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Comment: Tooth enamel mineralization in ungulates: Implications for recovering a primary isotopic time-series, by B. H. Passey and T. E. Cerling (2002)

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1. INTRODUCTION

Passey and Cerling (2002) presented both direct measurement and a theoretical model that describe rates of tooth enamel mineralization in ungulates (hoofed mammals), and the retrievability of environmental time-series. Their results are quite important because ungulate teeth are common in the fossil record and readily analyzed for stable isotope compositions, which makes them outstanding archives of paleoecological and paleoclimate information (e.g., Koch, 1998). Because tooth enamel grows progressively, isotopic zoning in enamel potentially encodes isotopic seasonality. However, Passey and Cerling show that enamel mineralization processes must cause records of isotopic seasonality to be damped relative to an environmental signal. According to their model, damping is strongly dependent on lengths corresponding to rates of enamel maturation (l_m) and lengthwise growth (t_Δ). They measured l_m , but provided no values for t_Δ , and in their models instead assumed various ratios of l_m/t_Δ . Unlike many comments, the purpose of this note is not to challenge their results per se, but rather to point out that published zoning profiles for several ungulates permit estimation of t_Δ . This in turn provides broad discrimination of their model results, and estimates for the degree of environmental damping likely present in tooth isotopic records.

2. LENGTH SCALES OF MINERALIZATION

Enamel forms via a two stage process, first by apposition, in which apatite crystallites are seeded into an organic matrix, then by a series of maturation stages, in which crystals infill and coarsen (e.g., Suga, 1982; Hillson, 1996). To what degree do these processes dampen primary environmental variation? As shown by Passey and Cerling's model, damping is primarily dependent on the ratio of two lengths along the enamel: (1) the length along the tooth over which enamel matures from its initial organic-rich state to its final state (l_m), and (2) the length of enamel laid down during the characteristic time span of a variable environmental signal (t_Δ). The ratio l_m/t_Δ is critical because it reflects the amount of time (relative to the time scale of environmental variation) needed for enamel at any location to mature from its initial to final states. Slow vs. rapid enamel maturation causes strong vs. weak damping of records of natural ecological and/or climate variability.

Many ungulate teeth that have been studied (e.g., cervids, bovids, equids, etc.) have ~1-mm-thick enamel "sheaths,"

which grow progressively from the occlusal, or wear surface towards the tooth root. Passey and Cerling show that l_m for large bovids (*Bison bison* and *Bos taurus*, both family Bovidae, subfamily Bovinae) is 15–30 mm. This value is indistinguishable from the results of an independent isotope study of experimental cattle ($l_m \sim 25$ mm; *Bos taurus*; Balasse, 2002). However, small bovids (*Ovis aries* and *Capra hircus*; subfamily Caprinae) have a much smaller value for l_m of 2–3 mm (Suga, 1982). Passey and Cerling also show that for $l_m/t_\Delta \geq 1$, damping is significant ($\geq \sim 50\%$), whereas for $l_m/t_\Delta \leq 0.5$, damping is much less severe ($\leq \sim 20\%$). However they do not suggest characteristic values for t_Δ , from which l_m/t_Δ and damping could be estimated, but rather show model calculations for a range of values of l_m/t_Δ , presumably applicable to a range of taxa. In fact, according to Passey and Cerling's definitions, for a sinusoidal perturbation, t_Δ is simply the half-wavelength of the environmental signal as recorded in a tooth (Fig. 1). Note that in comparison with Passey and Cerling's figure 4, it might appear that t_Δ should be the full wavelength, rather than the half-wavelength. However, that apparent disparity occurs simply because their figure is for a nonrepeating perturbation, whereas Figure 1 applies to a repeating signal.

Fortunately, if the environmental signal is regular, and if the material that records it forms at a constant rate, then the wavelength of the environmental signal will be preserved in the isotopic record, regardless of the degree of damping (e.g., Albarède, 1995). Thus, if isotope zonation that is recorded in a tooth can be correlated to a known seasonal duration, then a value for t_Δ corresponding to that seasonality can be assigned, and Passey and Cerling's model can be solved. In fact, modern and fossil ungulate teeth with enamel thicknesses of 0.5 to 2 mm commonly preserve quasi-sinusoidal oxygen isotope variations, interpreted as yearly seasonality, over typical enamel length scales of 30–60 mm (Table 1; Fricke and O'Neil, 1996; Fricke et al., 1998; Kohn et al., 1998, 2002; Feranec and MacFadden, 2000; Gadbury et al., 2000; Bocherens et al., 2001; Dettman et al., 2001; Zazzo et al., 2002; Balasse et al., 2002, 2003). Thus, for ungulates, t_Δ is typically 15–30 mm/6 months, albeit with important differences among families and subfamilies.

3. IMPLICATIONS

If the enamel maturation length scale is ~25 mm for large ungulates (as determined for *Bison* and *Bos*) and 2–3 mm for small ungulates (*Ovis* and *Capra*), then for yearly climate or dietary seasonality, l_m/t_Δ is approximately 0.1 to 1.0. These values for l_m/t_Δ overlap the model range considered by Passey and Cerling for large ungulates ($l_m/t_\Delta = 0.5$ to 2), and verify

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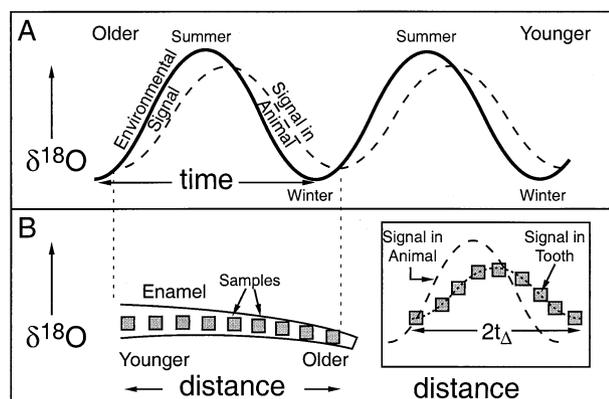


Fig. 1. Schematic diagrams showing quasi-sinusoidal oxygen isotope variation that could occur seasonally, and expected damped-signal responses. Note that the wavelength of the signal is always preserved regardless of the degree of damping (Albarède, 1995). (A) Isotope variability through time. The isotope signal in the animal (dashed line) is damped and time-shifted compared to predicted compositions (solid line) because of the isotope's residence time in the animal. For oxygen, damping is typically $\sim 10\%$ (Kohn et al., 2002). (B) Isotope zoning expected along the length of enamel. t_{Δ} is the distance along the enamel that corresponds temporally to the half-wavelength of the environmental signal. For yearly variations, t_{Δ} can be identified from oxygen isotope zoning studies. For large taxa, combination of measurements of l_m (Passey and Cerling, 2002; Balasse, 2002) and t_{Δ} values (Table 1) imply an average l_m/t_{Δ} of ~ 1 , or damping of $\sim 50\%$ (dotted line) relative to the isotope signal in the animal (dashed line). Different taxa may have different l_m/t_{Δ} (e.g., Hiller et al., 1975; Suga, 1982) leading to different degrees of damping.

the applicability of their results to many taxa. Because t_{Δ} corresponds to the half-wavelength of a yearly cycle, the maturation time encompassed by each part of enamel is therefore <1 to ~ 6 months (Table 1). Assuming apposition lengths of 15 mm for large ungulates (Passey and Cerling, 2002) and 3 mm for small ungulates (Suga, 1982), and a sampling length of 1–2 mm, the tooth isotopic record will be damped relative to a yearly sinusoidal environmental signal by <10 to 70%. Damping is defined here as the difference in amplitudes of the environmental and recorded signals, divided by the amplitude of the environmental signal, and ranges from 0% (perfect preservation of seasonal variation) to 100% (no response to seasonal variation). The residence time of the isotope in the animal causes additional damping. For oxygen this typically contributes an additional $\sim 10\%$ damping (Kohn et al., 2002). This might be important in taxa with $l_m/t_{\Delta} < 0.5$ but would increase total damping in taxa with $l_m/t_{\Delta} \sim 1$ by only a few percent. Obviously more damping would occur for higher frequency signals, such as semiannual or quarterly changes in climate or diet, whereas less damping would occur for faster tooth growth rates and/or higher oxygen turnover rates. Last, Passey and Cerling suggest that a sample spacing density of $\sim 0.125t_{\Delta}$ will result in a very good record of isotope variability, and that increased sample density is unwarranted. In practical terms, if t_{Δ} is 15–30 mm, this translates into a sample spacing of ~ 2 –4 mm, similar to that used in recent studies of yearly seasonality (e.g., Kohn et al., 1998, 2002; Bocherens et al., 2001; Dettman et al., 2001; Zazzo et al., 2002; Balasse et al., 2002, 2003).

Clearly, enamel maturation warrants further investigation, in

Table 1. Enamel growth and maturation rates, and damping factors for various taxa.^a

Family	Yearly enamel growth lengths (mm) (source)	Enamel maturation time	Average damping factor
Bovidae, large (cattle and bison)	40 (1), 40 (2), 40–50 (4), ≥ 50 (5), ≥ 45 (10)	6 months	50–70%
Bovidae, small (sheep, goats, antelope)	30 (2), 100 (3), >30 (6), 45 (9), 20–30 (10, 11)	≤ 1 month	$\leq 10\%$
Equidae (“horses”)	>40 (6), ≥ 60 (7), 50–60 (8)	5 months	40–50%
Cervidae, large (elk)	50 (2)	6 months	$\sim 50\%$
Castoridae (beavers)	150–440 (12)	2 weeks	$<10\%$
Muridae (rat)	180 (13)	2 weeks	$<10\%$
Proboscideae (gomphothere)	45 (14)	6 months	$\sim 50\%$

^a Data sources are: (1) Fricke and O’Neil (1996), archeological bison. (2) Fricke et al. (1998), modern cattle, sheep, and elk. (3) Kohn et al. (1998), modern antelope. (4) Feranec and MacFadden (2000), Pleistocene bison. (5) Gadbury et al. (2000), early Holocene bison. (6) Bocherens et al. (2001), archeological ovicaprid and equid. (7) Dettman et al. (2001), Miocene equids. (8) Kohn et al. (2002), Miocene and Pliocene equids. (9) Zazzo et al. (2002), late Miocene antelope. (10) Balasse et al. (2002), modern and archeological antelope, sheep, cow. (11) Balasse et al. (2003), sheep. (12) Stuart-Williams and Schwarcz (1997), modern and Pleistocene beaver. (13) Hiller et al. (1975), modern rat. (14) Fox and Fisher (2001), late Miocene gomphothere. Maturation times and damping factors are based on length scales for maturation and apposition of 25 mm and 15 mm respectively for large bovids (Passey and Cerling, 2002; Balasse, 2002), equids (assumed), large cervid (elk; assumed) and gomphothere (assumed); 10 mm and 10 mm, respectively, for modern beaver (from descriptions in Stuart-Williams and Schwarcz, 1997); 7 mm and 7 mm respectively for modern rat (Hiller et al., 1975); and 2–3 mm and 2–3 mm, respectively, for small bovids (Suga, 1982).

part because the length scale of maturation is known in only a few animals (e.g., Hiller et al., 1975; Suga, 1982; Stuart-Williams and Schwarcz, 1997; Passey and Cerling, 2002; Balasse, 2002), but also because zoning studies demonstrate that enamel growth is not identical in all herbivores. The paucity of data for l_m precludes accurate generalizations regarding its relationship to t_{Δ} . The l_m/t_{Δ} ratio is broadly linear with body mass for *Castor*, *Ovis*, *Capra*, *Bison*, and *Bos* ($l_m/t_{\Delta} \sim 0.002 \times \text{mass [kg]}$; Table 1). Although faster enamel maturation times for smaller animals make intuitive sense, the general applicability of this relationship is suspect because it mixes different subfamilies and orders. For example, both the rodents *Castor* and *Rattus* have similar l_m/t_{Δ} (~ 2 weeks; Table 1) despite a difference in body mass of two orders of magnitude. Nonetheless, different maturation rates are clearly critical for explaining why some taxa record predicted seasonality well whereas others do not (Fricke et al., 1998). That is, small bovids and some equids (?) are better recorders of seasonality because their enamel matures over a shorter period of time, whereas some large bovids are better averagers because their enamel matures slowly. Of course, other taxa could have similar or different enamel growth rates and hence damping, as illustrated for proboscideans (~ 45 mm/yr for gomphotheres; Fox and Fisher, 2001) vs. castorids (300–400 mm/yr for modern beaver; Stuart-Williams and Schwarcz, 1997). Ultimately,

establishing definite damping factors will require characterization of enamel maturation for each taxon. However, Passey and Cerling's contribution is a key exposition of the importance of enamel maturation and quantification of the process.

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