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ORIGINAL RESEARCH ARTICLE

# "Mind the gap"—Assessing methods for aligning age determination and growth rate in multi-molar sequences of dietary isotopic data

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**Abstract**

**Objectives:** Creating multi-tooth sequences of micro-sampled stable isotope (SI) analytical data can help track 20+ years of individual dietary history. Inferences about individual and population level behavioral patterns require cross-calibration of the timing of dietary changes recorded by each tooth. Dentin sections from contemporaneous tissues (eg, in M1 and M2) reflect dietary signature for the time of growth. Contemporary sections should produce similar values, allowing alignment of temporally overlapping portions of teeth into multi-tooth sequences. Published methods for determining the ages of incremental sections do not provide guidance for adjustment when poor alignment between individual tooth sequences is encountered. The primary objective is to address this problem; examine cause(s), assess the effects of the standard growth-model on available age-assessment techniques, and provide a viable solution.

**Methods:** Investigating difficulty in aligning a 3-molar sequence at Shamanka II, an Early Neolithic (7000-5700 BP) Kitoi hunter-gatherer cemetery in Cis-Baikal, Siberia, we employed 10 age assessment models and 13 variants of 2 published growth rate methods on 3 individuals of different age and sex.

**Results:** At Shamanka II, dentin initiation and/or growth rates were different from the mostly European, reference populations used to create published age-estimation/growth rate models. Initiation ages for M2 and M3 were delayed. Root formation rates were on the rapid end of known development parameters.

**Conclusions:** Age-assessment methods customized to dentin initiation ages and growth parameters of Siberian populations produced a hybrid growth rate model for dentin section ages and improved alignment for multi-tooth SI sequences over published models.

## 1 | INTRODUCTION

The recent development of micro-sampling (also termed incremental-, and sequential-sampling) methods of teeth and skeletal materials has revolutionized archeological biochemical research. Using bulk sampling methods, an individual is represented by a single set of measurements that give an average picture of behavior over the last 5-20 years of life depending on the bone tested, the age of the individual (Szulc et al., 2000; Valentin, 2003), and different physiological parameters (Han et al., 1997). For reconstructing individual life histories, bulk sampling has 2 critical limitations: (1) it masks entirely short-term events, such as starvation bouts or seasonal changes in diet; and (2) events occurring during the first segment of life, some potentially life-changing, such as weaning, differential parental investment, and relocation due to marriage, are lost during remodeling.

Using carbon and nitrogen isotopic analysis on micro-sampled dentin, researchers have recently uncovered variable weaning and dietary histories (eg, Beaumont et al.,

  

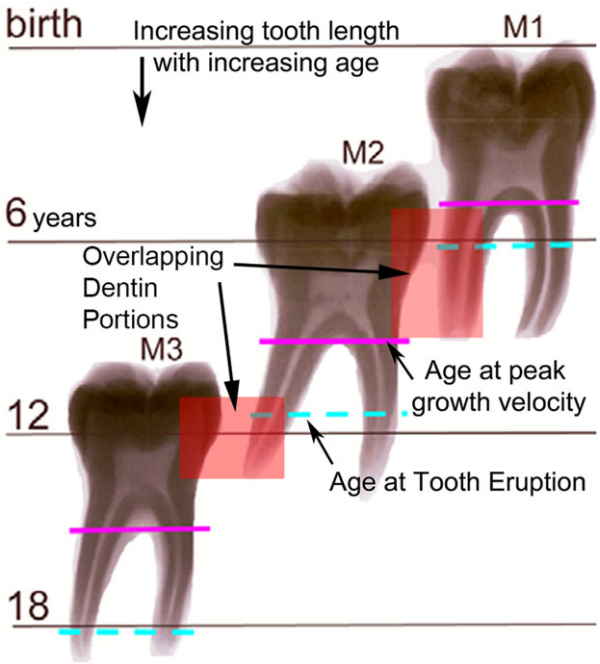


**FIGURE 1** Sequence of initiation of crown and root mineralization through to root completion compared for 3 molars, with approximate ages (years). Overlapping portions of dentin highlighted. Age at peak growth velocity and tooth eruption times following Dean and Cole (2013)

2013; Beaumont and Montgomery, 2016; Burt, 2015; Eerkens and Bartelink, 2013; Eerkens et al., 2011), invisible using bulk (ie, homogenized) bone sampling methods. Expanding incremental analyses to multiple molars, reconstructed dietary history has the potential to cover 20+ years of juvenile and early-adult life (AlQahtani, Hector, & Liversidge, 2010; Beaumont et al., 2013). Individual variation for molar initiation, eruption, age-at-peak-growth velocity, and root apex closure between populations can be substantial (Dean & Cole, 2014). Population-specific genetic histories should moderate within-population variability, particularly in small or isolated populations with limited gene flow.

Insights into an individual's life history require micro-sampled teeth to be accurately placed in temporal/developmental context. Incremental sections of each tooth are lined up to produce a continuous record/sequence of dietary history (Figure 1). Sections of dentin growing at the same time should match between the sampled teeth (eg, M1/M2 and M2/M3 overlap), or, at the minimum, demonstrate similar trend(s).

The Shamanka II cemetery (SHA) is located on the coast of Lake Baikal at its southwestern-most end (Figure 2; 103°42′11″E, 51°41′54”N) (Bazaliiski and Weber, 2004, 2006; Bazaliiskii, 2010). The Early Neolithic (EN) component of this cemetery, consisting of about 150 individuals, displays characteristics of the Kitoi mortuary tradition, including the extended supine body position, N-S/NE-SW orientation, multiple interments, toe-to-head arrangements, the use of red ochre, composite fishhooks, and items of zoomorphic art. The distribution of grave goods is quite variable, ranging from no objects, or very few, to interments with hundreds of items.

Biochemical research has shown interpersonal variation in dietary and mobility patterns at Shamanka II, as well as chronological trends showing increasing fish consumption through time (Scharlotta et al., 2016; Weber et al., 2016; Weber et al., 2011). Bulk bone samples yield a false appearance of dietary stability, obscuring seasonal/annual/multi-annual patterns targeting different terrestrial and aquatic resources. There also may be age-specific activities, as different hunting practices require variable levels of experience and coordination. Three-molar micro-sampled stable isotope (SI) sequences have the potential to refine dietary patterns at the individual scale and provide new life history insights about middle Holocene hunter-gatherers in Cis-Baikal.

Published models (Beaumont and Montgomery, 2015; Dean et al., 1993; Eerkens et al., 2011) for attributing ages to incremental dentin sections are based on a standard growth rate (eg, 4-5 μm per day). However, they do not provide guidance for how to rectify issues where poor alignment is encountered in multi-tooth sequences. Applying published models to incremental sections from 3 Shamanka II individuals (B.6, 34, and 66.1) produced poorly aligned sequences. Thus, the existing models for matching or aligning isotopic sequences across multiple teeth appear not to be applicable to this population. Age-estimation models may be biased by their genetic histories and should not be uncritically applied to archeological populations.

This study aims to assess the efficacy of different combinations of age-assessment methods and growth rate models in attributing ages to incremental dentin and aligning multi-molar sequences. The primary objective is to determine the underlying causes for poor performance of published models for linking multi-molar sequences by investigating the standard growth-model parameter's effects on age-assessment techniques. Effective methods are identified based on their ability to closely correlate multi-molar sequences within realistic developmental age-ranges without the need for “fine-tuning.”

## 2 | MATERIALS AND METHODS

### 2.1 | Skeletal materials

Mandibular molars used in this analysis come from 3 Shamanka II EN individuals: Burials 6, 34, and 66.1, all examined for pathology and age-at-death by Dr A. Lieverse (University of Saskatchewan) following Buikstra and Ubelaker (1994). The sampled teeth exhibited no evidence of enamel hypoplasia, dental caries, or any other tooth attrition. Molars produced 10-15 sections each (Tables 1 and 2, and see extraction method below), with adequate collagen for SI analysis, and consistently good collagen quality with C:N ratios between 2.9 and 3.4 (DeNiro, 1985).

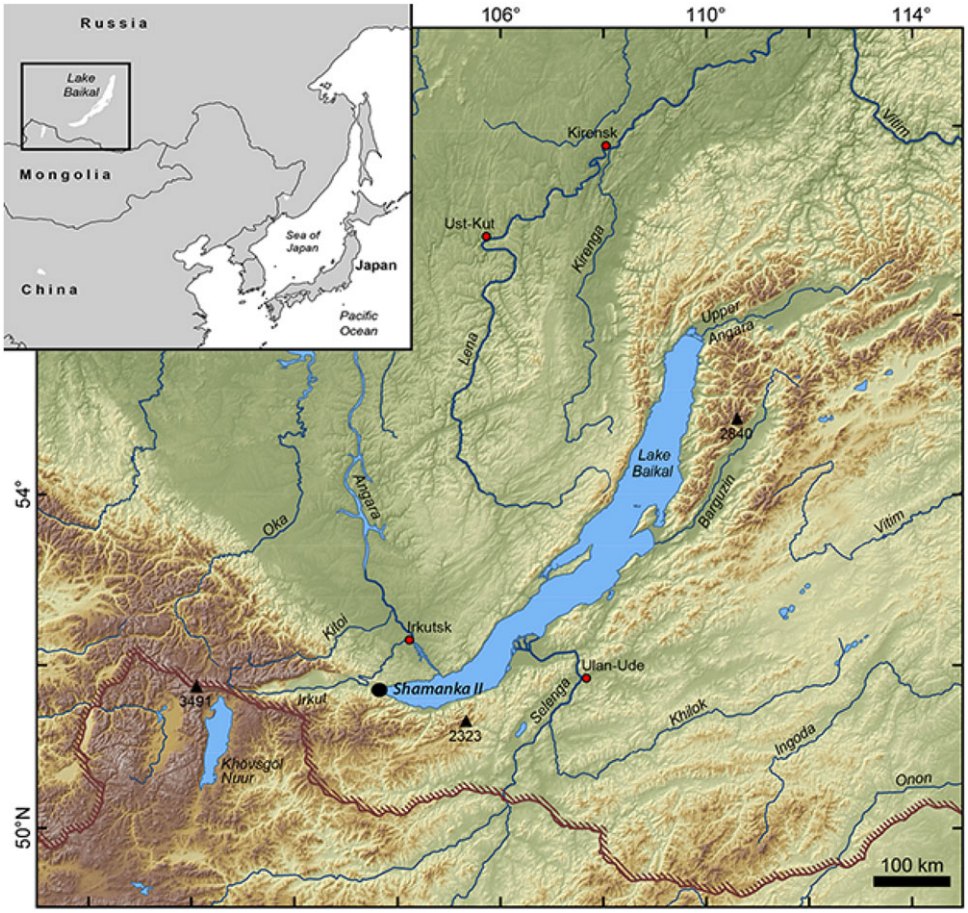


**FIGURE 2** Location map of cis-Baikal region, Siberia, within northern Asia. Topography is based on elevation shuttle radar topography mission v4.1 data (Jarvis et al., 2008); produced by Christian Leipe (FU berlin)

## 2.2 | Laboratory methods: Sectioning and collagen extraction

Molar crowns were scraped to remove any adhering calculus or exogenous material. Teeth were then sectioned with a low-speed saw (Buehler Isomet), first to remove enamel, and then to remove a longitudinal (ie, crown to root) section of dentin along the longest root. Enamel fragments were also collected for future analyses. Cut sections were sandblasted with aluminum oxide ($AlO_3$) powder (Bego Duostar) to remove any remaining enamel and cementum from the exterior and any secondary dentin from within the pulp chamber. Sandblasted sections were rinsed with deionized water and soaked in acetone for 24 h.

Rinsed samples were demineralized using 0.5 M hydrochloric acid (HCl) in a refrigerator at 5°C. HCl was changed every other day until the sample was completely demineralized (generally 1-2 weeks). Following demineralization, samples were immersed in 0.125 M NaOH (sodium hydroxide) for 18-20 h to remove humic acids. The sample was rinsed with $dH_2O$ to remove any residual NaOH.

Tooth sections were then sliced into parallel sections 0 mm thick, beginning at the dentin-enamel junction (DEJ) and working down to the apical root tip (Figure 3). These cuts were generally parallel to growth layers within the crown but cut across diagonal growth layers in the root (cf. Beaumont et al. 2013, Eerkens et al., 2011). The tangible impact of this overlap is a minor loss of chronological precision as each section averages a marginally (ie, 1-2 months) overlapping block of time, flattening that portion of the isotopic curve.

The number of serial sections varied depending on the degree of occlusal wear, and the size, length, and structure of the tooth. Current research (eg, Czermak et al., in press; Fernández-Crespo et al., in press) to refine the ability to either improve slicing methods or use smaller dental punches

**TABLE 1** Age-at-death (years), sex, radiocarbon date (corrected years BP), and carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) results for bone

| **Burial 6** | **Adult bone values** | | | | | |
|---|---|---|---|---|---|---|
| d13C | d15N | CN | 14C date | +/− | Age at death | Sex |
| −16.4 | 16.1 | 3.2 | 5875 | 74 | 16-18 years | Probable male |
| **Burial 34** | **Adult bone values** | | | | | |
| d13C | d15N | CN | 14C date | +/− | Age at death | Sex |
| −16.6 | 14.0 | 3.2 | 6609 | 73 | 35-45 years | Male |
| **Burial 66.1** | **Adult bone values** | | | | | |
| d13C | d15N | CN | 14C date | +/− | Age at death | Sex |
| −17.1 | 13.6 | 3.2 | 6653 | 70 | 25-35 years | Female |

**TABLE 2** Individual molar section $\delta^{13}C$, $\delta^{15}N$, and C:N ratios analyzed for M1, M2, and M3s

| Burial 6 Sample | Tooth sections Sample ID | S-01 | S-02 | S-03 | S-04 | S-05 | S-06 | S-07 | S-08 | S-09 | S-10 | S-11 | S-12 | S-13 | S-14 | S-15 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Lower L M1 | H 2012.033-C | −16.1 | −15.8 | −15.9 | −14.8 | −14.9 | −15.4 | −15.5 | −16.1 | −16.4 | −17.0 | −15.7 | −16.2 | | | |
| | H 2012.033-N | 16.1 | 14.2 | 13.8 | 14.3 | 14.8 | 14.5 | 15.1 | 15.0 | 15.3 | 15.9 | 15.5 | 15.6 | | | |
| | M1 C:N | 3.2 | 3.3 | 3.2 | 3.3 | 3.2 | 3.2 | 3.3 | 3.3 | 3.3 | 3.2 | 3.2 | 3.2 | | | |
| Lower L M2 | H 2012.034-C | −14.4 | −15.8 | −16.1 | −16.0 | −15.9 | −16.1 | −16.1 | −16.1 | −16.3 | −16.3 | −16.3 | −15.9 | −15.8 | −16.2 | −16.1 |
| | H 2012.034-N | 15.0 | 14.3 | 14.1 | 13.5 | 13.4 | 13.9 | 14.8 | 15.2 | 15.3 | 14.6 | 14.1 | 14.7 | 15.2 | 15.4 | 16.2 |
| | M2 C:N | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.4 | 3.3 |
| Lower R M3 | H 2012.035-C | −16.4 | −15.9 | −15.9 | −15.9 | −16.2 | −15.8 | −15.5 | −15.9 | −16.5 | −16.2 | −16.5 | −16.2 | | | |
| | H 2012.035-N | 15.2 | 14.4 | 15.0 | 15.4 | 15.4 | 16.0 | 16.6 | 16.6 | 16.4 | 16.5 | 16.7 | 16.7 | | | |
| | M3 C:N | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | | | |
| Burial 34 | Tooth sections | | | | | | | | | | | | | | | |
| Sample | Sample ID | S-01 | S-02 | S-03 | S-04 | S-05 | S-06 | S-07 | S-08 | S-09 | S-10 | S-11 | S-12 | S-13 | | |
| Lower R M1 | H 2003.681-C | −17.6 | −17.8 | −18.0 | −17.9 | −17.5 | −17.1 | −17.0 | −17.0 | −17.0 | −17.2 | −17.6 | −16.7 | | | |
| | H 2003.681-N | 14.0 | 13.6 | 13.2 | 12.8 | 13.0 | 13.8 | 14.6 | 14.8 | 14.7 | 14.7 | 14.4 | 15.0 | | | |
| | M1 C:N | 3.2 | 3.2 | 3.2 | 3.2 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.2 | 3.3 | 3.3 | | | |
| Lower L M2 | H 2003.682-C | −17.2 | −17.2 | −17.2 | −17.6 | −16.9 | −16.6 | −16.4 | −16.2 | −16.5 | −17.2 | −17.6 | −17.6 | −17.4 | | |
| | H 2003.682-N | 14.0 | 14.1 | 14.0 | 13.8 | 14.2 | 14.6 | 14.9 | 14.6 | 14.0 | 13.7 | 13.4 | 13.9 | 14.4 | | |
| | M2 C:N | 3.2 | 3.2 | 3.2 | 3.2 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.2 | 3.2 | 3.3 | 3.3 | | |
| Lower L M3 | H 2003.683-C | −17.3 | −17.4 | −16.9 | −16.6 | −16.6 | −16.4 | −16.5 | −16.5 | −16.3 | −15.9 | −16.0 | −16.3 | | | |
| | H 2003.683-N | 13.7 | 12.4 | 14.3 | 14.7 | 14.8 | 14.6 | 14.6 | 14.4 | 14.0 | 13.8 | 13.9 | 15.0 | | | |
| | M3 C:N | 3.2 | 3.2 | 2.9 | 3.3 | 3.2 | 3.3 | 3.3 | 3.2 | 3.2 | 3.3 | 3.2 | 3.3 | | | |
| Burial 66.1 | Tooth sections | | | | | | | | | | | | | | | |
| Sample | Sample ID | S-01 | S-02 | S-03 | S-04 | S-05 | S-06 | S-07 | S-08 | S-09 | S-10 | S-11 | S-12 | S-13 | S-14 | S-15 |
| Lower L M1 | H 2005.079-C | −17.3 | −17.3 | −18.3 | −18.2 | −17.8 | −17.1 | −17.0 | −16.7 | −16.6 | −16.6 | −16.8 | −16.8 | −17.3 | −17.2 | −16.6 |
| | H 2005.079-N | 16.7 | 13.8 | 13.0 | 13.6 | 13.5 | 14.0 | 14.6 | 15.0 | 15.3 | 15.3 | 15.1 | 15.3 | 15.4 | 15.4 | 15.5 |
| | M1 C:N | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 |
| Lower L M2 | H 2005.080-C | −17.5 | −17.0 | −16.9 | −16.9 | −16.3 | −16.4 | −16.7 | −16.9 | −17.1 | −17.5 | −17.9 | −17.7 | −17.6 | −17.0 | −17.2 |
| | H 2005.080-N | 14.5 | 14.7 | 14.8 | 14.9 | 14.6 | 14.5 | 14.5 | 14.4 | 13.9 | 13.6 | 13.7 | 14.4 | 14.6 | 14.6 | 14.8 |
| | M2 C:N | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.4 | 3.4 |
| Lower L M3 | H 2005.081-C | −17.0 | −16.6 | −16.9 | −16.5 | −16.4 | −16.4 | −16.7 | −16.9 | −16.7 | −16.1 | | | | | |
| | H 2005.081-N | 14.8 | 14.5 | 13.8 | 13.9 | 13.7 | 14.2 | 14.2 | 14.5 | 14.8 | 15.5 | | | | | |
| | M3 C:N | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 3.4 | | | | | |

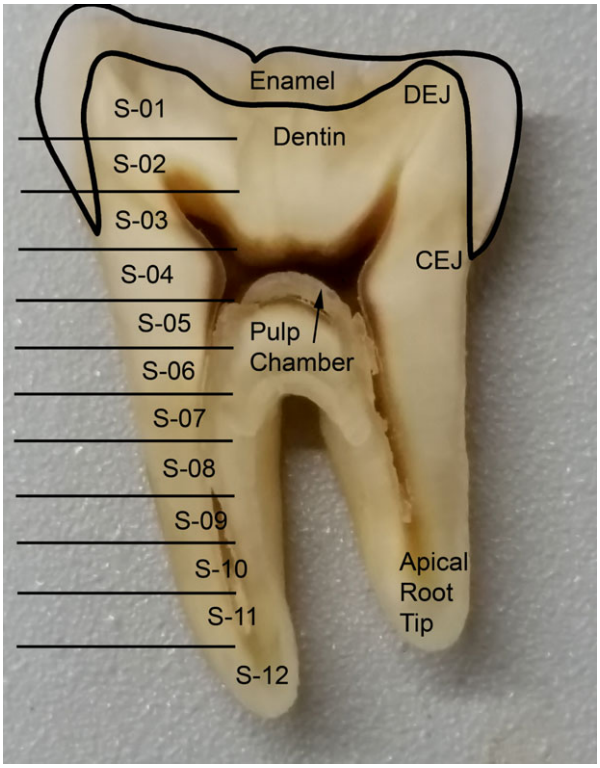


**FIGURE 3** Idealized model of human molar sequential-sectioning/micro-sampling of incremental dentin

may be able to further refine micro-sampling methods, but are not yet feasible for large comparative projects.

Dentin sections were moved to individual vials and placed in slightly acidic (pH 2, 0.01 M HCl) water and solubilized at 75°C. Solubilized collagen was then freeze-dried to remove all remaining water, isolating the collagen fraction. Between 0.9 and 1.1 mg of collagen was weighed out from each serial section for SI analysis. Carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) by isotope ratio analysis for each serial sample was measured at the Biogeochemical Analytical Service Laboratory of the Department of Biological Sciences, University of Alberta using a EuroEA Elemental Analyzer (EuroVector) coupled with Isoprime Mass Spectrometer (GV Instruments). Mass spectrometer precision was ±0.1‰ for $\delta^{13}C$ and ±0.2‰ for $\delta^{15}N$. Bulk bone values for $^{14}C$, $\delta^{13}C$ and $\delta^{15}N$ have been published by Weber and colleagues (Weber et al., 2016; Weber et al., 2016).

### 2.3 | Assessment of current methods of aligning incremental dentin sections

Variability in the levels of wear, root length, apex closure, and preservation condition (eg, overall root integrity, and caries) can impact the reconstruction of diets. To date, sequential sectioning of human dentin to reconstruct sub-adult diets through SI analysis has been tested on agrarian populations (Beaumont et al., 2013; Beaumont and Montgomery, 2015, 2016; Montgomery et al., 2013) and hunter-gatherer groups (Eerkens and Bartelink, 2013; Eerkens et al., 2011).

The British and Irish populations relied on terrestrial agrarian products and were examined to look for evidence of sporadic consumption of marine products and the

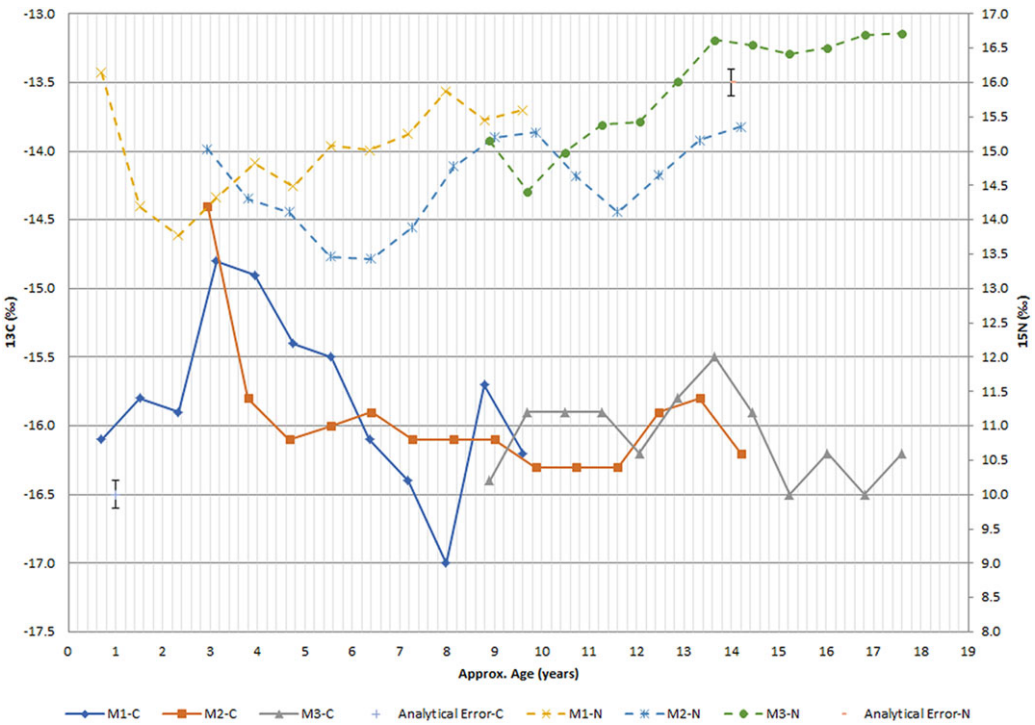


**FIGURE 4** Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) results for burial 6 using *method 2* and London atlas age-estimation method. Termination of M3 was scaled to 18 years based on the estimated age-at-death (years). Note the lack of alignment for any major slopes, changes or features like peaks or valleys on the sequence. Offsets between the $\delta^{13}C$ and $\delta^{15}N$ are outside of analytical error ranges. M2 appears to start 2 years early based on inferred M1/M2 sequence alignment. Also note the M2/M3 sequence has a $\delta^{15}N$ valley between 10 and 12 years that suggests that the M3 is already attributed approximately 2 years too early of an initiation time

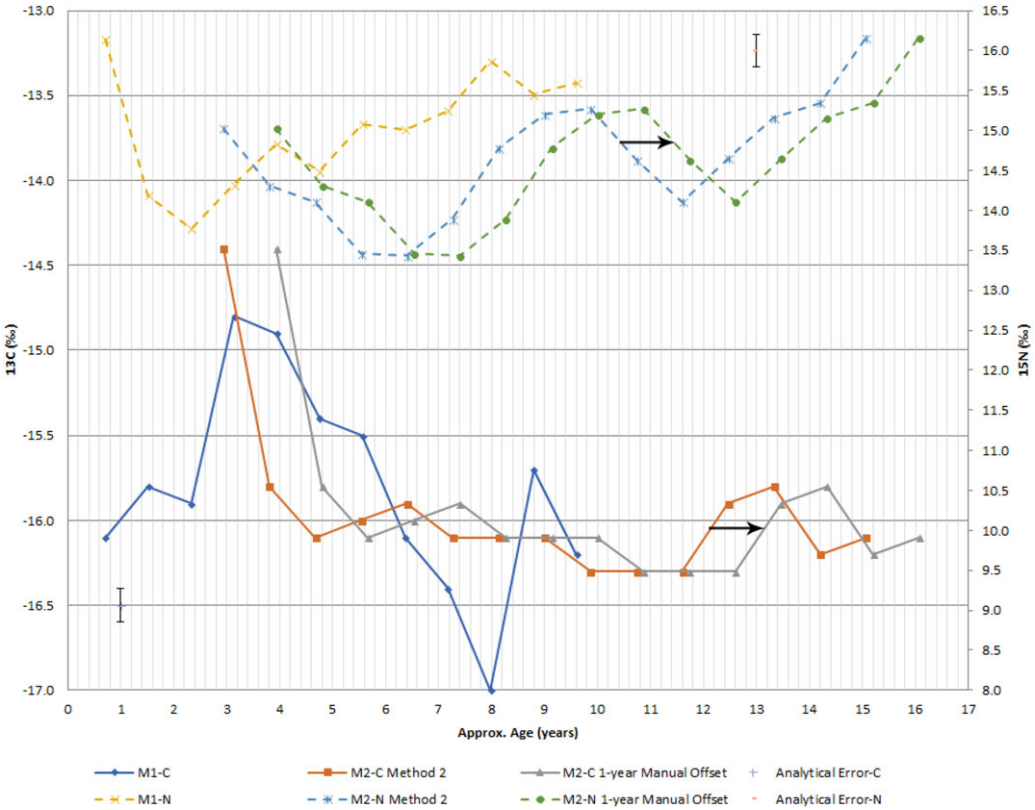


**FIGURE 5** Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) results for burial 6 M1 and the effects of manually shifting M2 values. M2 sequences are projected twice: (1) method 2 using London-atlas age-estimation, and (2) manually shifting the starting age for M2 1-year later. Note the 1-year manual adjustment improves alignment but does not solve problems associated with stretching or attenuation

importation of corn during famine periods. The California hunter-gatherers used storable natural resources (eg, acorns, shellfish) that produce relatively stable diets through time, like agrarian products. This dietary stability minimizes the potential problems of temporal offsets between incremental sections. Studies examining dietary histories using 2-(M1-M2) and 3-molar (M1-M2-M3) sequences have employed different growth rate models to produce satisfactory sequence alignments (Beaumont et al., 2013; Beaumont and Montgomery, 2015; Eerkens et al., 2011).

Published methods to attribute ages to incremental dentin sections are based on modifications of the Dean et al. (1993) growth rate parameters. See Supporting Information S1 for detailed descriptions of the published Methods and new Variants.

*Method 1*—(Eerkens et al., 2011)—is flat-rate method based on growth rates of 4-5 μm/day (Dean et al., 1993; Hillson, 1996; Liversidge et al., 1993) and calculations of the average size of the teeth used (≈ 18 mm) to produce linear growth rate estimates. This method incorporates variability in growth rate within individual teeth (Dean, 2009). Growth rate in the crown is 1.75 mm per year. From the cementum-enamel junction to the root tip, the rate is 1.87 mm per year (Eerkens et al., 2011:3107).

*Method 2*—(Beaumont et al., 2013; Beaumont and Montgomery, 2015)—is a variable method using standardized growth times for molars drawn from the London Atlas (AlQahtani et al., 2010). Teeth are measured and cut, each section then reflects an equal fraction of the total growth time. Estimated age is based on the number of sections cut from a tooth and the population averaged period of growth for that tooth.

*Method 2* is presumably the more flexible of the 2 as it inherently scales the growth rate to the actual size of the tooth based on a fixed age assessment, rather than applying a fixed growth rate to teeth of variable size. Although variability in the growth rate was expected between individuals (Dean et al., 1993; Dean and Vesey, 2008; Liversidge et al., 1993), this factor was not explicitly discussed in methods 1 and 2. The bulk of overlapping sections presented (ie, Beaumont et al. 2013: Figures 5–7; Beaumont and Montgomery, 2015: Figure 5; Eerkens et al. 2011: Figure 4) are flat, making it difficult to assess the model alignment between teeth. Sequence alignment was inferred as being satisfactory, as no further discussion is presented about possible reasons for poor alignment or recommendations for adjustments if other researchers encounter difficulties.

Using method 1, the alignment of multi-molar sequences from B.6 at SHA is poor and yields M3 apex termination at 16 years. In part, this may relate to the different size of the analyzed molars, 12-15-12 mm (M1-M2-M3) for B.6 at SHA, instead of the average length of 18 mm used by

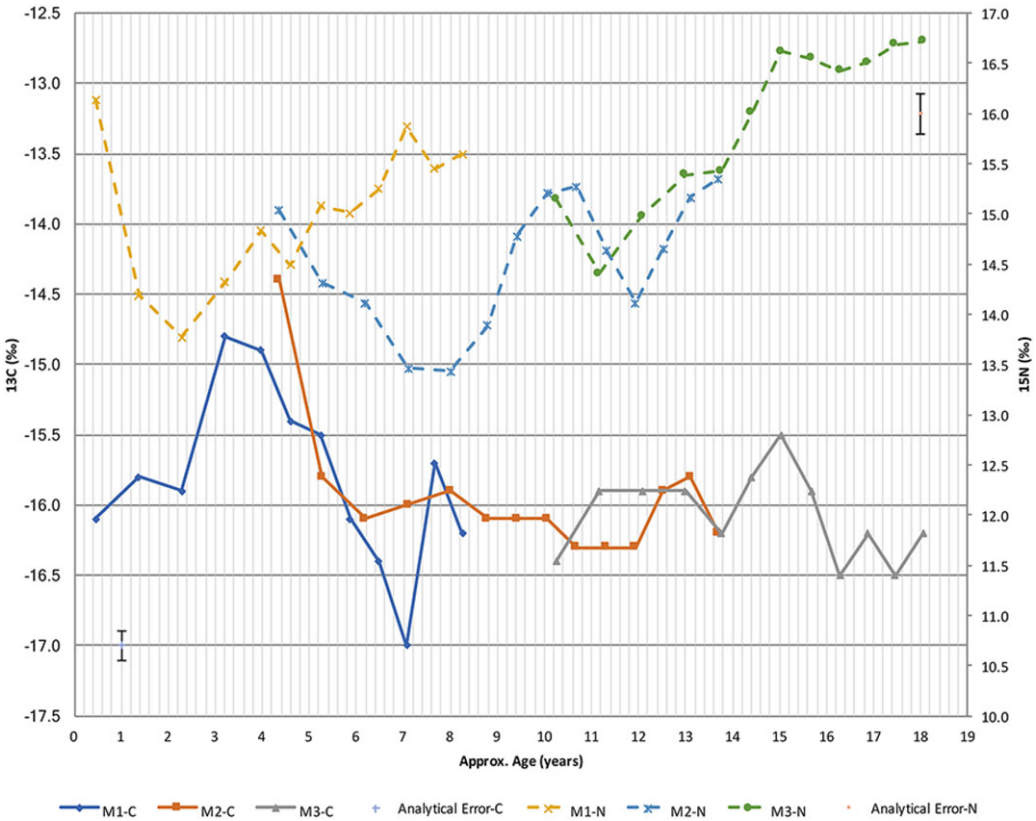


**FIGURE 6** Best fit example of multi-molar SI sequence. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) results for burial 6 using the variant 8 growth rate method and Haaviko age-estimation method. Note that the primary slopes of M1 and M2 now align, the valley along the nitrogen sequence still nearly fits between M2 and M3, and the tail end of M2 matches up with the dip in the M3 carbon sequence

Eerkens et al. (2011). Applying method 2 to B.6 (Figure 4) yielded results that were not as good as anticipated, compared with those reported for British archeological materials. Two additional SHA individuals (B. 34, 66.1) produced similarly poorly aligned sequences, suggesting that this likely was not the result of individual variability.

Shifting a tooth sequence 6-18 months older or younger for improved alignment of multi-molar sequences could be applied in an ad hoc manner (Figure 5). Such "fine-tuning" to ameliorate individual variations may be convenient when looking at an individual but is analytically problematic when trying to look at larger groups. Manual adjustments render any population-level statistics invalid. Fine-tuning can horizontally shift sequences older/younger but is unable to resolve issues associated with stretching effects that manifest using different growth rate models. For example, if the angle of sequences is misaligned and/or not parallel, a manual age shift will not correct this. If adjustments are required, a better age-attribution method should be identified and employed.

## 2.4 | Age-assessment and growth rate methods

Different age-assessment methods have been developed to investigate the possibility of significant differences between reference populations. This helps to address concerns that a method may be systematically under- or over-estimating the age at which different developmental markers are reached (AlQahtani, Hector, & Liversidge, 2014). Ten age-assessment methods, with different root initiation and completion times (Table 3; Supporting Information S1 and S2: Y-axis) were examined (AlQahtani et al., 2010, 2014; Anderson et al., 1976; Fanning and Brown, 1971; Haaviko, 1970; Liversidge, 2008; Liversidge et al., 2006; Schour and Massler, 1940; Smith, 1991), including modified versions (minimum, maximum, and values scaled to a termination age of M3 at 18 years) of the most recent London-Atlas method (AlQahtani et al., 2010).

These age-assessment models draw from comparative populations including North American, Australian, northern European, British, South African, Indian, and several population subgroups within these areas and have been used for estimating the age of fossil and archeological skeletons for many decades. These models give the timing of initiation for enamel, root at the crown, the timing and the root apex closure, and the total developmental (growth) time. However, these models do not provide comprehensive information about health quality, or other indicators of physiological stress, that could impact the results presented by the modern reference populations. Reference populations are ubiquitously agrarian and may not accurately reflect survival and growth patterns for populations reliant on seasonal or unstable subsistence patterns. While not exhaustive, they are

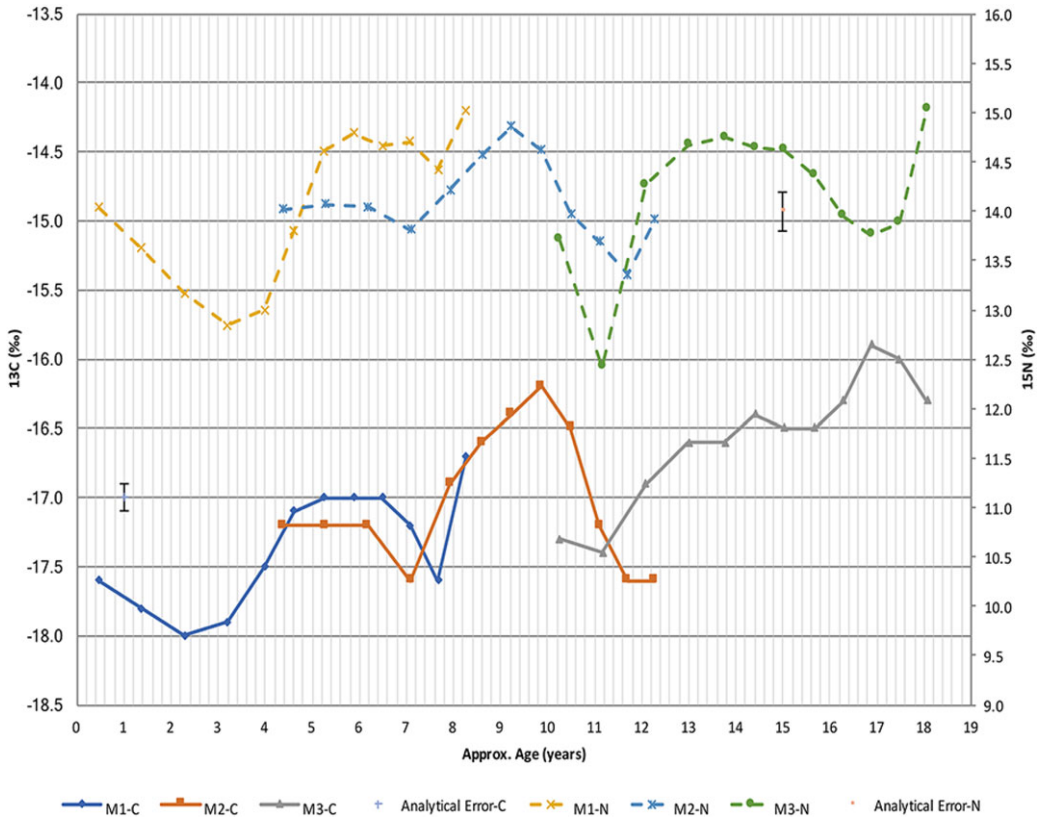


**FIGURE 7** Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) results for burial 34 using the variant 10 growth rate method and Haaviko age-estimation method. Sequence alignment is good, though M2 seems to still be younger than associated sections on M1 by perhaps 6 months. M3 is similarly shifted early by perhaps 9-12 months. Slope fits are visually clean, and many more sections are within the analytical error range when compared between different molars

representative of the mainstream methods used for age-assessment to date and a variety of genetic backgrounds for comparative purposes.

Growth rate variants determine the formation rate for individual incremental dentin sections along the root. Resultant end dates of the final section are hoped to fall within expectations for apex closure. Flat growth rate methods employ a fixed growth rate for either the entire tooth, or a fraction of the root length, without adjusting for the size of the tooth. Variable growth rate methods draw their initial growth rate from the length of the tooth and expected development time, as in *method 2*, and then adjust along portion(s) of the tooth. Overall, a total of 13 variants of growth rate methods were assessed, all employing the Shamanka multi-molar SI sequences (Table 4; Supporting Information S1 and S2: X-axis).

### 2.5 | Comparison method

The effectiveness of the different age-assessment models and growth rate methods was determined through a *fit score*. The closeness of fit was assessed using SD between the aligning section ages, carbon, and nitrogen isotopic results (Supporting Information S1). Comparisons included the total age of growth as determined by the model, the number of overlapping slices, the difference between the finishing age of the section, and the difference between overlapping $\delta^{13}C$ and $\delta^{15}N$ values.

$$\text{Fit Score} = 1 - \text{Average}(\text{STDev}\langle \text{C}|\text{N}|\text{section age}\rangle)$$

## 3 | RESULTS

Applying different method/models to Burial 6 yielded a large range of variability. The period of growth for individual molars ranged from 6.59 to 14.74 years, with unrealistic outlying values bracketing the parameter space. The number of sections overlapping between sequences varied from 3 to 10. The sequence alignment fit score (Supporting Information S1) demonstrates the impact of initiation age and formation rates on the alignment of individual sections throughout the multi-molar sequence. Model combinations minimizing overlapping sections and/or spanning shorter time ranges produced high fit scores, but unrealistic expectations for dentin development. If the resulting ages are not realistic then the model cannot be usefully applied for age-assessment.

### 3.1 | Age-assessment models

All the age-assessment models (Table 3) produced similar ranges of fit scores, but the distributions and realism of these

**TABLE 3** Crown initiation ($C_i$), root apex closure ($A_c$), and developmental ages (years) based on different published age-estimation methods

| | Mandible M1 | M2 | M3 |
|---|---|---|---|
| Schour and Massler '40 | | | |
| Ci | 0.0 | 2.8 | 8.5 |
| Ac | 9.5 | 15.0 | 21.5 |
| Development time | 9.5 | 12.3 | 13.0 |
| Haaviko '70 | | | |
| Ci-male | 0.0 | 3.9 | 9.8 |
| Ci-female | 0.0 | 3.9 | 9.6 |
| Ac-male | 9.8 | 15.7 | 20.4 |
| Ac-female | 9.2 | 14.7 | 20.8 |
| Development time-male | 9.8 | 11.8 | 10.6 |
| Development time-female | 9.2 | 10.8 | 11.2 |
| Fanning and Brown '71 | | | |
| Ci-male | 0.2 | 4.3 | 9.2 |
| Ci-female | 0.2 | 4.0 | 10.1 |
| Ac-male | 10.3 | 15.0 | 18.6 |
| Ac-female | 9.4 | 14.9 | 19.9 |
| Development time-male | 10.1 | 10.7 | 9.4 |
| Development time-female | 9.2 | 10.9 | 9.9 |
| Anderson et al. '76 | | | |
| Ci-male | 0.0 | 3.8 | 9.4 |
| Ci-female | 0.0 | 3.7 | 9.4 |
| Ac-male | 10.0 | 14.8 | 18.5 |
| Ac-female | 9.2 | 13.8 | 18.3 |
| Development time-male | 10.0 | 11.0 | 9.1 |
| Development time-female | 9.2 | 10.1 | 8.9 |
| Smith '91 | | | |
| Ci-male | 0.0 | 3.7 | 9.3 |
| Ci-female | 0.0 | 3.5 | 9.6 |
| Ac-male | 9.4 | 14.9 | 20.0 |
| Ac-female | 8.7 | 14.6 | 20.7 |
| Development time-male | 9.4 | 11.2 | 10.7 |
| Development time-female | 8.7 | 11.1 | 11.1 |
| Liversidge '08, Liversidge et al. '06 | | | |
| Ci-male | 0.0 | 3.5 | 9.0 |
| Ci-female | 0.0 | 3.4 | 8.3 |
| Ac-male | 10.0 | 15.3 | 19.1 |
| Ac-female | 9.3 | 14.8 | 19.6 |
| Development time-male | 10.0 | 11.8 | 10.2 |
| Development time-female | 9.3 | 11.3 | 11.3 |
| AlQahtani et al. '10 | | | |
| Ci | 0.3 | 2.5 | 8.5 |
| Ac | 10.0 | 15.5 | 22.0 |
| Development time | 9.7 | 13.0 | 13.5 |
| AlQahtani et al. '10 (M3 scaled for death at age 18) | | | |
| Ci | 0.3 | 2.5 | 8.5 |
| Ac | 10.0 | 15.5 | 18.0 |
| Development time | 9.7 | 13.0 | 9.5 |
| AlQahtani et al. '10 (minimum age values) | | | |
| Ci | 0.0 | 2.0 | 8.0 |
| Ac | 9.5 | 15.0 | 19.0 |
| Development time | 9.5 | 13.0 | 11.0 |
| AlQahtani et al. '10 (maximum age values) | | | |
| Ci | 0.5 | 3.0 | 9.5 |
| Ac | 10.5 | 16.0 | 23.0 |
| Development time | 10.0 | 13.0 | 13.5 |

Enamel and root formation have essentially synchronous beginnings for crown initiation times. Ci = crown initiation; Ac = apex closure, age in years.

outcomes varied. The best sequence alignment results were found using the age-assessment models outlined by Haaviko (1970) and the London Atlas (AlQahtani et al., 2010). The minimum age values from the London Atlas also outperformed the mean, maximum, and scaled versions of these models. The highest performing model/method combinations favored total development age ≤ 17 years.

The total fit scores were lower following Haaviko, but yielded a curve that visually fit both M1/M2 and M2/M3 in terms of clear periods of change (Figure 6). Later initiation age for M2 (Haaviko) produced poor M1-M2 alignment sequences; however, the highest average M2/M3 scores across the different growth rate methods. The age estimates were also more realistic than higher scoring variants, with the completion of M3 around the age of 19, and the individual having died shortly before reaching this point.

### 3.2 | Age-scaling issues

*Method 2* outlines scaling teeth completion ages for younger individuals to improve accuracy and preventing the erroneous attribution of growth years to a tooth that was not fully formed. Burial 6 died between the ages of 16 and 18 years, with M3 nearly complete in apex closure, suggesting an age closer to 18 years. Sequence alignment fit scores were higher with M3 completion at 22 years (M2/M3 Fit = 0.78), than scaled to a completion age of 18 years (M2/M3 Fit = 0.65). Each section represents a younger age, more rapid growth, and thus greater overlap with M2 than was expected following London Atlas values. The sequence alignment was possibly confounded by contracting the growth period to only 9.5 years (Supporting Information S2). This M3 development time was like those outlined by Fanning and Brown (1971) and Anderson et al. (1976); models that did not perform well overall.

### 3.3 | Poor-performance methods

Low fit scores were invariably correlated with poorly aligned sequences. This is not surprising; however, many of the moderate-to-high scoring methods (eg, method 1, variants 1-7) also produced unrealistic sequences. Reducing the

**TABLE 4** Summary of each *Variant* detail for growth rate (μm/day) and the proportional distribution along the length of the tooth root

| | (Crown→Root tip) | |
|---|---|---|
| **Methods** | **Growth rate (μm/day)** | **Distribution %** |
| Published | | |
| Method 1 | 4.8:5.1 | 27:73 |
| Method 2 | Variable | Variable |
| New variants | | |
| Variant 1 | 3.2:3.4 | 27:73 |
| Variant 2 | 2.3:3.2:3.5 | 40:40:20 |
| Variant 3 | 2.6:3.8:4.1 | 40:40:20 |
| Variant 4 | 3:4.3:4.6 | 40:40:20 |
| Variant 5 | 3.8:5.4:5.8 | 40:40:20 |
| Variant 6 | 2.3:3.2:3.5 | 33:33:33 |
| Variant 7 | 2.6:3.8:4.1 | 33:33:33 |
| Variant 8 | 3:4.3:4.6 | 33:33:33 |
| Variant 9 | 3.8:5.4:5.8 | 33:33:33 |
| Variant 10 | Variable | 25:25:25:25 |
| Variant 11 | Variable | 20:20:20:20:20 |
| Variant 12 | Variable | 20:20:20:20:20 |
| Variant 13 | Variable | 20:20:20:20:20 |

See supporting Information S2 for descriptions of new *Variants*.

number of overlapping sections also reduced differences for that overlap and could therefore produce better results. The goal of this study was to identify effective methods for aligning sequences, but not at the expense of realism.

Overlaps of 5+ sections were anticipated for most teeth analyzed, so methods that did not produce substantial overlaps could not be viewed as performing well. A second issue was that models yielding errant age ranges also tended to produce higher than expected fit scores. In this case the numbers were being driven by the reduced temporal offsets between overlapping slices; reduced time differences produced closer fit scores.

If only unrealistic age-assessment methods or growth rate models produced effective sequence alignments, then the entire approach would be flawed. That the most effective methods closely followed published values and described patterns of growth supports the efficacy of the current analysis.

### 3.4 | Good-performance methods

method 2, along with variants 8, 9, 11, and 13, consistently outperformed the other methods across the age-assessment models. Haaviko (1970) and AlQahtani et al. (2010) provided initiation ages that yielded the best fit-scores. With B.6, AlQatani produced higher scores, but, as noted, this was influenced by the age-ranges involved and Haaviko produced more realistic results.

To verify these results as indicating a superior method of age-assessment and growth rate, the top 5 performing growth rate methods (method 2, variants 8, 9, 11, and 13) all using the age-assessment methods of Haaviko and AlQahtani, were applied to 2 additional individuals (Burials 34 and 66.1), both with 3-molar dietary sequences (Supporting Information S3 and S4). Burial 34 yielded the best results using variant 8 following Haaviko age-estimates (Figure 7). Burial 66.1 also produced the best sequence alignment results following Haaviko, but using variant 9. The difference between these 2 curves is not surprising as Burial 34 had smaller teeth and would more closely follow a slower growth rate model.

The result of applying the different methods of age-assessment and growth rate to 2 additional individuals confirms that Burial 6 was not just a unique individual. All 3 individuals assessed performed better in curve alignment following Haaviko; age estimates differing most prominently on the initiation age of M2. This suggests that this EN population had a standard pattern of development with M2 starting relatively later than the populations used by the London Atlas. The total period of growth for M2 s and M3 s is also 2 years shorter than those given in the London Atlas.

### 3.5 | Diminishing returns

Research into the rate of growth along the length of tooth roots indicates that a near-continuous curve of growth velocity exists; the inference being that methods better approximating this variation should perform better in attributing ages to sections of that root. variants 10-13 failed to produce results superior to simpler methods.

### 3.6 | Attenuation

Temporal overlap between sections (see Eerkens et al. 2011) and the smoothing effects of sequence curves mask evidence of short-lived events. Bouts of starvation (triggering catabolism) or the boon from consuming large prey with a specific SI signature (eg, seal), will be averaged against all other protein sources over weeks/months, contributing to the collagen of dentin sections. Beaumont and Montgomery (2016) discuss how this attenuation of dietary isotopic signals hinder the prospects for identifying exact moments of transition, even when the diets are known.

The vertical offset between the M1 and M2 curves for B6 evidences the challenge of attenuation. In the DEJ section (age 4-5 years) of M2, $\delta^{13}C$ is ~0.8‰ higher than the highest $\delta^{13}C$ on the M1 curve (Figure 6). Similarly, between the ages of 7 and 8 years, the M1 shows a drop in $\delta^{13}C$ of ~1.0‰ relative to the M2 curve. These sections *should* represent similar blocks of time based on developmental times, but reflect dietary events differently. Protein source(s) responsible for these offsets were likely consumed in between the times represented by M1/M2 sections, getting averaged against other foods, more so in 1 tooth section than another.

Unless vertical offset clearly results from poor horizontal alignment, horizontal shifting and stretching through modifying method/model combinations cannot explain this

difference. Different growth rates along portions of the root, and/or localized recycling of collagen during portions of root formation may play a role. Additional research into the interrelationship between collagen formation, recycling, variable root growth rates, and recovery of proxy data will be needed to investigate this type of offset.

## 4 | DISCUSSION

This study examined the parameter space of various combinations of age-assessment models and growth rate methods (variants). Several yielded poorly performing sequence alignment results and unrealistic age ranges. The dramatic effects of minor differences in growth rate and/or starting times were surprising. Differences of ½ μ/day in growth rate can produce offsets of months, which compounded by different initiation ages produced multi-year variability in outcomes. Similarly, 1 method/model combination may work nearly perfectly for 1 individual with equal-length teeth and stable diet, while producing a dietary record with multi-month or -year offsets in another individual.

Flat rate methods rely on teeth being of similar size within and between individuals. Teeth vary in size (9-21 mm at SHA) and growth rate between M1, M2, and M3, between maxilla and mandible, even within the same individual. As such, flat rate methods were not anticipated to be particularly useful for broader application to the Shamanka II population, or to other cemeteries. Applying a variable rate of growth to different portions of individual teeth and scaling for the size of the tooth seems to be most effective for estimating age of specific sections.

The results of analysis with 3 individuals with multi-molar dietary sequences showed that using an average rate of 4 μm/day applied proportionally with a multiplier to equal thirds of the root length produced the best alignment (variant 8). As such, using a catalog of estimated growth rates for specific tooth sizes (eg, 4 μm/day for teeth 12-13 mm in length) is likely to produce the most reliable growth rate-informed age estimates. Employing flexible growth rate estimates as outlined in method 2 (Beaumont & Montgomery, 2015), and applying adjusted growth rates to proportional sections of the tooth will be easier and broadly applicable for researchers without such a catalog. This latter approach, employing the Haaviko (1970) initiation ages and periods of growth, provided the framework that removed the need to adjust tooth ages manually for multi-molar sequence alignment in the Shamanka II population.

The general poor alignment results following the London Atlas suggests several possible, though speculative, sources of difference between the reference population and the EN hunter-gatherers of Cis-Baikal. A difference in the genetic background of the populations seems likely. No Siberian indigenous populations were included in reference populations for the methods assessed, nor were any other populations that might be genetically closely related. Haaviko (1970) developed their age estimates using children in Helsinki rather than London. In the case of Shamanka II, the age-estimation method based on Finnish children was most effective.

## 5 | CONCLUSION

The goal of this study was to identify the most effective growth rate models and age-estimation methods based on specific reference populations with regional, genetic, or developmental age similarities. Manually adjusting multi-tooth sequences 6-18 months in 1 direction or another to align dietary records between teeth can be employed in an ad hoc fashion, at the cost of analytical rigor.

Employing published methods for attributing ages to sections of SHA individuals produced unrealistic multi-molar sequence alignments. The poor alignment observed at SHA is the result of poor correlations between population-specific age-assessment models and/or regional differences in development ages for tooth eruptions and dentin formation, but still within known growth parameters. Siberian EN populations in Cis-Baikal appear to have had later M2 and M3 initial formation times than modern European populations.

For future studies the results presented herein can be interpreted in 2 ways: (1) that it is necessary to take the time to produce a framework growth rate method wherein the best method will be determined by the tooth size; or (2) that for some regions/populations this level of effort will prove unnecessary, as methods 1 and/or 2 could produce suitable results.

The combined age-assessment model and growth rate methods that produced the best fitting sequence alignments at SHA were variants 8 and 9. Method/model combinations based on modern reference populations will yield a range of standard errors when applied to archeological populations. The amplitude and importance of these errors will vary by region, but should be kept in mind. The growth rate estimated by these methods can then be weighted to better approximate the known variability in growth throughout the length of the tooth roots to help refine the precision of resulting explanations.

This study was focused on aligning multi-tooth sequences of incremental dentin, but also provides insight into potential problems encountered while analyzing individual teeth. Taking a subset of a given archeological population and aligning a multi-molar sequence could help identify the magnitude of age-related errors. Using this information, the initiation time(s) for individual teeth could be corrected so that the aging of events within an individual's life is more accurate.

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## AUTHOR CONTRIBUTIONS

All authors read and approved the final version of the article.

*Designed the bioarchaeological study*: Scharlotta, Goude, Weber

*Conducted laboratory preparation of samples, analyzed the data, and drafted the article*: Scharlotta

*Contributed technical expertise, laboratory resources essential to this research and editorial input on the article*: Herrscher, Goude

*Provided access to the archeological teeth and contributed contextual knowledge about Siberian prehistory*: Weber

*Contributed background SI and $^{14}C$ data from Shamanka II, contextual archeological knowledge, and edited the article:* Weber

## CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest with the contents of this article.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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