Growth patterns in euconodont crown enamel: implications for life history and mode-of-life reconstruction in the earliest vertebrates

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Euconodonts were the first vertebrates to produce a mineralized skeleton. It is concluded that the minor increments in the crown enamels of *Protopanderodus varicostatus* and *Drepanodus robustus* are probable homologues of the cross striations in hominoid enamel, although they are much more variable in thickness and represent daily to weekly growth. Major increments are superficially similar to lines of Retzius, but represent a check in growth that is likely to have occurred at monthly intervals. Periods of above- and below-average growth are likely to have been seasonally moderated. The growth of *P. varicostatus*' elements are characterized by two distinct phases: the production of a triangular, asymmetrical juvenile 'proto-element' followed, in a second phase, by the development of the curved and twisted geometry of the adult element. These fundamentally different morphologies imply that juvenile and adult animals had different modes of life and/or feeding strategies. In these animals the growth of the elements was indeterminate. The growth model for euconodonts is clearly different from that of hominoid teeth as the enamel organ must have reformed repeatedly throughout life.

Keywords: euconodonts; enamel growth; mode of life

1. INTRODUCTION

Euconodonts are an extinct group of primitive gnathostomic vertebrates that ranged from the Cambrian to the Triassic (Donoghue *et al.* 2000). The oropharyngeal cavity of euconodonts contained an array of complex elements, which functioned as teeth (Purnell 1995); these were the only part of the skeleton to mineralize (Sansom *et al.* 1992). The apparatus was retained throughout life as indicated by morphometric study of bedding-plane assemblages (Purnell 1993, 1994) and microstructural analysis (Donoghue 1998; Donoghue & Purnell 1999). Histological studies suggest four hierarchical modes of formation (Donoghue 1998), homologous with the development of hard tissues in other vertebrates, and demonstrate that elements developed through four or more growth-function cycles (Zhang *et al.* 1997; Donoghue & Purnell 1999). The crown enamel in euconodonts is an accretionary tissue and grows by the appositional addition of increments (Donoghue 1998).

Organisms with accretionary skeletons record the effects of circadian or environmental rhythms on their metabolic processes as fine growth increments grouped into cyclical hierarchies within the skeleton. The periodicity of these hierarchies has been used to estimate day length through geological time, in palaeoecological studies and in the reconstruction of life histories (e.g. Scrutton 1978). It is known that the incremental growth of dental enamel in other vertebrates preserves tracks of growth (Boyde 1963), and the conditions under which the tooth grew can be used to interpret the life history. In this paper we report that protopanderodontid euconodont elements record life-history events.

2. METHODS

Protopanderodus varicostatus (Sweet & Bergström 1962; order Protopanderodontida; figure 1a,b) and *Drepanodus robustus* (Hadding 1913; order Protopanderodontida; figure 1c) were chosen because they are relatively large and have simple morphologies. Specimens were sectioned and polished as recommended by Donoghue (1998). Specimen 692/14 was mounted on a scanning electron micrograph stub to allow an orientated view into the basal cavity. Increment thickness was measured directly from photomicrographs.

Thickness data are plotted as bivariate plots (figures 2a–d, f and 4a–d) and Fischer plots (figures 2d, 3b,c and 4d). The latter were devised to elucidate cycle hierarchy within sedimentary successions (Sadler *et al.* 1993) and are ideal for delimiting periods of above- and below-average growth. As increment duration cannot be assumed to be constant, the horizontal scales on Fischer plots represent cumulative thickness. In these plots the rate of deposition of enamel is assumed to be similar throughout growth, as indicated by the linear relationship between cumulative thickness and cumulative number of growth events in both taxa (figures 2d and 4d).

Growth events are defined as the time taken to secrete the minimum-thickness minor increment. A growth cycle is arbitrarily defined as constituting a peak of growth on either a Fischer plot or a thickness versus increment plot.

3. RESULTS: PATTERNS OF ENAMEL GROWTH

(a) *Protopanderodus varicostatus*

Specimen GLAHM 109171 comprises two hierarchies of growth increment: minor increments are grouped in sets of five to ten to form major increments (figures 1a,b and 2). The mean minor-increment thickness is 1.5 µm (range

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Figure 1. Photomicrographs of specimens analysed in this study. (a) *Protopanderodus varicosatus* (specimen GLAHM 109171), scale bar = 200 μm . (b) High-magnification image of box in figure 1a illustrating major and minor increments, scale bar = 50 μm . (c) Oblique view into the basal cavity of *Drepanodus robustus* (specimen 692/14); minor and major increments can be seen on the inner surface of the crown, scale bar = 100 μm . All specimens are from Mid-Ordovician *P. anserinus* biozone limestone clasts from Culzean Bay, UK (grid reference NS 245130 sample D842) deposited in the University of Durham Micropalaeontological Collection. Specimen GLAHM 109171 is housed in the Hunterian Museum, University of Glasgow, UK.

0.8–3.3 μm ; figure 2a). The earliest minor increments could not be observed in this specimen, which comprises 72 minor and 9 major increments. The mean major-increment thickness is 12 μm (range 7.2–16.7 μm). The thicknesses of the minor increments vary as approximate multiples of 0.8 μm (figure 2a). If 0.8 μm is taken as the minimum thickness of enamel that could be deposited in

a single growth event in this species, then the number of growth events per minor increment varies from one to four (figure 2b). The number of growth events per major increment varies from 9 to 23, with a mean of 15 (figure 2g). The Fischer plot of minor-increment thickness separates periods of above- and below-average growth (figure 2e); growth was terminated part-way through a growth cycle. Despite having a polycyclic growth pattern, this element exhibits a linear increase in size over its entire growth period (figure 2c,f). There is no apparent correlation between major-increment boundaries and changes in growth on the Fischer plot.

Specimen 9799-12D (figure 3) comprises 95 minor increments visible in the distal region of the crown. Major increments are defined by low-angle discontinuities. The upper 30 minor increments have a mean thickness of 1.5 μm ; the lower 65 minor increments have a mean thickness of 1.6 μm . The Fischer plots for the upper and lower parts of the element are distinct (figure 3b,c). Up to minor increment 15, the upper part is characterized by above-average growth; the lower part is characterized by average growth followed by parallel and then by declining growth. The effect of differential growth in the two parts of the specimen produces a 'proto-element' that is triangular and asymmetrical about the midline. If we assume that 0.8 μm is the minimum amount of enamel that could be secreted during a growth event in this species, then the 'proto-element' took 29 growth events to form.

(b) *Drepanodus robustus*

Specimen 692/14 (figures 1c, 4 and 5) comprises 136 minor increments with a mean thickness of 2.5 μm (range 1.3–9.3 μm ; figure 4a) and 16 major increments with a mean thickness of 21.5 μm (range 10.4–30.3 μm ; figure 5a). Minor increments are grouped in sets of four to ten to form major increments. The thicknesses of the minor increments vary as approximate multiples of 1.3 μm (figure 4a,b). If 1.3 μm was the minimum thickness of enamel that could be deposited in a single growth event in this species, then the number of growth events per minor increment varies from one to four with occasionally as many as seven (figure 4b). The number of growth events in a major increment varies from 8 to 23 (mean = 16.6; figure 5c). Major-increment thickness and the number of growth events per major increment vary systematically and in parallel, with five peaks indicating that the element grew over five growth cycles (figure 5a,c). The Fischer plot of minor-increment thickness shows five growth cycles, each comprising periods of above- and below-average growth (figure 4e). This element also shows a linear increase in size throughout its growth, despite a polycyclic growth pattern (figures 4c,d and 5b,d).

4. DISCUSSION

(a) *Timing of growth and implications for mode of life*

Incremental growth patterns in marine invertebrates are notoriously difficult to interpret, as organisms consistently preserve fewer growth events than is theoretically possible (Scrutton 1978). Additionally, incremental growth can

Figure 2. Growth patterns in *Protopanderodus varicostatus* (specimen GLAHM 109171), oldest increments to the left in all cases. For explanation see text. (a)–(d) Bivariate plots of raw thickness (a), number of growth events (b) and cumulative thickness (c,d) for minor increments. (e) Fischer plot illustrating periods of above and below average growth. (f) Cumulative thickness per major increment. (g) Number of growth events per major increment. Vertical scales in (a), (c), (d) and (f) in micrometres.

Figure 3. (a) Tracing of the enamel microstructure in the longitudinal section of *Protopanderodus varicostatus* (specimen 9799-12D), scale bar = 100 µm. Major-increment discontinuities and the 'proto-element' were interpreted on axially compressed images. (b,c) Fischer plots of minor-increment thickness. Increments are measured from the midline to the edge of the element. The deflection in the plots (at minor increment 15) marks the edge of the 'proto-element' and a marked change in growth style between the two parts of the element.

Figure 4. Growth patterns in *Drepanodus robustus* (specimen 692/14) (a) Bivariate plots of raw thickness. (b) Number of growth events. (c) Cumulative thickness of minor-increments. (d) Cumulative thickness against cumulative number of growth events showing linear increase in size and a mean minor-increment thickness of $1.3\text{ }\mu\text{m}$. (e) Fischer plot showing polycyclic growth. Vertical scales in (a), (c), (d) and (e) in micrometres.

record endogenous circadian rhythms and/or exogenous environmental cycles. Short-term diurnal, tidal and lunar cycles can often entrain growth and dominate the preserved patterns.

The minor increments in euconodont enamel have a minimum thickness similar to that of the diurnal enamel cross striations in hominoids (Risnes 1998) and other primates (FitzGerald 1998), but are more variable in thickness. A minor increment thicker than the minimum was produced by multiple growth events. If a growth event represents daily growth then the *Protopanderodus* (specimen GLAHM 109171) would have grown over a minimum of 137 days. A major increment would then represent between 9 and 23 (mean=15) days' growth. *Drepanodus* (specimen 692/14) would have grown over 265 days, with the major increments representing, on average, checks in growth every 17 days. A synodic lunar cycle in the Ordovician has been estimated to be approximately 21 days (Scrutton 1978).

Incremental growth in many marine animals can also be entrained by a variety of seasonal cycles (for a review of these in fishes see Helfman *et al.* (1997) and Müller & Nogami (1972) for euconodonts). The studied taxa exhibit polycyclic growth. Growth cycles are best preserved in *Drepanodus* (specimen 692/14). Periods of above-average growth lasted for between 30 and 60 growth events (figure 4e). If the growth events were daily then these periods could represent monthly or bimonthly phases of growth and could reflect seasonal variation in environmental conditions correlating with a local increase in nutrient availability and/or temperature, the primary ecological limiting factors in other marine vertebrates (Helfman *et al.* 1997).

The most parsimonious explanation is that *Protopanderodus* and *Drepanodus* deposited a minimum of $0.8\text{ }\mu\text{m}$ and

$1.3\text{ }\mu\text{m}$, respectively, of enamel in a day, values comparable to hominoids and other primates. This results in a reasonable hierarchy of scales, comparable with those found in other organisms. Minor increments would be deposited either daily or, more commonly, represent several days of uninterrupted growth. Major increments in the two species comprise tens of growth events and are more likely to record monthly checks in growth. Periods of above- and below-average growth represent seasonal fluctuations in nutrient availability and/or temperature.

(b) *Implications for life history and mode of life*

Hatching or birth and the onset of exogenous feeding represent two landmark events in the early life history of fishes. The loss of larval characters and the acquisition of the axial skeleton, exogenous feeding, new organ systems, pigmentation, squamation and fully-developed fins mark the change from the larval to the juvenile stage. The change from juvenile to adult is marked by the onset of sexual maturity. Growth commonly ceases at this point but can continue at a reduced rate until death (Helfman *et al.* 1997).

The growth of *Protopanderodus* was characterized by two distinct phases. The first phase lasted approximately 29 days and resulted in a short triangular 'proto-element'. The curved and twisted geometry of the adult element was only initiated in the second phase, which continued until growth ceased. If the growth of the skeleton in euconodonts was initiated at the beginning of the juvenile stage then the 'proto-element' represents the juvenile condition and the change in growth style probably occurred on reaching adulthood. Growth is then likely to have continued throughout life (indeterminate growth). Alternatively, the 'proto-element' could represent a larval condition, with the change in growth style

Figure 5. Growth patterns in *Drepanodus robustus* (specimen 692/14 based upon major-increment thickness) (a) Raw thickness illustrates polycyclic thickness variations in major increments. (b) Linear correlation of cumulative number of growth events per major increment. (c) Number of growth events per major increment varies systematically with five growth cycles in this element. (d) Cumulative thickness against cumulative number of growth events illustrates the linear increase in the size of this element. Vertical axis in (a) and (d) in micrometres. Oldest increments are on the left in all cases.

occurring during the transition to the juvenile phase. Growth in this case is likely to have ceased at adulthood (determinate growth). Comparison with other fishes suggests that the former is the more likely hypothesis.

Further, different element morphologies are likely to have had different functions, different feeding efficiencies or were used to process different prey. This implies that juvenile protopanderodontid euconodonts had a different mode of life from adults.

In hominoid teeth the enamel organ is destroyed on the eruption of the permanent teeth. If protopanderodontid euconodonts exhibited similar cycles of function and growth to those seen in more derived taxa, then the functional phase must have occurred between major increments, and it is therefore only possible to give a minimum age to a euconodont element. The enamel organ in euconodonts must have repeatedly reformed throughout life.

5. CONCLUSIONS

The minor increments in euconodont crown enamel are probable homologues of the cross striations in hominoid enamel, although they are much more variable in thickness, representing daily to weekly growth. Major increments, though superficially similar to lines of Retzius, represent a monthly check in growth.

Two phases of growth are documented in *Protopanderodus*. The 'juvenile' proto-element is short and triangular, whilst the adult element is markedly curved, implying different functionalities and suggesting that juvenile and adult animals had different modes of life or feeding strategies. In these animals the growth of the elements was indeterminate.

The growth model for euconodonts is clearly different from that of hominoid teeth as the enamel organ must have reformed during functional phases. Growth-pattern analysis is potentially a powerful tool in the elucidation of life histories and modes of life in euconodonts.

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