skeletal remains

of individual conodonts, including articulated element pairs, but they are held together by indurated sedimentary matrix or by diagenetic minerals, and the occlusal surfaces of elements are not visible. Thus almost all previous work on occlusion in conodonts has relied on indirect methods, and all previous functional reconstructions of element pairs are hypothetical. Jeppsson (1971) for example, reconstructed *Idiognathodus* Pa elements as an interlocking occlusal pair but based this on line drawings of elements in Lindström (1964: Fig. 43f,g). The elements upon which these drawings were based are approximately equal in size and came from the same formation, but almost certainly did not come from a single individual. Furthermore, although the spacing of the supposedly interlocking ridges and furrows was measured, their depth and height are entirely hypothetical (Jeppsson 1979). Nicoll (1987, 1995) took Jeppsson's approach further by physically reconstructing opposed pairs of Pa elements belonging to a variety of taxa. Pairs of sinistral and dextral elements of similar size were selected from collections of isolated elements and reconstructed according to patterns of articulation in fused element clusters (Nicoll 1985). He then photographed the element pairs and evaluated the nature of the fit between the elements' opposed articulating surfaces. Nicoll (1987) concluded that because the pairs in his study did not fit closely together conodont elements must have been permanently covered by soft tissue in life. However, the poor degree of interlocking between the elements observed by Nicoll may have resulted from his use of discrete element collections; like Jeppsson (1971), the elements he put together almost certainly came from different individuals and had not worked together in life.

Weddige (1990) drew on these earlier studies in proposing antagonistic "see-saw" interaction between ozarkodinid P elements, and Purnell and von Bitter (1992) later proposed similar interaction and element motion for *Vogelgnathus*. Purnell (1995) used an opposed pair of Pa elements of *Idiognathodus* as a diagrammatic illustration of bilateral occlusion and left-behind-right pairing in ozarkodinid conodonts. This was based on the model of

skeletal architecture subsequently published by Purnell and Donoghue (1997, 1998) but the details of interlocking occlusion between the platforms of the opposed elements were hypothetical.

Material and Methods

Our analysis is based on elements of *Idiognathodus* (sensu Baesemann 1973) from natural assemblages on bedding planes of the unnamed black shale unit in the Modesto Formation (McLeansboro Group, Pennsylvanian) below the La Salle Limestone Member at Bailey Falls, Illinois (locality 1 of Rhodes 1952). Together with coeval deposits in the vicinity, this represents the most prolific source of natural assemblages (e.g., Du Bois 1943) and provided the material for the recent reconstruction of the ozarkodinid feeding apparatus (Purnell and Donoghue 1997, 1998). One of the element pairs illustrated here (Birmingham University, Lapworth Museum specimens BU 2683a and BU 2683b; hereafter referred to as the BU pair) was recovered using the methods outlined in the appendix. The other illustrated pair (University of Illinois specimens UI X-1509a and UI X-1509b; hereafter referred to as the UI pair) is from the same horizon and locality but was recovered by Rhodes (1952) (deposited with the figured material). We are unsure of the techniques used to extract these elements from the matrix of the bedding plane assemblage, but we suspect that the process was essentially mechanical.

The details of occlusion in these element pairs were investigated directly by placing the Pa elements in opposition. Gum tragacanth was used as a temporary adhesive to hold the elements together for SEM examination.

Note that throughout this paper we use anterior and posterior not in the conventional arbitrary sense, but to indicate the in vivo orientation of the elements. The terms dorsal, ventral, sinistral, and dextral also refer to in vivo orientation and position (Fig. 1).

Morphology, Occlusion, Motion, and Microwear

Morphology.—In life, the paired elements were opposed across the animal's axis of bi-

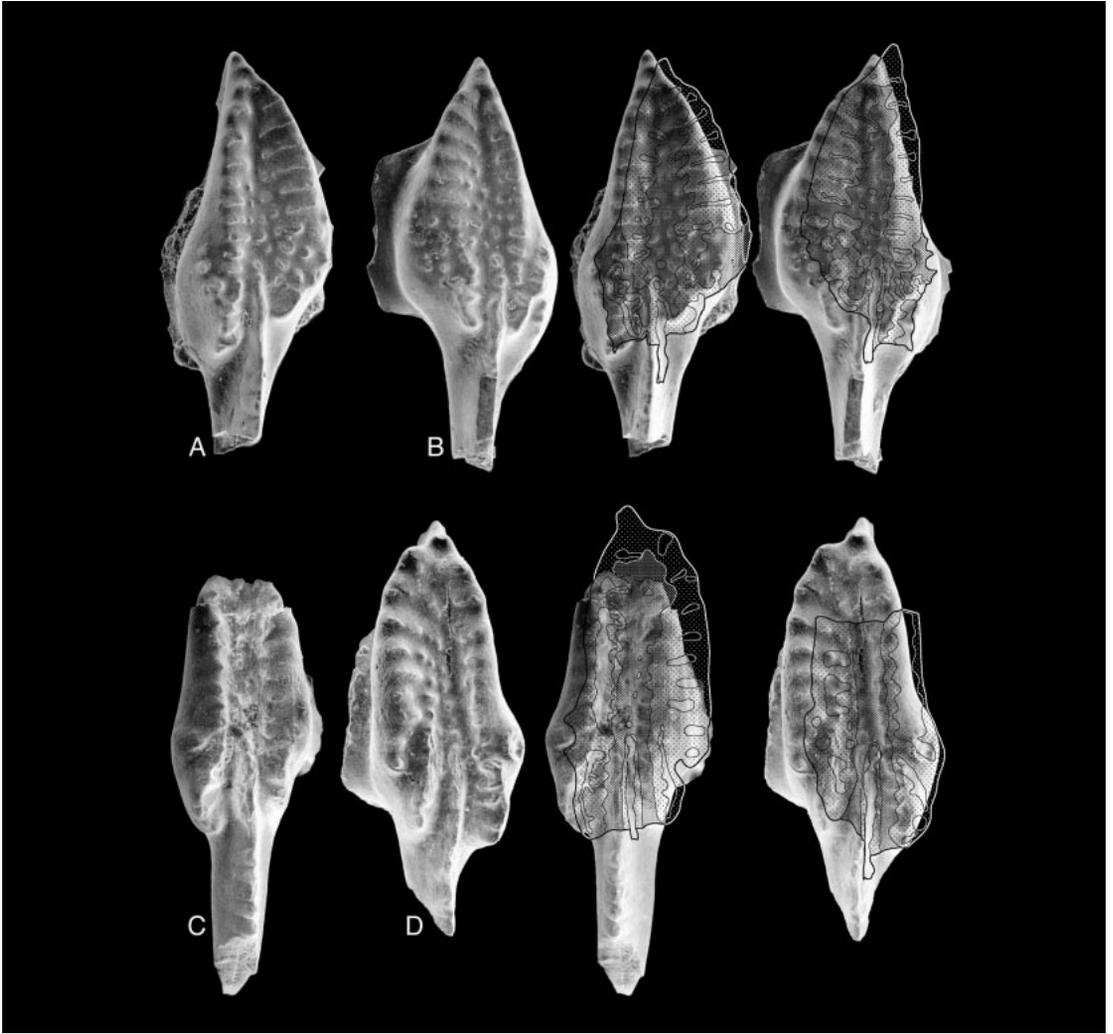


FIGURE 2. Stereo pairs of the Pa elements of *Idiognathodus* studied. The overlays are traced from the elements and indicate approximate contouring of the surface (highest dot densities correspond to lowest topography). These have been inverted and superimposed on the opposed element to show the inverse correspondence of morphological features when occluded. A, Sinistral element BU 2683a, $\times 48$. B, Dextral element BU 2683b, $\times 48$. C, Sinistral element UI X-1509a, $\times 52$. D, Dextral element UI X-1509b, $\times 53$.

lateral symmetry (see Purnell and Donoghue 1997, 1998), yet the elements dissected from the bedding plane assemblages do not exhibit mirror-image symmetry and differ in significant morphological details of their oral surfaces (Figs. 2, 3). Compared with the sinistral element of the BU pair (Figs. 2A, 3A), the platform of the dextral element (Figs. 2B, 3B) is slightly wider: the maximum width of the raised area forming the anterior side of the platform is approximately 0.2 mm, whereas the maximum width of the same area on the sinistral element is approximately 0.14 mm.

On both elements, these raised anterior margins are strongly convex anteriorly (Figs. 2A,B, 3A,B), and considerably wider than the raised area on the posterior side of the platform (up to twice as wide). They bear transverse ridges that are asymmetrical, their ventral faces steeper than the dorsal faces. The posterior margins of the two elements are less convex. Between the raised margins, both elements have a slightly depressed medial trough that extends from the end of the ventral blade to the dorsal tip of the element. The central area of the platform (i.e., above the

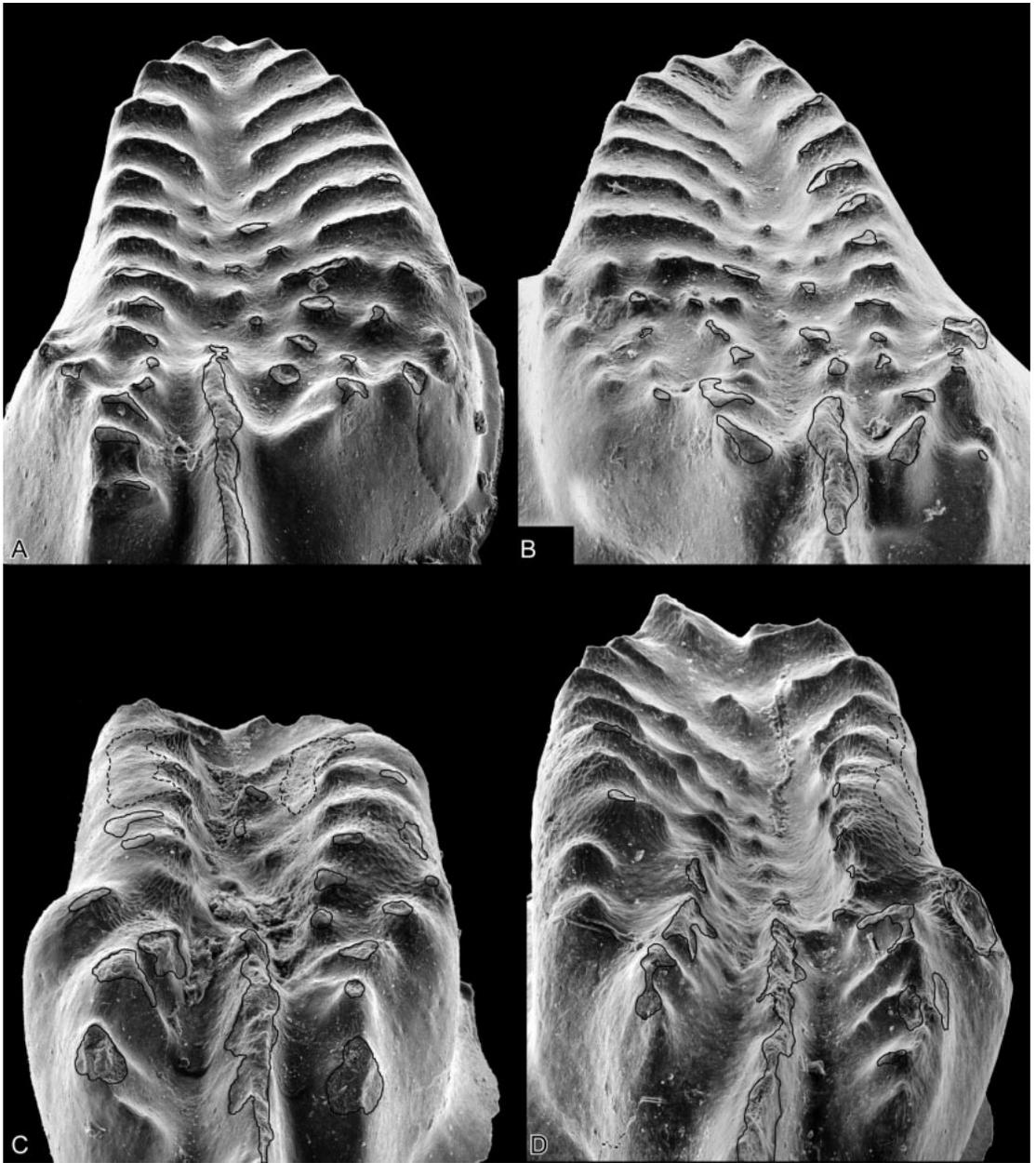


FIGURE 3. Wear and surface damage on the Pa elements of *Idiognathodus*, oblique ventral views. Areas of damage and wear are outlined in black, the dashed lines indicate equivocal areas of damage. See text for details. Images are photomontages of several photomicrographs. A, Sinistral element BU 2683a, $\times 140$. B, Dextral element BU 2683b, $\times 140$. C, Sinistral element UI X-1509a, $\times 180$. D, Dextral element UI X-1509b, $\times 180$.

apex of the basal cavity) is covered with small nodes, but it grades dorsally into the smooth medial trough. The ventral part of the oral surface, in the area around the junction of the platform and blade, is dominated by a complex arrangement of topographic highs and lows that together form a series of alternating

dorso-ventrally oriented ridges and furrows that lie in subparallel alignment on either side of the blade. In the sinistral element the ventral blade is aligned with the medial axis of the dorsal part of the platform and the ridge flanking the blade on the posterior side is aligned with the posterior margin. In the dex-

tral element, however, the blade and its lateral ridges and furrows are offset posteriorly with respect to the dorsal portion of the platform. The platforms of the two elements are similar in length and differ only slightly in area (sinistral platform area 0.2 mm², dextral 0.23 mm²).

The sinistral element of the UI pair is broken toward the dorsal end (Fig. 2C), presumably as a result of extraction from the shale. The platform of the dextral element (Figs. 2D, 3D) is slightly wider than that of the sinistral element (Figs. 2C, 3C). The raised area forming the anterior side of each element is ornamented with transverse ridges. These ridges are rather blunt on the sinistral element, but those of the dextral element are sharp and descend toward the medial trough of the platform where they break up into nodes. The raised areas forming the posterior margins of the elements are narrower, but approximately equal in height to the anterior margins. Their ornament is more nodose than ridgelike, the nodes rather flattened and forming a serrated posterior side to the medial trough. Both elements have a deep, steep-sided medial trough, the floor of which is ornamented with small nodes. As in the other element pair, the ventral portion of the oral surface, in the area around the junction of the platform and blade, takes the form of a series of alternating dorso-ventrally oriented furrows and nodose ridges lying in subparallel alignment on either side of the blade. In the sinistral element these are approximately aligned with the axis and margins of the dorsal part of the platform. In the dextral element, as in the other pair, they are offset posteriorly. Both elements have a marked posterior protuberance at this point.

In both pairs, the ventral part of the platform of the Pa elements is morphologically the most complex part of the element; this is typical of *Idiognathodus sensu lato*.

Occlusion of the Element Pairs.—Rather than infer the details of occlusion between opposed elements from their morphology, we physically placed the elements together to observe occlusion directly. In each pair, the sinistral element was positioned so that its blade lay behind that of the dextral element, as indicated in natural assemblages (Purnell 1995; Purnell

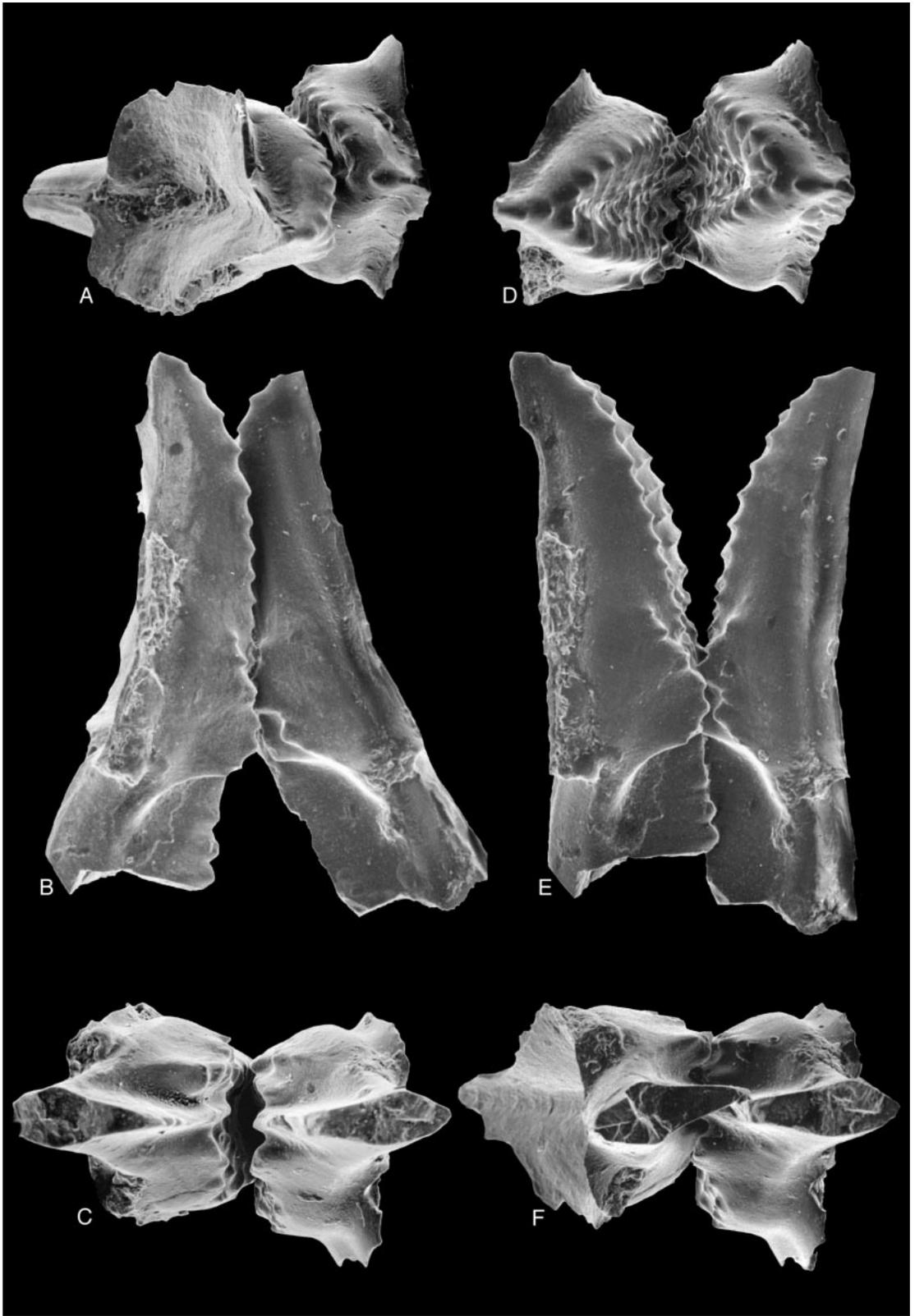
and Donoghue 1997, 1998). Juxtaposed in this manner, as the oral surfaces of the platforms are brought together they lock into position (Figs. 4D–F, 5D–F, 6).

Like the blades, the opposing platforms are offset so that the sinistral platform sits slightly to the posterior of its dextral counterpart (Figs. 4D,F, 5D,F). The principal point of articulation is the ventral part of the platform around the area where the blade joins the platform. The complex morphology of this area leads to very precise articulation of the opposing platforms; they interlock much more closely than the more dorsal parts of the oral surfaces, largely because the depth and height of the opposed articulating components allow considerable interpenetration (Figs. 4D–F, 5D–F, 6). The alternating dorso-ventrally oriented furrows and ridges on either side of the blade (Figs. 2, 3, 6) also incorporate a number of transverse protuberances that result in a very stable three-dimensional interlocking of the opposing platforms. Each morphological structure is mirrored by an “inverted” or negative structure in the opposing element, so that each alternation of ridge and furrow is matched by a furrow and ridge on the opposing element (Figs. 2–6).

Rotating the elements about this point of articulation brings more dorsal areas of the oral surfaces of the platforms together. They also interlock, but less precisely: in each pair the raised posterior margin of the dextral element and the raised anterior margin of the sinistral element occlude with the medial trough of the opposed element. Continued rotation, bringing the dorsal parts of the platforms together, causes the interlocking furrows and ridges of the complex ventral area of the platform to disengage (Figs. 4A–C, 5A–C).

The anterior edge of the dextral elements and the posterior edge of the sinistral elements are nonocclusal, protruding anteriorly and posteriorly, respectively (Figs. 4, 5). When the dorsal parts of the platforms on the BU pair are occluded, the transversely oriented ridges of the opposing surfaces interdigitate.

Element Motion.—The complex interpenetrative interlocking of the furrows and nodose ridges in the ventral area of the platform effectively restricts movement between the ele-



ments to simple opening and closure. When the furrows and ridges are engaged, anterior-posterior motion between the elements is not possible, as the elements can only move in the transverse plane, articulating about the anterior-posterior axis. Viewed along this axis, the surfaces of the platforms are convex and the whole oral surface cannot be in simultaneous contact (Figs. 4, 5). Instead the platforms come into contact by rocking from ventral to dorsal, the various matching morphological structures interlocking as they meet. Concomitantly, as the platform surfaces occlude from ventral to dorsal, the surfaces of the blades move past each other, then part; reversal of this motion causes the platforms to occlude from dorsal to ventral and the sides of the blades to overlap once more (Figs. 4, 5, 7).

Surface Damage, Wear, and Microwear.—Because the elements studied here are from articulated natural assemblages preserved in black shales, they cannot have undergone post mortem transport, and surface damage cannot be the result of sedimentary abrasion. Thus the wear on the surfaces of these elements must have been produced in vivo, providing important and unequivocal corroboration of surface wear observed on specimens from collections of disarticulated elements (Purnell 1995). Damage produced in vivo during the normal use of feeding structures provides a type of evidence regarding function fundamentally different from that derived from interpretations of morphology; for fossils, it is the closest possible approximation to direct observation of function (Purnell in press).

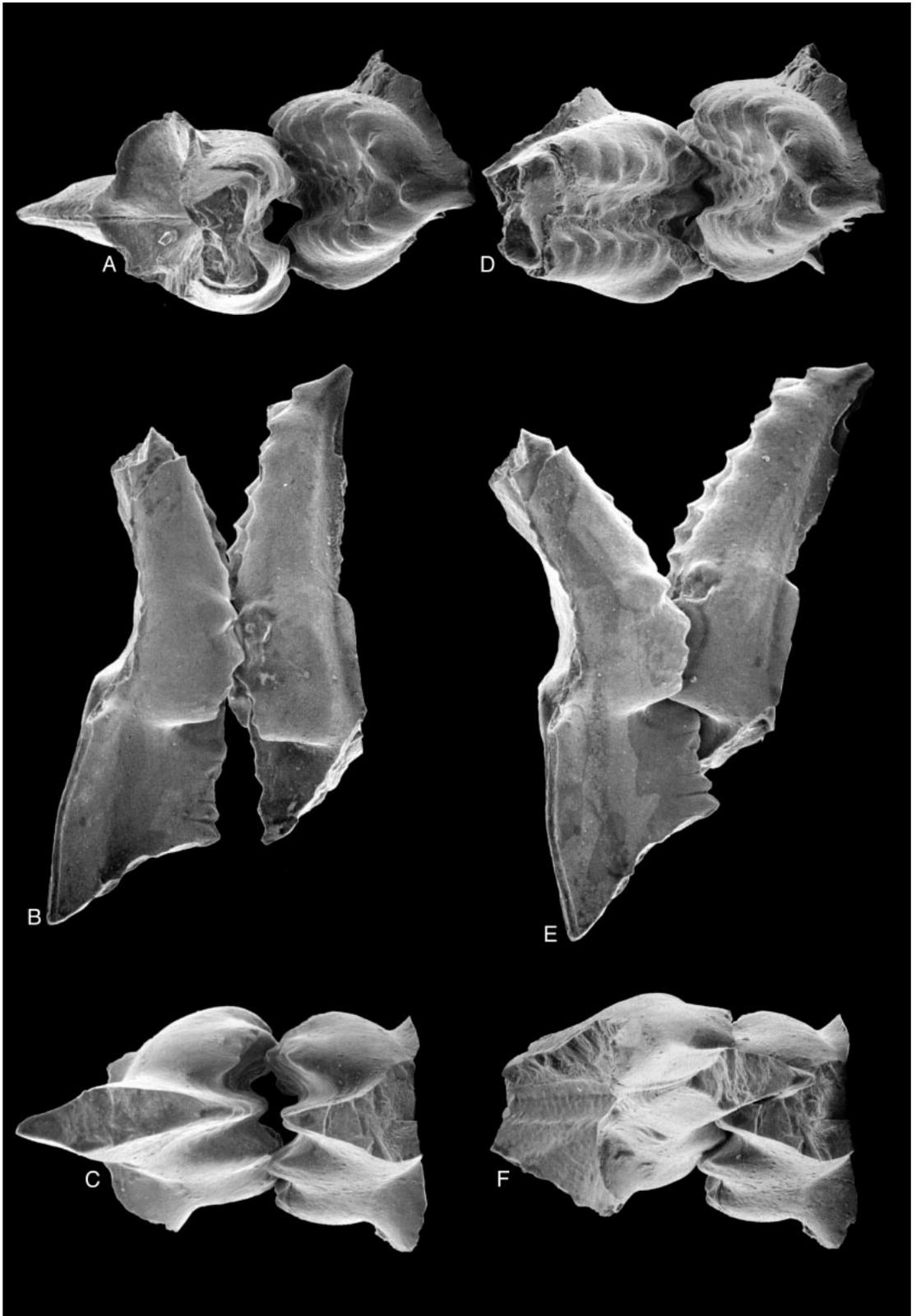
On the dextral element of the BU pair (Fig. 3B), surface damage is evident on the tips of nodes and ridges toward the ventral part of the platform, particularly in the area where the blade joins the platform. Surface damage is most intense on the crest of the blade in this area. Damage is also present on the crests of the ridges in the posterior margin, but the

ridges on the anterior margin retain sharp crests and primary polygonal micro-ornament. On the sinistral element (Fig. 3A), damage is also concentrated in the ventral part of the platform and is especially evident on the crest of the blade. The transverse marginal ridges toward the dorsal part of the platform are pristine, with primary polygonal micro-ornament. On the dextral element of the UI pair (Fig. 3D), damage is clearly evident along the crest of the blade and on the crests of the adjacent ridges. The posterior protuberance has a marked central depression that is also the result of surface damage. Except for two small areas of damage, the ridges of the anterior margin of the platform are pristine and have particularly well-preserved polygonal micro-ornament. Polygonal ornament is also preserved on the posterior margin, except for an area near the crest that is smooth, possibly as a result of wear. The sinistral element (Fig. 3C) also exhibits clear damage on the crest of the blade and tips of adjacent nodes and ridges. The anterior margin preserves some primary polygonal micro-ornament, especially between ridges, but has some small patches of damage on ridge crests. The posterior margin preserves polygonal ornament on its medial face, but the crest is smooth, possibly as a result of wear. There is a patch of surface damage toward the dorsal end of the medial trough, but as this end of the platform is broken, damage during preparation cannot be excluded as the cause.

Surface damage on the elements provides an independent test of our reconstructed pattern of occlusion and hypothesis of element motion. The distribution of surface damage accords well with the reconstructed pattern of element occlusion. The nonocclusal anterior margin on the dextral elements and the posterior margin on the sinistral elements exhibit the least damage and the best-preserved primary micro-ornament. Possible wear on the crest of the posterior margin of the UI sinistral

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FIGURE 4. Occlusal juxtaposition of the *Idiognathodus* Pa element pair BU 2683. A, B, C, Dorsal and middle parts of platforms occluded, dorsal, posterior, and ventral views respectively; D, E, F, Ventral area of platform occluded, dorsal, posterior and ventral views respectively. The sinistral element is on the left in all views. A, $\times 77$; B, $\times 77$; C, $\times 75$; D, $\times 77$; E, $\times 78$; F, $\times 77$.



element is slightly anomalous, but it may have been produced by contact with the posterior side of the posterior margin of the dextral element, which also exhibits possible wear. However, the damage in these two areas is somewhat equivocal as it is possible that the lack of polygonal ornament on these surfaces is original. On all the elements damage is lightest toward the dorsal end of the platform, and heaviest on the blade and adjacent nodes and ridges (the crest of the blade would originally have been denticulated but has been worn almost flat). This is consistent with the stresses that would have been generated in this area if it was the hinge point about which the element articulated, with the interlocking of opposed ridges and furrows constraining element motion to the transverse plane. Damage to the tips of nodes in the central area of the medial trough in the elements of the BU pair (Figs. 3A,B) is also consistent with our reconstruction of occlusion, as this is an area where nodes opposed nodes.

In addition to the distribution of surface damage and wear on the element pairs, the microscopic textures developed within facets can also yield valuable information. Many of the areas of damage on these elements exhibit chipped or pitted textures, but in some areas, particularly where surface damage extends down the sides of the blade, for example, the pitted appearance is probably the result of an irregular fracture rather than pitted microwear. However, pitted microwear is well developed on the crests of the blades of all elements (the BU pair especially), on several of the damaged nodes on the platforms of the BU elements, and on the nodes and ridges flanking the blade on the UI elements (Figs. 3C,D). Such pitting or chipping in teeth is diagnostic of crushing or compression (Gordon 1982; Maas 1994). Smoothly polished surfaces, another characteristic microwear texture, are developed on the blades of the elements: on the anterior side of the sinistral elements and on

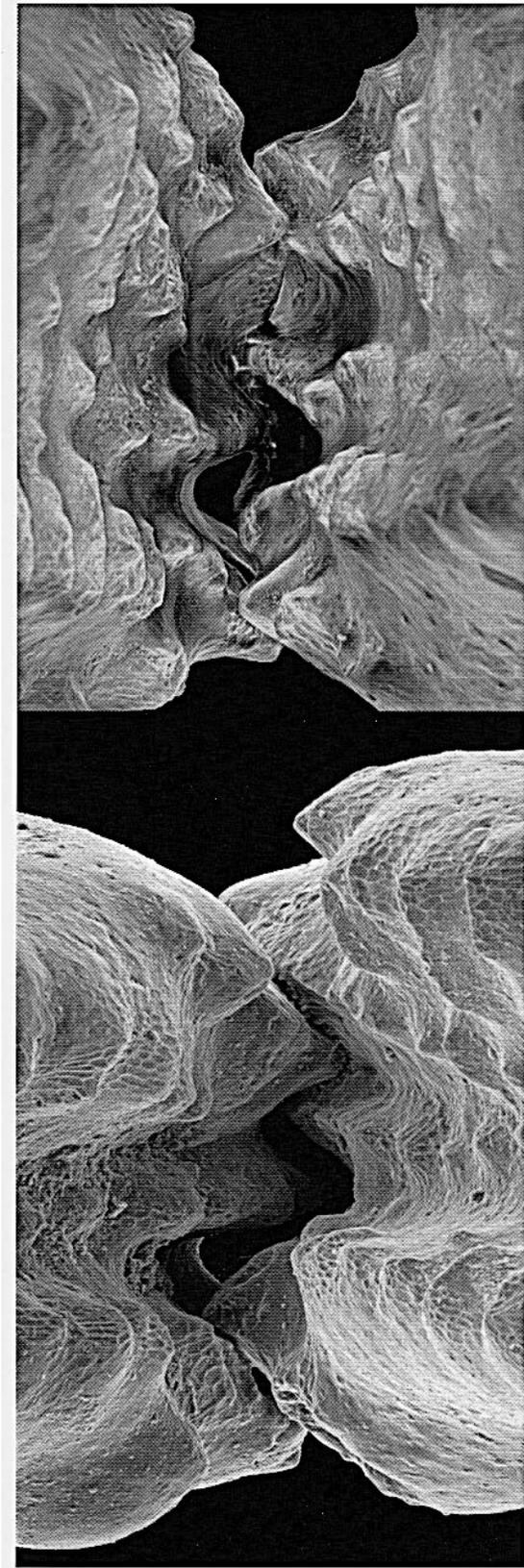
the posterior side in dextral elements (i.e., on the occlusal surfaces) (Fig. 8). Similar microwear has been observed in the same position on the blades of *Gnathodus bilineatus* Pa elements (Purnell 1995); it indicates element-on-element contact either in the absence of food (Teaford 1988) or with nonabrasive food (Rensberger 1978). The smooth areas on the posterior margins of the UI element platforms (Figs. 3C,D) may be the original surface texture, or they could be exhibiting polished microwear textures. Perhaps the most significant feature of the microwear on the elements is the absence of any finely striated or scratched textures seen on some other conodont elements (Purnell 1995). Scratched textures are produced by shearing (Gordon 1982; Teaford 1988; Maas 1991), and although the lack of scratching represents negative evidence, taken with the development of pitted textures it supports the hypothesis that element motion was constrained to a single transverse plane.

Function

Analyses linked to apparatus architecture (Aldridge et al. 1987; Purnell and Donoghue 1997), ontogeny of elements and apparatuses (Purnell 1993, 1994), and microwear patterns (Purnell 1995) all indicate that the Pa elements of *Idiognathodus*, and other ozarkodinids, were involved in the processing of food rather than its acquisition. Our analysis of element morphology, the nature of occlusion and interlocking of the elements, and the patterns of surface damage and microwear provide several lines of evidence from which we have interpreted in detail how the Pa elements of *Idiognathodus* performed this function. All the evidence of our analysis of the natural pairs indicates that motion between the elements was restricted to bilateral occlusion in the transverse plane, and that this was accomplished by rotation (Fig. 7). The complex interlocking morphology of the ventral part of the platform, the presence of pitted microwear

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FIGURE 5. Occlusal juxtaposition of the *Idiognathodus* Pa element pair UI X-1509. A, B, C, Middle parts of platforms occluded, dorsal, posterior, and ventral views respectively; D, E, F, Ventral area of platform occluded, dorsal, posterior and ventral views respectively. The sinistral element is on the left in all views. A, $\times 87$; B, $\times 76$; C, $\times 89$; D, $\times 87$; E, $\times 76$; F, $\times 89$.



textures on occlusal areas of the platforms, the presence of smooth-polished areas on the blades, and the absence of any evidence of shearing all indicate that *Idiognathodus* Pa elements processed food by crushing. The asymmetry of the transverse ridges on the dorsal parts of the platforms (particularly on the BU elements) indicates that the power-stroke in the occlusal cycle involved closure of the platforms from ventral to dorsal, the steeper ventral faces of the ridges acting to prevent food particles from being squeezed dorsally during closure. The reverse action reset the elements for another powerstroke, analogous to the opening of jaws in preparation for biting.

Much of the most significant information for understanding the details of how the elements interacted and functioned comes from the ventral part of the platform. Morphologically, this area seems to be an adaptation to constrain element motion to the transverse plane, but the surface damage and microwear developed in this area provide more detail. The crest of the blade in this area of the element bears clear evidence of breakage and pitting, indicating element-on-element contact and crushing. This pitting cannot simply be the result of crushing brittle foodstuffs as this would have left clear evidence in the form of scratches on the sides of the blades, but as noted above, they are smoothly polished. The damage on the crests must have been produced by direct contact of one blade crest on another as the elements were brought together. This hypothesis is also supported by the lack of wear in the furrows adjacent to the blades. This indicates that at some phase in the occlusal cycle the ventral platform areas on opposed elements were parted. When parted these areas would have provided no constraints on element motion and could not have acted together as a hinge. Thus the function of the morphologically complex ventral platform probably changed through the occlusal cycle.

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FIGURE 6. Complex interlocking occlusion of the ventral area of the platform in the Pa element pairs of *Idiognathodus*. Dorsal views, sinistral elements to the left. Upper image BU 2683, ~ ×260; lower image UI X-1509, ~ ×280.

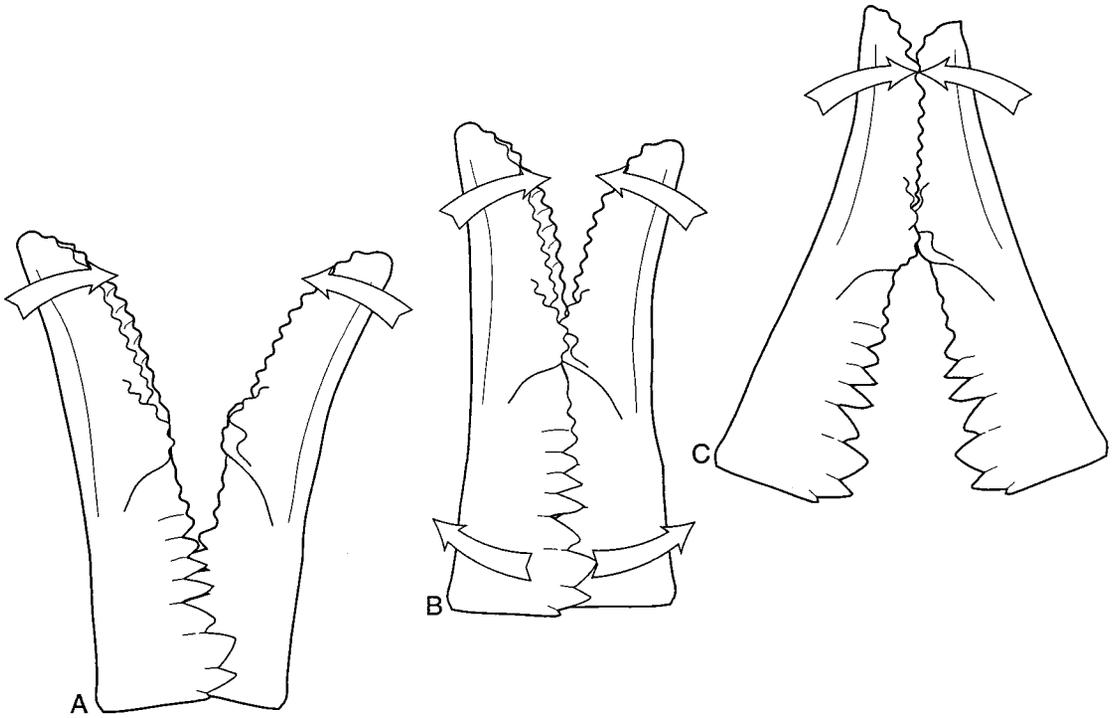


FIGURE 7. Operation of *Idiognathodus* Pa elements. A, Ventral blades partially occluded. B, Ventral area of the platform occluded and interlocking. C, Dorsal areas of the platforms occluded. Reversal of this motion resets the elements for another powerstroke.

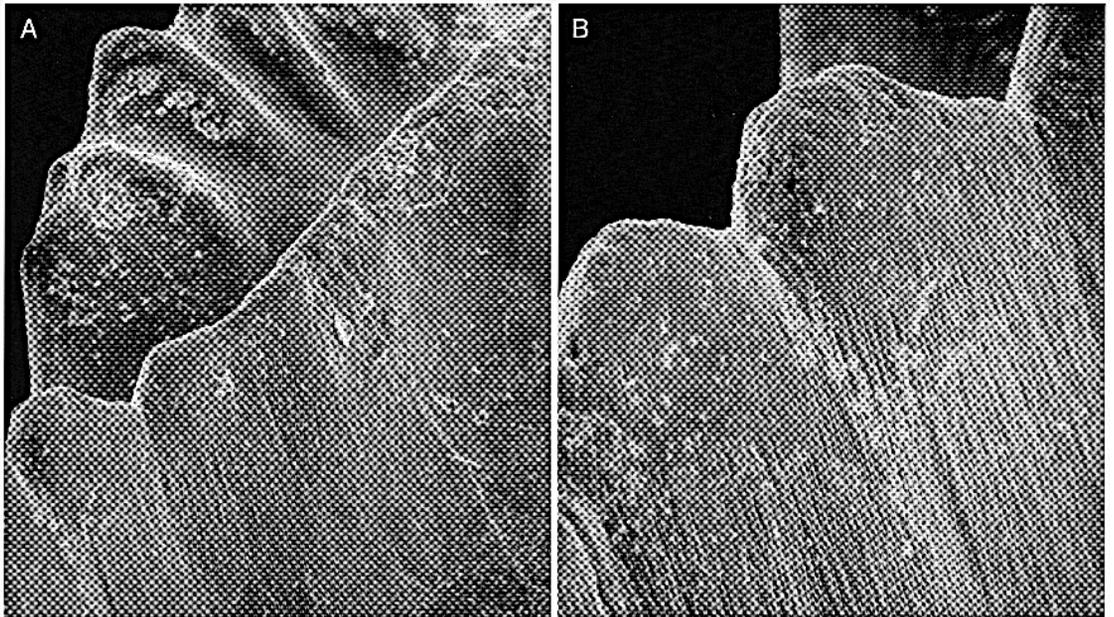


FIGURE 8. Surface damage and microwear on *Idiognathodus* Pa element BU 2683a. A, Oblique view showing blunting and damage to the crest of the blade, $\sim \times 390$. B, Enlargement of part of A showing where the primary striated ornament has been worn away to form smooth polished facets on the anterior surfaces of the denticles, $\sim \times 880$.

In the early stages of closure, the area functioned in simple crushing as the ridges and nodes were brought together, with the long, ventrally extended, flat-sided blades acting as the primary means of element alignment. As closure continued, however, the furrows and nodose ridges would have started to interlock, and through the middle part of the crushing cycle this area would have provided a high level of constraint and prevented translational motion between the elements, thus maximizing the efficiency of crushing between the platforms. As the dorsal parts of the platforms come into contact, however, the interlocking furrows and ridges disengage and occlusion is poorly constrained (Figs. 4A–C, 5A–C). In life, occlusion may not have proceeded to this point, and this may account for the lack of wear toward the dorsal ends of the platforms.

The cycle of closure in *Idiognathodus* is analogous to the way in which interlocking occlusal molars operate in mammals (e.g., Crompton and Hiiemae 1970). The surface morphology of the element platforms is also similar to that of mammalian crushing teeth (cf. Rensberger 1995). The raised ridges of mammal teeth act to reduce the surface area of tooth-food-tooth contact, concentrating applied stress into a much smaller area and increasing the efficiency of food breakdown (Rensberger 1995). However, there must be a trade-off between the apical angle of the ridges and the mechanical strength of the brittle tissue from which the elements are composed; the more acute the apical angle, the higher the concentration of applied stress, hence the greater the likelihood of brittle failure. A serious constraining factor is thus the rheology of enamel and its microstructure. Although enamel is the most hard wearing of all vertebrate hard tissues, it is also one of the most brittle because of its low organic content in comparison with other dental hard tissues such as enameloid, dentine, or bone. In *Idiognathodus* the problem is exacerbated because unlike most vertebrate teeth, conodont elements were almost entirely composed of enamel (Donoghue 1998).

Growth and Function of Idiognathodus Pa Elements.—The Pa elements of *Idiognathodus* underwent considerable morphological change

during ontogeny (von Bitter 1972: Pl. 1; Purnell 1994: Fig. 4) and this must have affected element function. Juvenile Pa elements have a much smaller platform than those of adults; they are basically blade-shaped with secondary ridges above the basal cavity aligned parallel to the blade (e.g., Purnell 1994: Fig. 4f), more closely resembling ancestral taxa. This morphology may have facilitated overlapping occlusion similar to that displayed by *Gnathodus bilineatus* (e.g., Nicoll 1987: Pl. 5.3: Fig. 2), but without complex platforms these elements could not have performed a crushing function as efficiently as larger specimens. This must have influenced prey selection. The smallest recognizable juvenile may not, however, represent a functional stage. Some studies of the internal structure of conodont elements indicate periodic growth (Müller and Nogami 1971, 1972; Zhang et al. 1997), and use may have been restricted to the end of each growth cycle (Donoghue and Purnell in press). Mature platform morphology is attained at an early stage in ontogeny (see von Bitter 1972: Pl. 1; Purnell 1994: Fig. 4) and platform growth in elements of more than 0.4 mm in length is isometric (Purnell 1994). The smallest forms may thus represent an animal that died during initial growth of the feeding elements prior to eruption. However, this can only be rigorously evaluated by analysis of microwear in relation to ontogeny.

Cyclical growth of the feeding elements causes enormous problems in modeling histogenesis, because it requires that the elements be returned to the epidermis for subsequent growth to occur (Donoghue 1998). But how does this tissue-cover hypothesis stand up to our current view of element function? Bengtson (1976, 1983) reconciled the need for soft tissue cover and toothlike function by suggesting that elements were everted during function and subsequently retracted into an epithelial pocket. However, recent advances in the understanding of conodont element growth (Müller and Nogami 1971; Sansom 1996; Donoghue 1998) render Bengtson's paradigm untenable, and we must now view elements as either permanently or only periodically covered by soft tissue in a manner

analogous to growing denticles and scales (Donoghue 1998).

Previous Interpretations of Occlusion and Function.—The results of this study highlight a number of errors in previous hypotheses of Pa element occlusion and function. The diagrammatic reconstructions of Jeppsson (1971: Fig. 3) and Purnell (1995: Fig. 1) incorrectly show Pa elements of *Idiognathodus* in opposition without the anterior-posterior offset between the platforms of the sinistral and dextral element. In this position the medial troughs of the elements would have opposed each other and the occlusal surfaces of the elements could not have been brought into interactive articulation. Our demonstration of accurate occlusion between Pa elements also indicates that the lack of close articulation in many of Nicoll's reconstructed pairs (1987) is an artifact of combining elements from different individuals. His hypothesis that the main functional surfaces of the platforms did not come into close contact and were covered in soft tissue is undermined by the lack of space between the elements, and is effectively falsified by the traces of damage observed at points of contact between the interactive surfaces. Previous interpretations of rotational occlusion between elements (Weddige 1990; Purnell and von Bitter 1992; Purnell 1995) are supported by our analysis of *Idiognathodus*, but the limits of element movement demonstrated by the natural element pairs in this study indicate that it is unlikely that the ventral surfaces of the elements would have parted to the degree illustrated by Weddige (1990: Text-fig. 15b). Although his hypothesis is based on another ozarkodinid, *Polygnathus*, this genus also exhibits complex morphology in the area of the platform-blade junction that would have controlled element alignment and articulation. Purnell and von Bitter's (1992) interpretation of *Vogelgnathus campbelli*, with the occlusal sides of the ventral blades as primary functional surfaces, implies that the powerstroke in *V. campbelli* was during closure of the elements from ventral to dorsal, opposite to that in *Idiognathodus* and most other taxa (see below).

Asymmetry and Function.—Gross asymmetry between sinistral and dextral elements of

the same species has been widely recognized in the past, but all previous pairings have been inferred from criteria such as common range, co-occurrence, and statistical association. This is the first demonstration of asymmetrically paired elements from an individual conodont. The recognition of asymmetry in element pairs can be important taxonomically. There are several examples where elements originally assigned to different taxa have been recognized as sinistral and dextral elements of a single species (e.g., Voges 1959; Lane 1968; Klapper 1971; Klapper and Lane 1985; Sandberg and Ziegler 1979; Kuz'min 1990). Lane (1968) recognized several possible types of pairing in conodonts and erected a scheme of classification. This has proven useful, but it is now clear that when small but functionally significant details of morphology are considered, all ozarkodinid Pa elements are asymmetrical (symmetry Class III).

From a functional perspective, the importance of recognizing asymmetry in element-pairs cannot be overstated (cf. Purnell and von Bitter 1992). Asymmetry in element morphology does not imply asymmetrical feeding behavior in conodonts (Purnell 1995; contra Babcock 1993) but is related to their complex bilateral interaction. Perfect mirror image pairs of elements could not perform an efficient tooth-like function requiring occlusal contact because a degree of asymmetry is necessary to allow the functional pairs to interlock ("complementary symmetry" of Weddige [1990]; Purnell 1995). Preliminary work indicates that ozarkodinid conodonts evolved a consistent pattern of pairing, with the sinistral element behind the dextral (Purnell and von Bitter 1992; Purnell 1995; Purnell and Donoghue 1997), and the apparent absence of intrapopulation variation in asymmetry indicates that this phenomenon is not a manifestation of handedness. Only one example of the opposite asymmetry has so far come to light (a species of *Idiognathodus* [Stamm 1996], not *Icriodus* as reconstructed by Weddige [1990]).

Occlusion and Function in Other Taxa.—The most important constraint on element motion in *Idiognathodus* was undoubtedly provided by the ridge and furrow system of the ventral area of the platform. Similar structures can be

found in numerous other conodont taxa including gnathodids and some polygnathids. *Siphonodella*, for example, developed as many as three or four ridges and intervening furrows parallel to the blade, and once occluded these would have provided unmatched constraint over the relative motion. The lack of transverse structures in the complex may have led to axial slippage between the elements unless this was prevented by the transverse ridges on the dorsal part of the platform. Many taxa, however, exhibit no morphological features apart from the ventral blade that would have enhanced alignment between opposed Pa elements (e.g., *Palmatolepis*). But microwear on the blade-shaped Pa elements of *Ozarkodina confluens* (Purnell 1995) indicates that, in some at least, the relative motion between the elements was highly constrained and that dorsal parts of the elements met in a manner very similar to the platforms of *Idiognathodus*. The denticles of the opposing elements must have met in an offset intermeshed arrangement, shearing food as they came together. However, the physical constraints on relative motion and the means by which occlusion was controlled remain unknown.

Conclusions

Morphology, physical juxtapositioning, patterns of surface damage, and microwear provide compelling evidence that the Pa elements of *Idiognathodus* crushed food by rotational closure constrained by complex interpenetrative occlusion of the ridges and troughs in the ventral part of the platform. This supports the hypothesis that, even without jaws, conodonts developed dental occlusion of mammal-like complexity. Other conodonts with similar molariform Pa elements probably crushed food in a manner similar to that of *Idiognathodus*.

Our hypothesis of element motion, function, and food processing is better constrained and more detailed than previous hypotheses of feeding proposed for conodonts or any other groups of fossil agnathans, but it also has important implications for more general understanding and analysis of morphology and function in conodonts. Features of the oral surface of conodont Pa elements that have long been used, somewhat arbitrarily, as tax-

onomic characters, and that thereby underpin the biostratigraphic utility of conodonts, can finally be understood in a paleobiological context.

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Literature Cited

- Aldridge, R. J., M. P. Smith, R. D. Norby, and D. E. G. Briggs. 1987. The architecture and function of Carboniferous polygnathacean conodont apparatuses. Pp. 63–76 in R. J. Aldridge, ed. *Palaeobiology of conodonts*. Ellis Horwood, Chichester, England.
- Aldridge, R. J., and M. A. Purnell. 1996. The conodont controversies. *Trends in Ecology and Evolution* 11:463–468.
- Babcock, L. E. 1993. Trilobite malformations and the fossil record of behavioral asymmetry. *Journal of Paleontology* 67: 217–229.
- Baesemann, J. F. 1973. Missourian (Upper Pennsylvanian) conodonts of northeastern Kansas. *Journal of Paleontology* 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.
- . 1983. The early history of the conodonts. *Fossils and Strata* 15:5–19.
- Carroll, R. L., and W. Lindsay. 1985. The cranial anatomy of the primitive reptile *Procolophon*. *Canadian Journal of Earth Sciences* 22:1571–1587.
- Clark, J. M., L. L. Jacobs, and W. R. Downs. 1989. Mammal-like dentition in a Mesozoic crocodylian. *Science* 244:1064–1066.
- Crompton, A. W., and K. Hiiemae. 1970. Molar occlusion and mandibular movements during occlusion in the American

- opossum, *Didelphis marsupialis* L. Zoological Journal of the Linnean Society 49:21–47.
- DeMar, R., and J. R. Bolt. 1981. Dentitional organization and function in a Triassic reptile. *Journal of Paleontology* 55:967–984.
- Donoghue, P. C. J. 1998. Growth and patterning in the conodont skeleton. *Philosophical Transactions of the Royal Society of London B* 353:633–666.
- Donoghue, P. J. C., and M. A. Purnell. In press. Growth, function, and the conodont fossil record. *Geology*.
- Du Bois, E. P. 1943. Evidence on the nature of conodonts. *Journal of Paleontology* 17:155–159.
- Fox, R. C., G. P. Youzwyshyn, and D. W. Krause. 1992. Post-Jurassic mammal-like reptile from the Palaeocene. *Nature* 358:233–235.
- Gordon, K. D. 1982. A study of microwear on chimpanzee molars: implications for dental microwear analysis. *American Journal of Physical Anthropology* 59:195–215.
- Janis, C. M. 1990. The correlation between diet and dental wear in herbivorous mammals and its relationship to the determination of diets of extinct species. Pp. 241–259 in A. J. Boucot, ed. *Evolutionary paleobiology of behavior and coevolution*. Elsevier, Amsterdam.
- Jepsson, L. 1971. Element arrangement in conodont apparatuses of *Hindeodella* type and in similar forms. *Lethaia* 4:101–123.
- . 1979. Conodont element function. *Lethaia* 12:153–171.
- Kemp, A. 1977. The pattern of tooth plate formation in the Australian lungfish, *Neoceratodus forsteri* Krefft. *Zoological Journal of the Linnean Society* 60:223–258.
- Klapper, G. 1971. Sequence within the conodont genus *Polygnathus* in the New York lower Middle Devonian. *Geologica et Palaeontologica* 5:59–79.
- Klapper, G., and H. R. Lane. 1985. Upper Devonian (Frasnian) conodonts of the *Polygnathus* biofacies, N.W.T., Canada. *Journal of Paleontology* 59:904–951.
- Kuz'min, A. V. 1990. Asymmetrical pairs of platform elements of *Polygnathus* (conodonts). *Paleontological Journal* 1990:62–70.
- Lane, H. R. 1968. Symmetry in conodont element-pairs. *Journal of Paleontology* 42:1258–1263.
- Lindström, M. 1964. Conodonts. Elsevier, Amsterdam.
- Maas, M. C. 1991. Enamel structure and microwear: an experimental study of the response of enamel to shearing force. *American Journal of Physical Anthropology* 85:31–49.
- . 1994. A scanning electron-microscope study of *in vitro* abrasion of mammalian tooth enamel under compressive loads. *Archives of Oral Biology* 39:1–11.
- Müller, K. J., and Y. Nogami. 1971. Über die Feinbau der Conodonten. *Memoirs of the Faculty of Science, Kyoto University, Series of Geology and Mineralogy* 38:1–87.
- . 1972. Growth and function of conodonts. Pp. 20–27 in 24th International Geological Congress, Montreal.
- Nicoll, R. S. 1985. Multielement composition of the conodont species *Polygnathus xylus xylus* Stauffer, 1940 and *Ozarkodina brevis* (Bischoff and Ziegler, 1957) from the Upper Devonian of the Canning Basin, Western Australia. *Bureau of Mineral Resources Journal of Australian Geology and Geophysics* 9:133–147.
- . 1987. Form and function of the Pa element in the conodont animal. Pp. 77–90 in R. J. Aldridge, ed. *Palaeobiology of conodonts*. Ellis Horwood, Chichester, England.
- . 1995. Conodont element morphology, apparatus reconstructions and element function: a new interpretation of conodont biology with taxonomic implications. *Courier Forschungsinstitut Senckenberg* 182:247–262.
- Norby, R. D. 1976. Conodont apparatuses from Chesterian (Mississippian) strata of Montana and Illinois. Ph.D. dissertation. University of Illinois at Urbana-Champaign.
- Pough, F. H., J. B. Heiser, and W. N. McFarland. 1996. *Vertebrate life*, 4th ed. Prentice Hall, Upper Saddle River, N.J.
- Purnell, M. A. 1993. Feeding mechanisms in conodonts and the function of the earliest vertebrate hard tissues. *Geology* 21:375–377.
- . 1994. Skeletal ontogeny and feeding mechanisms in conodonts. *Lethaia* 27:129–138.
- . 1995. Microwear on conodont elements and macrophagy in the first vertebrates. *Nature* 374:798–800.
- . In press. Conodonts: functional analysis of disarticulated skeletal structures lacking extant homologues. Pp. 129–146 in E. Savazzi, ed. *Functional morphology of the invertebrate skeleton*. Wiley, Chichester, England.
- Purnell, M. A., and P. C. J. Donoghue. 1997. Skeletal architecture and functional morphology of ozarkodinid conodonts. *Philosophical Transactions of the Royal Society of London B* 352:1545–1564.
- . 1998. Architecture and functional morphology of the skeletal apparatus of ozarkodinid conodonts. *Palaeontology* 41:57–102.
- Purnell, M. A., and P. H. von Bitter. 1992. Blade-shaped conodont elements functioned as cutting teeth. *Nature* 359:629–631.
- Rensberger, J. M. 1978. Scanning electron microscopy of wear and occlusal events in some small herbivores. Pp. 523 in P. M. Butler and K. A. Joysey, eds. *Development, function and evolution of teeth*. Academic Press, New York.
- . 1995. Determination of stresses in mammalian dental enamel and their relevance to the interpretation of feeding behaviors in extinct taxa. Pp. 151–172 in J. Thomason, ed. *Functional morphology in vertebrate paleontology*. Cambridge University Press, Cambridge.
- Rhodes, F. H. T. 1952. A classification of Pennsylvanian conodont assemblages. *Journal of Paleontology* 26:886–901.
- Robinson, P. L. 1956. An unusual sauropod dentition. *Zoological Journal of the Linnean Society* 43:283–293.
- Sandberg, C. A., and W. Ziegler. 1979. Taxonomy and biofacies of important conodonts of Late Devonian *styriacus* Zone, United States and Germany. *Geologica et Palaeontologica* 13:173–212.
- Sansom, I. J. 1996. *Pseudooneotodus*: a histological study of an Ordovician to Devonian vertebrate lineage. *Zoological Journal of the Linnean Society* 118:47–57.
- Sansom, I. J., M. P. Smith, H. A. Armstrong, and M. M. Smith. 1992. Presence of the earliest vertebrate hard tissues in conodonts. *Science* 256:1308–1311.
- Smith, K. K. 1993. The form of the feeding apparatus in terrestrial vertebrates: studies of adaptation and constraint. Pp. 150–196 in J. Hanken and B. F. Hall, eds. *The skull*. University of Chicago Press, Chicago.
- Stamm, R. G. 1996. Reversals of misfortune: a new species? of *Idiognathodus* (Conodonts) based on functional surface morphology. In J. E. Repetski, ed. *Sixth North American Paleontological Convention Abstracts of Papers*. Paleontological Society Special Publication 8:369. Smithsonian Institution Press, Washington, D.C.
- Sweet, W. C. 1985. Conodonts: those fascinating little whatzits. *Journal of Paleontology* 59:485–494.
- Teaford, M. F. 1988. Scanning electron microscope diagnosis of wear patterns versus artefacts on fossil teeth. *Scanning Microscopy* 2:1167–1175.
- Voges, A. 1959. Conodonten aus dem Untercarbon I und II (Gatendorfia- und Pericyclus-Stufe) des Sauerlandes. *Paläontologische Zeitschrift* 33:266–314.
- von Bitter, P. H. 1972. Environmental control of conodont distribution in the Shawnee Group (Upper Pennsylvanian) of

- eastern Kansas. University of Kansas Paleontological Contributions 59:1–105.
- Weddige, K. 1990. Pathological conodonts. Courier Forschungsinstitut Senckenberg 118:563–589.
- Wild, R. 1978. Die Flugsaurier (Reptilia, Pterosauria) aus der Oberen Trias von Cene bei Bergamo, Italien. Bollettino della Societa Paleontographica Italiana 17:176–256.
- Wu, X.-C., H.-D. Sues, and A. Sun. 1995. A plant-eating crocodyliform reptile from the Cretaceous of China. *Nature* 376:678–680.
- Young, J. Z. 1978. Programs of the brain. Oxford University Press, Oxford.
- Zhang, S., R. J. Aldridge, and P. C. J. Donoghue. 1997. An Early Triassic conodont with periodic growth? *Journal of Micro-palaeontology* 16:65–72.

Appendix

Elements were removed from their indurated black shale matrix using a modified version of a technique established by Norby (1976). Samples were immersed in a solution of approximately 10% sodium hypochlorite with 10 grams of sodium hydroxide added per 100 ml to promote the reaction; after 24 hours or more, the shale surface had usually disaggregated and the conodont elements were readily removed from the matrix; shale still adhering to the elements was removed by repeated treatment with sodium hypochlorite. Invariably, sediment loading and compaction of the shale resulted in fracturing of elements in situ, and all attempts at reattachment of broken fragments using organic and dental bonding resins have failed. Bedding plane assemblages with the least evidence of fracture, particularly of Pa elements at the point where the platform and blade join, were therefore preferentially selected for study.