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Proc. R. Soc. B 2012 **279**, 2849-2854 first published online 14 March 2012

doi: 10.1098/rsjb.2012.0147

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The sharpest tools in the box? Quantitative analysis of conodont element functional morphology

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Conodonts have been considered the earliest skeletonizing vertebrates and their mineralized feeding apparatus interpreted as having performed a tooth function. However, the absence of jaws in conodonts and the small size of their oropharyngeal musculature limits the force available for fracturing food items, presenting a challenge to this interpretation. We address this issue quantitatively using engineering approaches previously applied to mammalian dentitions. We show that the morphology of conodont food-processing elements was adapted to overcome size limitations through developing dental tools of unparalleled sharpness that maximize applied pressure. Combined with observations of wear, we also show how this morphology was employed, demonstrating how *Wurmiella excavata* used rotational kinematics similar to other conodonts, suggesting that this occlusal style is typical for the clade. Our work places conodont elements within a broader dental framework, providing a phylogenetically independent system for examining convergence and scaling in dental tools.

Keywords: conodont; tooth; dental tools; finite-element analysis; *Wurmiella excavata*

1. INTRODUCTION

Conodonts, an extinct clade of jawless vertebrates [1], possessed an oropharyngeal skeleton of elements that formed a feeding apparatus [2,3]. The extensive wear and damage developed on these elements, which could result only from attrition and abrasion of exposed element surfaces [4–6] and clear morphological convergence with other dentitions ([6,7] and references therein), strongly supports the interpretation of conodont elements as functional analogues, if not homologues, of gnathostome teeth.

However, qualitative analyses of conodont elements have revealed that the architecture, growth and basic kinematics of the feeding apparatus differed fundamentally from the teeth of jawed vertebrates [6,8], reflecting independent origin [1,9]. Moreover, at approximately 0.2–2 mm long, conodont elements are at least an order of magnitude smaller than many teeth. Likewise, because conodont oropharyngeal muscles must necessarily have been small, and lacked jaws for anchorage, the absolute force available for fracturing and fragmenting food with these elements is likely to have been miniscule. How then could such structures function effectively as a dentition?

We addressed this issue quantitatively for the first time, using finite-element (FE) analysis, to test loading hypotheses in structures too small and delicate for empirical experimentation [10]. We also analysed elements morphologically, as tools for food fracture, an approach that has

formalized the application of engineering principles to teeth and illuminated the influence of shape upon function in mammals [11–16]. Finally, we combine results from these analyses with observations of surface wear to constrain element kinematics and function during food processing.

2. MATERIAL AND METHODS

We focus on *Wurmiella excavata*, which possessed a skeletal morphology common in conodonts [17] and is represented by well-preserved specimens from the Silurian Eramosa Member Lagerstätte, Canada [18]. We analysed eight P₁ elements (paired, dedicated food-processing structures at the posterior of the feeding apparatus), using three-dimensional models constructed with synchrotron radiation X-ray computed micro-tomography (SR μ CT) on the 20XU beamline of the SPring-8 synchrotron, Japan. Surfaces were extracted from this volume data using AVIZO v. 6 (VSG). From these surfaces, three-dimensional sharpness measurements were obtained in GEOMAGIC STUDIO v. 12 (Geomagic, USA) and two-dimensional angular measurements in IMAGEJA v. 1.44b [19]. P₁ element morphology and the functional variables we measured are illustrated in figure 1. Occlusal models were produced in BLENDER v. 2.49b (<http://www.blender.org>). To contextualize our measurements, we compare our data with those acquired from microchiropteran molars [11,14], which overlap the size range of conodont elements and are the only teeth from which comparable data are available. We selected the cusps of a P₁ element pair (Royal Ontario Museum 61381) as representative geometries (figure 2) on which to apply FE modelling to test two alternative loading hypotheses: a uniform pressure to either the dorsal cusp edge, simulating a

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsob.2012.0147> or via <http://rsob.royalsocietypublishing.org>.

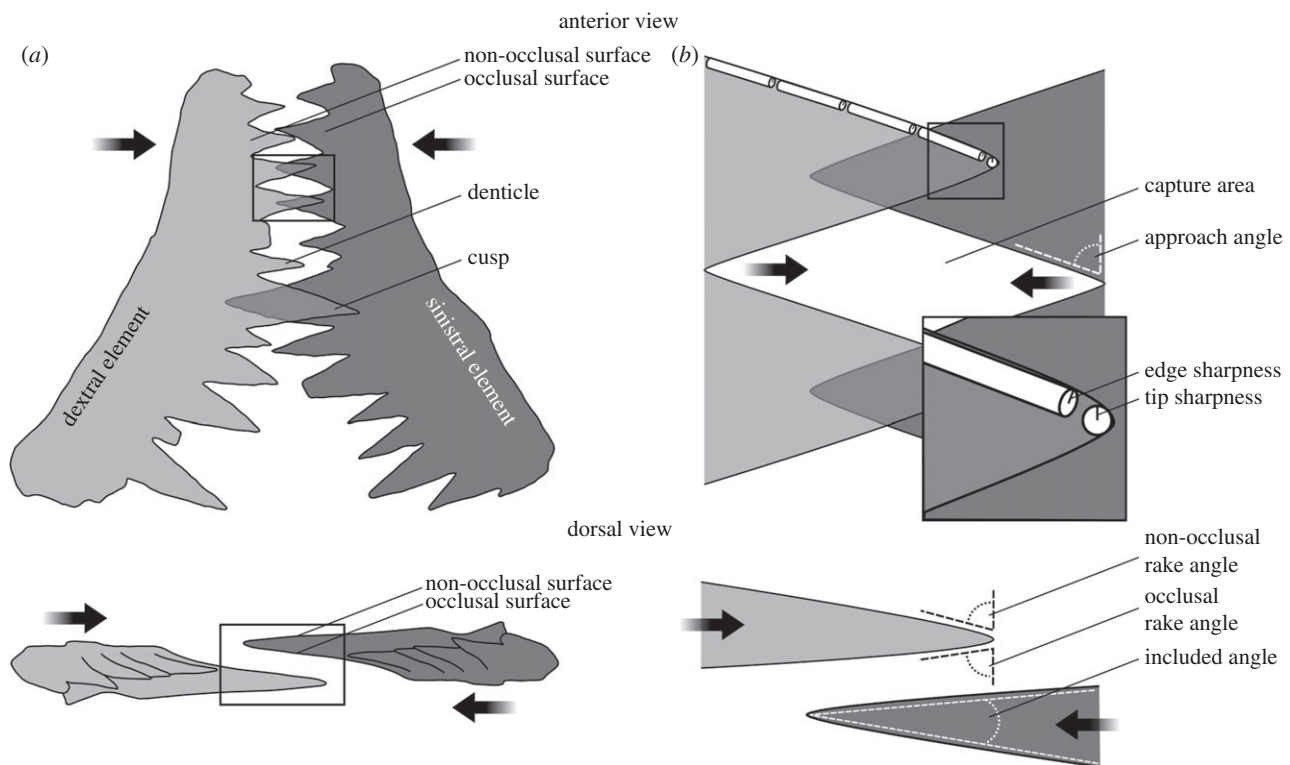


Figure 1. Functional characteristics of conodont elements, using *Wurmiella excavata* P₁ elements as illustrative example. (a) Occluding element pair, illustrating morphology, with boxed areas enlarged in (b) to show measurements. Arrows indicate probable occlusal vectors for initial occlusal phase (see text). In conodonts, the cusp is defined simply as the structure closest to the point of first growth; the remaining pointed structures are denticles.

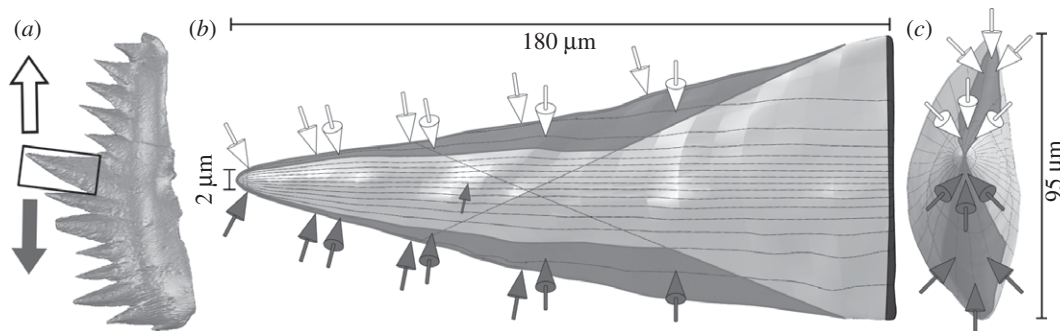


Figure 2. Model geometry and load parameters for FE analysis of the sinistral *Wurmiella excavata* P₁ element cusp (ROM 61381). (a) Whole element in anterior view, highlighting cusp in boxed area; arrows indicate direction of cusp motion during dorsal (white) and ventral (grey) draw cuts. (b) Anterior and (c) occlusal view of cusp model. Dark grey regions indicate area of applied load and arrows indicate its approximate direction for dorsal (white) and ventral (grey) pressure. Black area in (a) demarcates basal constraints.

dorsal draw cut, or the ventral cusp edge, simulating a ventral draw cut. Each comprises movement orthogonal to the cusp long axis. These models were created and analysed in ABAQUS v. 6.7 (Simulia, USA), based on surfaces imported from GEOMAGIC STUDIO. See the electronic supplementary material for further details.

3. RESULTS

(a) Element morphology

Our measurements are summarized in table 1 (see the electronic supplementary material for full results). All elements have an included angle of less than 15°; they therefore possess effectively two rake (leading) surfaces, with positive rake angles. The dorsal and ventral surfaces of the cusps and denticles are narrowed to form distinct ridged edges; the element therefore forms a blade. The

dorsal edges of the cusp and dorsal process denticles are typically sharper than the ventral edges. The interdenticle spaces are developed to form sharp, V-shaped notches, sometimes extended into slits. The dorsal denticles and cusp are coaxial, whereas the ventral denticles exhibit a splayed configuration.

(b) Constraints on element occlusion

Pristine *W. excavata* cusps and denticles possess pronounced micro-ornament (figure 3a) that shows frequent evidence of *in vivo* wear along its entire length (figure 3b,c) on the occlusal surface of the element. This polishing is smooth, exhibiting no microtexture (i.e. pits and scratches). Moreover, wear is present along most of the denticle row on both processes, although its extent diminishes away from the cusp (figure 3d). Lighter wear is also present along

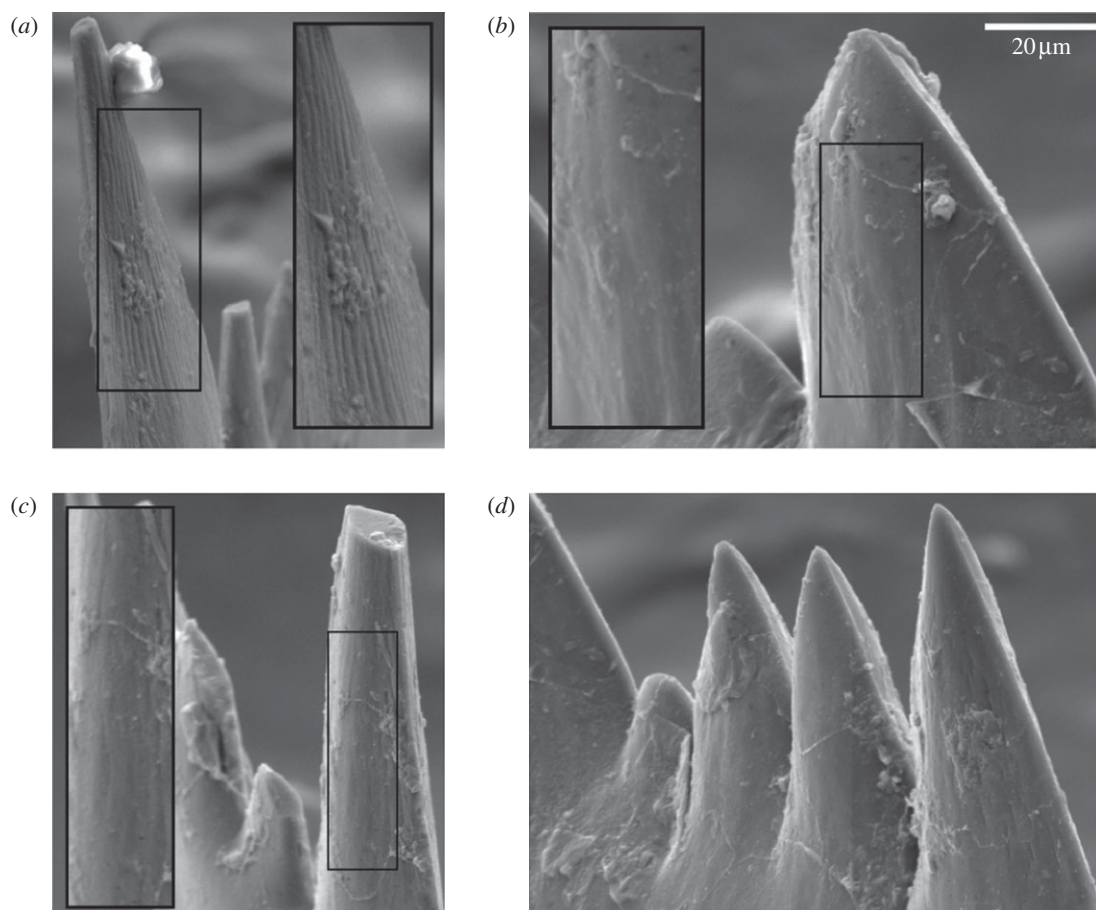


Figure 3. Scanning electron micrographs of *W. excavata* elements (Silurian, UK). (a) Unworn occlusal surface of cusp; (b,c) occlusal surfaces of two cusps, illustrating worn state; (d) ventral denticle row, showing progressive decrease in extent of wear from proximal to distal (left to right). Scale applies to non-inset images.

Table 1. Summary values for functional measurements from *W. excavata* P₁ elements from the Eramosa Lagerstätte, Canada. Equivalent data are provided from microchiropteran molars [11,14].

	<i>W. excavata</i>	microchiroptera
length (μm)	270–850	1087–2110
tip sharpness (radius of curvature; μm)	1–3	15–40
cuspal sharpness ($10^3 \mu\text{m}^3$ at $100 \mu\text{m}$ from tip)	3–42	600–1700
edge sharpness (radius of curvature; μm)	1–4	10–20
rake angle ($^\circ$)	83–85	–11–40
approach angle ($^\circ$)	60–80	24–42

both denticle rows on the non-occlusal surface of the cusp and denticles.

The results of the FE analysis of P₁ element cusps (figure 4 and table 2) reveal that mean maximum principal stresses are lower when cusps are loaded on the dorsal edge compared to when loaded on the ventral edge.

4. INTERPRETATION OF THE OCCLUSAL CYCLE

Figure 5 illustrates our occlusal model. Articulated *W. excavata* P₁ elements reveal that the dextral element was positioned anterior to the sinistral [20], as in other conodonts [2]. However, smoothly polished wear is characteristic of element–element attrition [4]. Its presence on the non-occlusal surface suggests that elements sometimes occluded dextral caudal to sinistral and so must have

separated during the occlusal cycle (figure 5a). This allows food to move between the elements, which would otherwise be difficult. The development of occlusal wear along the length of both denticle rows requires a rotational component to occlusion, because element curvature would prevent such wear occurring were movement purely orthogonal to the element long axis. The sharper dorsal edges of the cusp and denticles (electronic supplementary material, table S1) indicate that the *direction* of rotation for the primary power stroke was dorsal. FE analysis tests and supports this conclusion: cusp morphology is better able to resist tensile stress during a dorsally directed draw cut (table 2). This suggests that the elements initially occluded with the dorsal process long axis of each element vertical and parallel. Rotation then separated the dorsal processes, moving the dorsal denticles and cusp upward

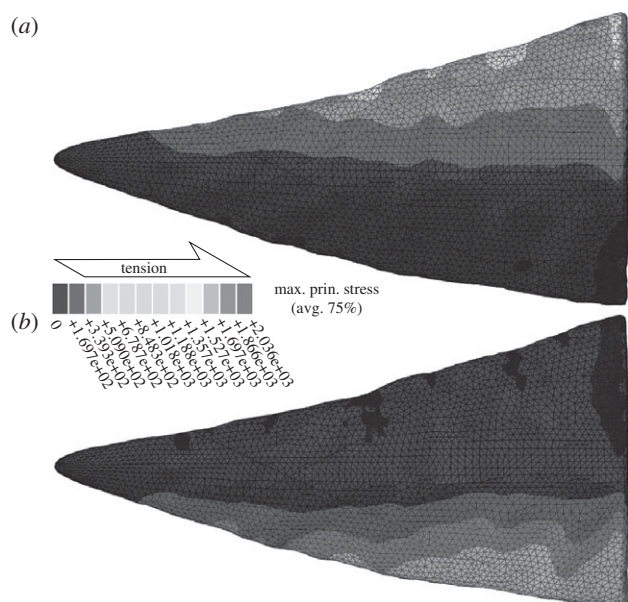


Figure 4. Maximum principal stress patterns in the FE model of the sinistral *W. excavata* P₁ element cusp (ROM 61381) under (a) dorsal and (b) ventral loading. Black areas indicate negative values (compression).

and outward, and bringing the ventral processes and their denticles into occlusion (figure 5*b,c*). The extent of occlusal wear reveals that occlusion was deep; i.e. the cusp and denticles overlapped almost completely.

Cusp tip spalling in P₁ elements with *W. excavata* morphology further suggests that these elements separated during the occlusal cycle; by analogy with teeth [21], this would also have resulted from element–element contact. Cusp size can estimate the separation distance: dental tools are of similar dimensions or smaller than the food being fractured [22]; using a large cusp to fracture much smaller food items is ineffective. Consistent with this are the typically larger cusps of the P₂ elements in *W. excavata* [20], which are anterior to the P₁, encountered food first and, thus, larger fragments. A similar pattern of relative P element cusp sizes is observed in many conodonts.

Initial occlusion in *W. excavata* takes advantage of the sharp tips of cusps and dorsal denticles (table 1), which reduce the contact area between element and food, concentrating force and increasing penetration efficiency [12,23,24]. The sharp, bladed edges of the cusp and denticles (table 1) functioned similarly. Their influence becomes increasingly important as they enter and so displace a progressively larger volume of the food, thus requiring higher force to maintain penetration, because the edges direct force towards crack propagation rather than plastic deformation [13,24,25]. Likewise, the high cusp sharpness (table 1) reduces the energy required for the cusp or denticle to drive through tough food, needing fewer bonds in the material to be broken or strained, reducing the force required for crack propagation [13]. The high approach angles of the cusp and denticle edges (table 1) increase the elements' mechanical advantage [13] by decreasing the area of contact between the two elements, increasing pressure and decreasing friction. Deep occlusion exploits the acute inter-denticle notches, further concentrating forces [13,26,27], and enclosing

Table 2. Mean maximum principal stress in the model of the sinistral *W. excavata* P₁ element cusp (ROM 61381) in the FE analyses.

cusp	element no.	force direction	force (Pa)	mean maximum principal tensile stress (Pa)
dextral	175 156	dorsal	101	195
dextral	175 156	ventral	100	237
sinistral	205 859	dorsal	76	84
sinistral	205 859	ventral	100	133

the food before it is fully divided, making it more likely to be fractured. Subsequent rotation exploits the sharp tips (table 1) of the splayed ventral denticles.

5. DISCUSSION

(a) Comparison to other conodonts

The P₁ element morphology of *W. excavata* is common in conodonts [17], and so insights derived here can be generalized to furnish functional hypotheses for many species. Similar rotational kinematics have also been proposed for two taxa with morphologically different P₁ elements. The ventral processes in *Idiognathodus*, which form denticulated blades, are interpreted principally to have guided the alignment of the dorsal processes during occlusion, which are expanded into food processing platforms [6]. Nodes on the occlusal surfaces of the ventral processes of P₁ elements of *Vögelgnathus campbelli* were argued to improve food processing, through slicing and cutting food, with rotation about the dorsal processes [28]. In both interpretative models, elements remain in contact throughout the occlusal cycle. However, non-occlusal wear and tip spalling in *Idiognathodus* suggests separation occurred [5]; the same is probable and testable for *V. campbelli*. Therefore, our occlusal model of separation and rotation may be general for conodonts. However, whereas the power stroke in *V. campbelli* was dorsal to ventral, as the evidence suggests for *W. excavata*, in *Idiognathodus* it was opposite in sense: ventral to dorsal. It may be that the evolution of platforms was associated with a reversal of initial rotation direction; this is also testable using our approach.

The development of sharp, bladed cusps and denticles suggests facultative consumption of tough, viscoelastic food. To fragment this food, deep occlusion would be required to drive the elements completely through it, as cracks would not self-propagate [22,29]. However, conodonts were not constrained to produce elements with sharp, bladed cusps and denticles: the morphology and orientation of these structures varies greatly, even between processes on a single element. The absence of sharp blades in many conodont species that lack platforms like *W. excavata*, suggests a reliance on puncture rather than draw cutting in these taxa, and concomitantly orthogonal occlusion with little rotational movement. Our approach provides a means of understanding and testing these scenarios.

(b) Comparison to other vertebrate dentitions

Our analytical approach places conodont elements within a broader dental framework. Convergence with the bladed

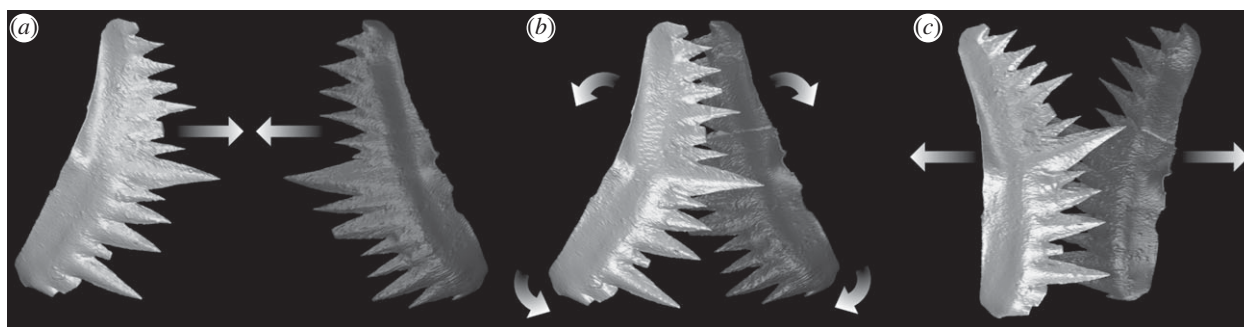


Figure 5. (a–c) Occlusal cycle in *W. excavata* P₁ elements in anterior view, based on SR μ CT models of P₁ element pair ROM 61381. Dextral element in light grey, sinistral element in dark grey, arrows indicate movement. See the electronic supplementary material for animation.

edges of conodont element cusps and denticles is evident in chiropteran canines [30] and various marine predators [7], and convergence with the inter-denticle notches is apparent in chondrichthyan, theropod dinosaur and mammalian carnassial teeth [31,32]. Although high sharpness renders the elements demonstrably vulnerable to wear and breakage [5], the external appositional growth of elements meant that conodonts could re-sharpen worn tips and edges, and replace damaged cusps and denticles through life. Although this largely releases the constraint on sharpness in conodonts, many gnathostomes could achieve the same result by replacing teeth. The larger absolute muscular force available to gnathostomes for fracturing food probably allows them to apply the same effective pressure to food with the blunter teeth that higher dental stresses necessitate to minimize tooth fracture [24,33].

6. CONCLUSIONS

Using quantitative analyses based on engineering approaches applied to conodont food-processing elements, we show that their morphology is adapted to overcome size limitations by developing dental tools of unparalleled sharpness which maximize applied stress. We also show how this morphology is employed in *W. excavata* using rotational kinematics similar to other conodonts, suggesting that this occlusal style is typical, though not universal, for the clade. Using these techniques to improve our understanding of conodont element function has broad implications. Conodonts provide a resource for establishing the generality of functional principles derived from teeth, and for exploring convergence in food-processing structures from different groups. Their small size places them in a position to elucidate the little-studied effects of scaling in dental morphology [22,34]. The key position they occupied within marine ecosystems means that increased constraints on their diet will allow more comprehensive reconstruction of trophic structure in ancient oceans.

We extend grateful thanks to Peter von Bitter and Mark Purnell for specimen loan, and thank Ian Stewart for specimen mounting materials and the two reviewers who provided helpful comments on an earlier version of the manuscript. Work was funded by Marie Curie POF-GA-2009-235868 (to D.J.) and the Australian Research Council DP0880120 (to A.R.E.). Travel to Japan was funded by the International Synchrotron Access Programme of the Australian Government, managed by the Australian Synchrotron. Synchrotron Proposal no. 2010A1047 was performed with

the approval of the Japan Synchrotron Radiation Research Institute.

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