Microstructural variation in conodont enamel is a functional adaptation

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Recognition that conodonts were the earliest vertebrate group to experiment with skeletal biomineralization provides a window in which to study the origin and early evolution of this developmental system. It has been contended that the conodont skeleton comprised a classic suite of vertebrate hard tissues, while others suggest that conodont hard tissues represent divergent specializations within the early diversification of vertebrate hard tissues, supporting a view that the hard tissues of conodonts, particularly enamel, exhibit a range of microstructural variation beyond that seen in vertebrates. New evidence reveals that, although variable, conodont enamel microstructure is consistent between homologous portions of homologous dentitions. Although there is a correlation between morphology and microstructure, this belies a stronger correlation between the commonality of microstructure and dental function. The enamel of conodonts evolved in response to changes in dental function and differentiation of the microstructural layer into a number of enamel types and can be linked to dental occlusion, heterodonty, a permanent dentition, enamel thickness and, probably above all, the small size of the dental elements.

Keywords: Conodonts; enamel; structure; function; vertebrate; evolution

1. INTRODUCTION

Conodonts comprise an extinct clade that occupies a phylogenetic position intermediate between the living jawless vertebrates, which lack a mineralized skeleton, and all other extinct and extant groups of jawless and jawed vertebrates, the majority of which are heavily skeletonized (Donoghue *et al.* 2000). This implies that the characteristic mineralized feeding apparatus of conodonts represents the first vertebrate experiment in skeletonization. Furthermore, comparison of the histology and morphogenesis of conodont and vertebrate hard tissues indicates that the developmental basis for the vertebrate dermal and visceral skeleton was already established in the latest common ancestor of conodonts and all more derived vertebrates (Donoghue 1998; Donoghue & Aldridge 2001). Thus, conodonts provide a unique insight into the plesiomorphic condition of the vertebrate skeleton.

Notwithstanding these observations, precise homology between conodont and vertebrate hard tissues remains controversial. One of the main criticisms of homology between conodont crown tissue and 'true' (i.e. sarcopterygian) enamel relates to the degree of microstructural variation within conodont crown tissue. For instance, Forey & Janvier (1993) argued that the orientation of crystallites within conodont crown tissue fails to correspond precisely to that seen in vertebrate enamel and that 'the extreme variation in crystal orientation is puzzling' (p. 133). However, more recent work has demonstrated that the variation in crown tissue microstructure within a single element can go beyond that hitherto documented between taxa (Donoghue 1998). This would appear to make the homology of conodont crown tissue even more problematic. However, there is reason to doubt the canonical view of the microstructure of enamel. For instance, even the geometric constraints of a curved surface (i.e. the enamel–dentine junction of most vertebrate teeth) dictate that the crystallites cannot all be orientated

perpendicular to the outer surface. Furthermore, a number of authors have documented instances where the microstructure of enamel and enamel-like tissues is differentiated topologically into a number of microstructural types (e.g. Reif 1979).

2. A SURVEY OF THE MICROSTRUCTURE OF ENAMEL AND ENAMEL-RELATED TISSUES IN NON-CONODONT VERTEBRATES

Although it has been proposed that enamel is a synapomorphy of vertebrates (Smith 1995), the phylogenetic distribution of enamel-like tissues indicates that enamel is a synapomorphy of the Sarcopterygii (Maisey 1988) and that all non-sarcopterygian enamel-like tissues have been acquired independently. Nevertheless, there is reason to consider all enamel-like tissues together given that they have evolved within a homologous organ system, the odontode (see Reif 1982). Given the number of times that enamel-like tissues have evolved independently during vertebrate phylogeny, it should come as no surprise to find that the canonical view of enamel-type microstructures, where component crystallites are orientated perpendicular to the oral surface, is incomplete. In practice, approximately surface-normal crystallites are found in simple tooth morphologies and functions, whereas more complex tooth morphologies and functions are generally associated with enamel microstructures that are much more variable (e.g. Clemens 1997). The following is a brief account of the variation in enamel-like tissues amongst vertebrates.

Amongst the jawless vertebrates, enamel-like tissues are known in only two heterostracomorphs, *Eriptychius* and *Astraspis*. Although little is known of the microstructures of these tissues, available evidence suggests that they are very simple (Smith *et al.* 1995). The tissues are topologically restricted to dermal scales. Enameloid is ubiquitous amongst the chondrichthyans, both in scales and teeth. Reif (1979, 1981 and references therein) documented

differentiation of the microstructure of enameloid in concert with specialized tooth functions, including shearing and crushing teeth. Actinopterygian histology is variable, but teeth commonly include an enameloid tip and an enamel collar. Adaptation to bending resistance in shearing and cutting teeth appears to have evolved at least twice within the Actinopterygii (Reif 1979, 1981). The microstructure of the collar enamel appears to be restricted to radial crystallite enamel (RCE) (Smith 1992) where crystallites are arranged in parallel, approximately perpendicular to the oral surface.

Smith (1989, 1992) surveyed enamel microstructures amongst basal sarcopterygians and found examples of RCE as well as more complex microstructures such as columnar enamel and micro-unit enamel (see Sander 1999 for definitions). Dental morphologies and functions are simple.

Sander (1999) examined enamel microstructures amongst 'reptile' dentitions and found a high degree of variability, from RCE to microstructures in which the crystallites are arranged into domains of varying complexity. Sander (1999) has argued persuasively that microstructures more complex than simple RCE are not necessarily linked to function, a conclusion that is borne out by the fact that, although such microstructures are organized into domains, the dental enamel layers of most non-mammals are composed of a single enamel type. Sander (1999) cited examples of enamel-like microstructures that develop in the absence of cellular control, such as the development of a prismatic structure within bivalve shells, which arises solely because of geometric constraints on spherulitic growth (Ubukata 1994). Sander (1999) associated all 'reptilian' enamel microstructures more complex than RCE as resulting from increased growth and reduced cellular control on crystal precipitation and growth. It is likely that this model can be extended to explain the occurrence of complex microstructures in lower sarcopterygians.

The greatest degree of microstructural variation is encountered amongst mammals. The microstructure of almost all mammalian enamels is organized into distinct domains known as prisms. True prisms differ from the microstructural domains encountered amongst other sarcopterygians in that they are bordered by interprism material comprising the prism 'sheath'. Most mammal groups exhibit further organization of the enamel microstructure into a series of enamel types that are distributed anisotropically throughout the enamel layer of a tooth; the distribution patterns are consistent between homologous teeth of different individuals (von Koenigswald & Clemens 1992). Invariably, the differentiated microstructures represent adaptations to abrasion resistance and/or brittle failure in complex dentitions (Rensberger 1995). This obtains because enamel crystallites are more resistant to wear if they are arranged perpendicular to a surface rather than more approximately parallel (Rensberger & von Koenigswald 1980). If prisms are arranged in layers of more than one orientation, cracks that tend to propagate along prism boundaries are likely to be decussed upon reaching a layer of prisms of differing orientation (Rensberger 1995).

Clemens (1997) has argued that microstructural adaptations are more prevalent amongst mammals than any

other group because mammals exhibit the highest degree of dental specialization. Furthermore, increased enamel thickness and reduced tooth replacement in mammals with respect to non-mammalian amniotes ensures that adaptations to the maintenance of tooth integrity are placed at a premium (Grine *et al.* 1979; Clemens 1997).

The inextricable linkage between the function and differentiation of the microstructure of enamel into a number of distinct types can be demonstrated through examples of convergence and loss that serve as tests of the null model that microstructural variation is phylogenetically and/or developmentally constrained. Cooper & Poole (1973) described the occurrence of mammal-like occlusal dentition in *Uromastix*, an agamid lizard, a condition that can only have been arrived at through convergence. Examination of the enamel microstructure demonstrated the occurrence of prismatic enamel that must also have evolved independently of the prismatic enamel of mammals. Ontogenetic analysis of a series of skulls revealed no evidence of tooth replacement. It is likely that dental microstructure and function evolved in concert under selective pressures analogous to those in mammals.

Examples of secondary absence of a complex enamel microstructure within mammals also serve to demonstrate the structure–function linkage. Perhaps the best example is provided by the evolution of cetaceans in which dental morphologies have simplified while the enamel microstructure has reverted to RCE (Sahni & von Koenigswald 1997).

Examples of convergence are not limited to true enamel. By far the most convincing case of microstructural convergence in response to analogous functional selective pressures has been presented by Reif (1979) who documented an example of precise convergence between enameloid microstructures in the cutting teeth of sharks and two groups of actinopterygians.

The examples of complex enamel and enamel-like microstructures evolving in the absence of direct functional selective pressures in 'reptiles' provide a healthy air of caution in which to consider the implications of enamel and enamel-like microstructures. However, examples of microstructural convergence also demonstrate that enamel and enamel-like tissues differentiated into a number of microstructural types are invariably associated with structural adaption to complex dental function. It is therefore pertinent to consider the microstructural differentiation of conodont crown tissue in the perspective of an adaptation to function. However, given that adaptational arguments should be framed within functional, developmental and phylogenetic perspectives, below I compare the crown tissue microstructure, rheology and functional morphology of conodont elements from three related taxa that exhibit combinations of similarity and difference in morphology and inferred function. This provides a test of the hypothesis that conodont crown microstructure is a functional adaptation.

3. MATERIAL AND METHODS

Double-polished thin sections and ground sections were cut from the crown tissue of *Ozarkodina*, *Palmatolepis* and *Idiognathodus* P₁ elements (for terminology see Purnell *et al.* 2000). The study

was restricted to these taxa and elements because of the paucity of well-constrained functional morphological data, because the interrelationships of these taxa are well constrained and because they exhibit both similar morphologies and contrasting functions. Based on the most widely accepted hypothesis of relationships, *Ozarkodina* is a sister taxon to *Palmatolepis* and *Idiognathodus* and its condition is representative of the latest common ancestor of *Palmatolepis* and *Idiognathodus* (cf. Sweet 1988); thus, the platforms of these two taxa are convergent. Thin sections and ground sections were examined using a scanning electron microscope after surface etching with 0.5% orthophosphoric acid for 10 min.

Figured specimens have been repositied in Birmingham University Lapworth Museum of Geology (BU) and the Royal Ontario Museum, Toronto (ROM).

4. MICROSTRUCTURE OF THE 'ENAMEL' LAYER

(a) *Ozarkodina*

The crown tissue of *Ozarkodina* is differentiated into a number of microstructural types. The lower two-thirds of the element is composed of crystallites arranged in parallel, perpendicular to the outer surface (figure 1*b,c,e–g*). The upper portion of the element is composed of crystallites arranged subparallel to the outer surface, either in line with the orientation of the denticles (figure 1*d*), in line with the long axis of the element (figure 1*e*) or in gradation between these extremes (figure 1*f*). The occlusal side of the element exhibits greater development of subparallel crystallites than the non-occlusal side (figure 1*b,c*). The apex of the element is composed of surface-normal crystallites (figure 1*b*). The junction between these distinct enamel types can be abrupt (figure 1*e*) rather than transitional in nature. This combination of microstructural types is common to all species of *Ozarkodina* studied to date.

(b) *Palmatolepis*

The microstructure of the ventral blade is directly comparable to the condition met with in *Ozarkodina* except that there is no evidence of asymmetry in the distribution of the microstructural types comprising opposing sides of the blade in *Palmatolepis*. The immediate oral subsurface of the platform in the *Palmatolepis* P₁ element is composed of surface-normal crystallites (figure 2*b–d*) and the overhanging underside of the platform is

Figure 1. *Ozarkodina* P₁ elements. (a) A fused natural assemblage of a pair of *Ozarkodina* sp. P₁ elements in functional opposition with maximum dimension 570 µm (BU 3308). (b) Transverse section through a P₁ element of *Ozarkodina confluens* cut ventral ('anterior') to the cusp with maximum height 620 µm (BU 3306). (c) Transverse section through a P₁ element of *O. confluens* cut dorsal ('posterior') to the cusp with maximum height 420 µm (BU 3307). (d) Detail of the microstructure immediately below the occlusal surface of a P₁ element of *O. confluens* with frame height 51 µm (BU 3309). (e) Detail of different enamel microstructural types comprising the non-occlusal side of the P₁ element figured in (c) with frame height 45 µm. (f,g) Longitudinal 'horizontal' section through a P₁ element of *O. confluens* demonstrating the range of crystallite orientations in a single section through a single element with (f) frame height 90 µm and (g) 1530 µm maximum length (BU 2621).

composed of crystallites that are orientated subperpendicular to the surface. The crown tissue also includes vacuities and areas of hypomineralization (figure 2c) (Donoghue 1998) and there is poor crystallographic continuity between the increments of growth, as evidenced by prominent incremental growth lines (figure 2b–d). There is no evidence of any differentiation of the crown microstructure within the platform.

(c) *Idiognathodus*

Although the microstructure of the blade in *Idiognathodus* P₁ elements conforms to the condition in *Ozarkodina*, the microstructure of the platform is quite distinct from that of the blade or the microstructure of the platform in *Palmatolepis*. The most prominent difference lies in the organization of the crystallites into domains (figure 3b–d). The crystallites within each domain are arranged in an outwardly diverging cone-shaped fan that has a distinct boundary from all adjacent domains. The microstructure within the platform is organized into two broad zones. The immediate sub-surface of the platform is composed of a series of domains in which the crystallites are all arranged normal or approximately normal to the oral surface (figure 3c). Surface ornamentation, such as nodes and ridges, appears to be composed of individual domains, and acid etching of the oral surface reveals that the borders to the domains coincide with the margins of the ornamental structures. Blade-parallel sections through the platform reveal that the crystallite domains comprising the transverse ridges are asymmetric and the main axis of crystallite orientation is orientated at an oblique angle to the surface such that the axis is directed slightly ventrad. The domains are interwoven (figure 3d) below the immediate oral sub-surface, converging about a plane parallel to the oral surface of the platform.

The crystallite domains lack an intervening matrix of crystallites (also known as prism 'sheaths') that distinguishes true prismatic enamel from non-prismatic enamel. The tissue is more directly comparable to the protoprismatic enamel of some lower sarcopterygians (e.g. Smith 1989) and non-mammalian tetrapods (e.g. Sander 1999). Unusually, the differentiated condition met with in *Idiognathodus* is unparalleled amongst other vertebrates bearing a protoprismatic microstructure. Furthermore, with a diameter approaching 30 µm, the crystallite domains in *Idiognathodus* are larger than in prismatic and protoprismatic enamels and compare most closely in size with multituberculate gigantoprismatic enamel (Fosse *et al.* 1978). The microstructure of the *Idiognathodus* platform is interrupted by at least one major structural discontinuity (arrowed in figure 3b) that is aligned obliquely to the oral surface.

Figure 2. *Palmatolepis* P₁ elements. (a) A fused natural assemblage of a pair of *Palmatolepis* sp. P₁ elements preserved in functional opposition (specimen lost). (b–d) Transverse section through a P₁ element of *Palmatolepis* sp. figured under progressively higher magnification: (b) 290 µm maximum dimension, (c) 125 µm frame width and (d) 42 µm frame width (BU 2640).

5. FUNCTION OF CONODONT ELEMENTS

The P_1 element of *Ozarkodina* is of a blade-shaped morphology (figure 1a) and it is interpreted to have performed a slicing scissor-like function based upon microwear analysis (Purnell 1995) using its dorsal process (Donoghue & Purnell 1999a,b). The P_1 elements of *Idiognathodus* (figure 3a) and *Palmatolepis* (figure 2a) also possess ventral blade-shaped processes as in *Ozarkodina*, although the dorsal processes of the P_1 elements in *Idiognathodus* and *Palmatolepis* are developed into a platform.

The function of *Idiognathodus* has been studied more intensively than any other conodont taxon (Purnell 1995; Purnell & Donoghue 1997; Donoghue & Purnell 1999b). The oral surface of the *Idiognathodus* P_1 platform exhibits a complex series of nodes and pits in association with an array of transverse ridges and sulci that constrain the movement of the opposing elements such that they occlude bilaterally (Donoghue & Purnell 1999b). Analysis of microwear and functional morphology demonstrates that the *Idiognathodus* P_1 element performed a crushing function (Purnell 1995; Donoghue & Purnell 1999a,b). Asymmetry in the transverse ridges on the oral surface indicates that the power stroke was from ventral to dorsal (Donoghue & Purnell 1999b).

Analysis of the function of the *Palmatolepis* P_1 element reveals that the platforms did not occlude (Nicoll 1987) (figure 2a), although the blades did interact in a manner comparable to the P_1 elements in *Ozarkodina*. This observation is supported by the lack of evidence of microwear on the oral surface of the platforms, although microwear is found on the blades. Together, this evidence suggests that the P_1 elements of *Palmatolepis* performed a function comparable to *Ozarkodina* P_1 elements and, while the platforms could have been employed in food processing (cf. Nicoll 1987), they could not have performed a mechanical function comparable to the P_1 elements of *Idiognathodus*.

6. RHEOLOGICAL CONSIDERATION OF CONODONT CROWN TISSUE

The rheological properties of various microstructures under different functions have been widely considered (see Rensberger 1995 for a review). Microstructures with component crystallites orientated perpendicular to the functional surface are more resistant to abrasion than microstructural types where the component crystallites are more approximately parallel to the surface (Rensberger & von Koenigswald 1980). However, the

Figure 3. *Idiognathodus* P_1 elements. (a) A pair of *Idiognathodus* P_1 elements in functional opposition from a natural assemblage of elements with maximum length 1181 μm (BU 2683) (reproduced from Donoghue & Purnell (1999b) with permission of the Paleontological Society). (b,c) Transverse fracture section through a P_1 element of *Idiognathodus magnificus* under progressively higher magnification: (b) 720 μm maximum dimension and (c) 235 μm frame width (ROM 53261). (d) Longitudinal 'vertical' section through the platform component of an *Idiognathodus* P_1 element with frame width 135 μm (ROM 53264).

general occurrence of surface-perpendicular crystallites within conodonts and, indeed, all other vertebrates that possess enamel and enamel-like tissues, suggests that this microstructural type represents a plesiomorphic and potentially non-adaptive condition. This equates well with the occurrence of a surface-perpendicular crystallite layer comprising the immediate subsurface of the P₁ element platforms of *Palmatolepis* which did not come into contact during the occlusal cycle and exhibit no evidence of wear.

The properties of surface-parallel/subparallel crystallites are not so obvious because, as has been pointed out, there are no clear comparisons for this enamel type amongst other vertebrates. However, a surface-parallel microstructure is found preferentially in conodont elements and portions of conodont elements that are inferred to have performed a shearing function or, at the very least, were subject to shearing forces. Furthermore, where there is an anisotropic distribution of a surface-parallel microstructure, it can be observed to occur preferentially along occlusal surfaces (figure 1d). The alignment of (immediately) subsurface crystallites parallel to inferred shearing forces appears counterintuitive as this is the orientation in which the crystallites are least resistant to wear (Rensberger & von Koenigswald 1980). However, evidence suggests that this may be an adaptation to the functional development of a flatter occlusal surface with sharper cutting edges. For instance, worn specimens of *Ozarkodina* commonly exhibit evidence of events where sheets of enamel have been dislocated from the occlusal surface of the denticles (Donoghue & Purnell 1999a, fig. 2) resulting from crack propagation along crystal boundaries in the surface-parallel microstructure and along prominent incremental growth planes.

The microstructural types comprising the platform of *Idiognathodus* P₁ elements are also problematic because they combine organization of microstructural domains reminiscent of true prismatic enamel in mammals with characters of domain organization that are simpler than prismatic enamel and are more similar to the enamel of non-mammalian amniotes. Analysis of microwear demonstrates that mechanical abrasion is a significant factor in *Idiognathodus* P₁ platforms (Purnell 1995; Donoghue & Purnell 1999b). This equates with a surface-normal crystallite orientation that is optimal for abrasion resistance (Rensberger & von Koenigswald 1980). The asymmetrical orientation (in blade-parallel section through the platform) of the crystallite domains (figure 3d) places the component crystallites directly perpendicular to the main direction of force in the power stroke of the elements, which Donoghue & Purnell (1999b) identified as ventral to dorsal. Organization of the microstructure into domains reduces the homogeneity of the tissue, thereby conferring enhanced resistance to crack propagation (Rensberger 1995). This obtains because the energy required for crack propagation is proportional to the radius of the crack tip. When reached by a propagating crack, the domain boundaries act as decussation planes by vastly increasing the radius of the crack tip and, at the same time, the energy required for further propagation (cf. Rensberger 1995). The inhomogeneity and, therefore, crack propagation resistance of *Idiognathodus* crown tissue is even greater than it would otherwise be

because the domains are interwoven, such that the domain boundaries are not all aligned in a common orientation.

7. HYPOTHESIS TESTING

Given the combination of characteristics displayed by the taxa in this study, it is possible to reject the null models outlined above. First, it is possible to reject the hypothesis that the microstructure of conodont crown tissue is developmentally constrained because similar morphotypes, as in the platforms of *Palmatolepis* and *Idiognathodus*, exhibit dissimilar microstructures. The second possibility, that the microstructure of conodont crown tissue is phylogenetically constrained, does not arise with respect to the platforms of *Idiognathodus* and *Palmatolepis*, because the microstructures comprising those platforms are dissimilar and, further, the currently accepted hypothesis of relationships suggests that these structures are not homologous. Even when the microstructures of homologous structures are compared, such as the blades of *Ozarkodina*, *Palmatolepis* and *Idiognathodus* P₁ elements, although the microstructural patterns are broadly similar, there are nevertheless detailed differences such as asymmetry, and the similarities that remain are explained equally as well by common function. Thus, based on evidence from histological, functional, rheological and phylogenetic analysis, it is possible to conclude that the consistent correspondence between the microstructure of conodont crown tissue and the function of the element fully corroborates the hypothesis that microstructural variation in conodont crown tissue is a functional adaptation.

8. DISCUSSION AND CONCLUSIONS

Although enamel and enamel-like tissues are the most hard-wearing of all vertebrate biomaterials, the high ratio of mineral to organic constituents results in a tissue that is also amongst the most brittle of all vertebrate biomaterials. As a result, many groups of vertebrates with complex dental functions have independently evolved complex enamel microstructures that serve to counter associated increases in dental stress and/or dental wear. The problem of brittleness is particularly problematic in conodonts because their dental elements are composed almost entirely of crown tissue and their oral morphology is generated solely within the enamel layer (Donoghue & Aldridge 2001). This contrasts markedly with the situation in the teeth of most vertebrates, which are composed of a thin skin of enamel overlying a relatively expansive dentine core that cushions the enamel layer and maintains the integrity of a tooth even in the event of complete brittle failure of the enamel layer. The situation in conodonts is further exacerbated by the minute size of the dental elements wherein the loss of a portion of a tooth is more problematic in small rather than large dentitions (cf. Janis & Fortelius 1988). Given these perspectives, it might be considered all the more surprising if conodont elements did not possess a differentiated crown tissue microstructure. Nevertheless, it remains surprising that the microstructure of conodont crown tissue should be so extensively differentiated into

distinct microstructural types that exhibit no intergradation and remain so topologically consistent between homologous elements.

While differentiated microstructures are met with in the hypermineralized tissues covering the dentitions of a wide range of vertebrates, the condition in conodonts appears to exhibit greater comparison to mammalian dentitions than to any other group. For instance, it has been argued that enamel microstructural differentiation has arisen in mammals because of a number of factors including the relative thickness of their enamel layer. Other parallels can be observed. These include the 'reduced replacement' that mammal dentitions exhibit in contrast to the vertebrate norm in which dentitions are replaced wholly and serially (Grine *et al.* 1979). Although conodonts exhibit a manifestation of replacement in which growth is facilitated by augmentation of the existing dentition, this requires that the existing dentition is maintained and not completely replaced (Donoghue & Purnell 1999a). Further, Clemens (1997) has argued that selection favouring heterodonty, precise occlusion and increasingly complex and specific masticatory functions are all implicated in the development of differentiated enamel microstructures in the dentitions of mammals. While conodont evolution was clearly non-directional, conodont phylogeny nevertheless exhibits an increasing range of heterodont apparatus diversity through much of the Palaeozoic era, whereas homodont dentitions are present only at the very earliest interval in the evolutionary history of the clade. Although work assessing the range of conodont dental histology and function remains at a preliminary stage, it is clear from the available data that the most complex enamel microstructures are met with in dentitions that exhibit the most complex dental functions, in this instance documented herein, linked to precise occlusion.

Notwithstanding parallels in the nature and evolutionary history of conodont and mammalian dentitions, it is nevertheless surprising to observe broad similarities between conodont and mammalian dentitions and dental microstructures. This is because, although the dental stresses invoked for complex dentitions in conodonts and mammals are analogous, these dental stresses would be orders of magnitude greater in mammals, which have jaws, than in conodonts, which are jawless. Thus, amongst the factors implicated in the functional adaptation of the microstructure of enamel, those exclusive to conodonts are probably the most important. These are (i) the greater impact of brittle failure on small dentitions, (ii) relative reduction of the supporting tissues, and (iii) the fact that dental morphology is developed entirely within the enamel layer.

While the number of taxa for which microstructural data are available remains small, future work undertaken in hand with careful functional analysis (e.g. Purnell 1995) and phylogenetic analysis is likely to reveal much more regarding the nature of how enamel, a uniquely vertebrate tissue, adapted in response to the varied functional strategies adopted during conodont phylogeny. As such and with the caveats noted above, the conodont fossil record represents the results of a unique and extensive natural experiment that can be used for calibrating patterns of dental structure–function relationships throughout vertebrate phylogeny.

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