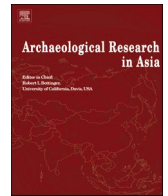




Contents lists available at ScienceDirect

Archaeological Research in Asia

journal homepage: www.elsevier.com/locate/ara

Full length article

Skeletal and dental maturation relative to tooth formation in prehistoric hunter-gatherers from Cis-Baikal, Siberia

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ARTICLE INFO

Keywords:

Ontogeny
Epiphyseal union
Tooth eruption
Growth

ABSTRACT

This study reconstructs fusion of skeletal elements and tooth emergence relative to tooth formation among prehistoric hunter-gatherers from Cis-Baikal, Siberia (ca. 8000 to 5200 BP). Tooth formation was recorded using standard protocols. Ages were estimated based on tooth formation stages within an individual. Tooth emergence was recorded as not emerged, emerged beyond the alveolus, or in occlusion. Skeletal epiphyses and apophyses were recorded as fused or unfused. Fisher's exact tests were used to test heterogeneity in each developmental stage. Tooth emergence occurred in the order reported by earlier studies and ages-at-emergence were similar to those of reference standards. Skeletal epiphyses and apophyses also had low degrees of heterogeneity in each age group and fused in the predicted order. Fusion of the presacral vertebrae and upper limb was similar to reference standards, though maturation in the lower limb was delayed. Low heterogeneity may be attributed to the small sample sizes, though genetic conservation in tooth emergence may also be inferred from these results. In addition, skeletal maturation in the vertebral column confirms that some measurements of the neural canal may be used as appropriate measures of stress exposure in the early life environment. Low levels of heterogeneity in skeletal maturation suggests that these elements may be used to estimate age at death, though caution should be expressed when using the lower limb as fusion of these elements may have been delayed by stress events.

1. Introduction

The study of life history provides fundamental knowledge of the developmental underpinnings surrounding the biology and behavior of living primates (Harvey and Clutton-Brock, 1985). Living primates are distinguished from other mammals on the basis of larger brains and slower development, and within primates, anatomically modern humans are further distinguished by a continued emphasis on slow growth and relatively large brains (Walker et al., 2006; Robson et al., 2006). Paleoanthropologists and bioarchaeologists work with human skeletal and dental remains and are unable to directly observe the association between life histories, behavior, and biology. However, skeletal and tooth maturation are frequently used as proxies that describe the timing and variation of life history events. Factors such as age at tooth emergence and ordering of tooth emergence are frequently

tethered to the life history of living, and by extension, extinct primates. At present, variation in the timing and ordering of events such as tooth emergence and elemental fusion is well documented among select contemporary human samples (Moorrees, 1957; McKern and Stewart, 1957; Demerjian et al., 1973; Smith, 1991; Albert and Maples, 1995; Ubelaker, 1989; Albert and Greene, 1999; Liversidge and Molleson, 2004; Cardoso, 2007, 2008a, 2008b; Sciulli, 2007; AlQhatani et al., 2010; Cardoso and Ríos, 2011; Conceição and Cardoso, 2011; Oziegbe et al., 2013). Results suggest general correspondence between tooth formation, emergence, and elemental fusion, though tooth emergence and elemental fusion may be delayed in accordance with environmental stress.

Stress is an external perturbation that disrupts physiological homeostasis (Goodman et al., 1988). This concept is derived from the Seylean model that conceptualizes stress under the guise of a general

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<https://doi.org/10.1016/j.ara.2020.100239>

Received 4 February 2020; Received in revised form 27 October 2020; Accepted 28 October 2020

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adaptation syndrome (Seyle, 1936). The organism responds to external perturbations through a three-stage response: alarm, resistance, and exhaustion. Survival of stress events is associated with adaptive plasticity as growth disruptions produce a series of energetic trade-offs that help thwart mortality during physiological perturbation (Kuzawa, 2005; Kuzawa and Quinn, 2009). That said, future energetic investments in growth and survival are limited due to the physiological trade-offs required to survive early life stress events—energy is redirected to the growth and maintenance of essential tissue, while investment in long-term growth and survival is diminished (Worthman and Kuzara, 2005).

Tooth development is the process by which teeth form and emerge (Smith, 1991). Tooth formation includes three stages associated with the production and mineralization of enamel: presecretory, secretory, and maturation (Nanci, 2008). First, ameloblast cells are differentiated from precursor cells in the inner enamel epithelium. Next, secretory ameloblasts produce the organic component of enamel, mostly made up of proteins and enzymes. Finally, ameloblasts secrete ions responsible for the mineralization of enamel during the maturation stage. This process also occurs in the dentine via odontoblasts that are signaled during the termination of the presecretory stage of amelogenesis. Elevated “heritability” values for tooth formation combined with low coefficients of variation suggest minimal environmental influence over this process (Garn et al., 1960; Demerjian et al., 1973; Pelsmaekers et al., 1997; Merwin and Harris, 1998; Cardoso, 2007; Townsend et al., 2009). As such, tooth formation provides an important baseline indicator of chronological age in pre-adult human skeletal remains, particularly when assessing the relative maturation of dental and skeletal tissues during the first two decades of life.

Relative maturation of the dentition is often measured using tooth eruption, though the term “eruption” remains imprecise as most studies observe the emergence of teeth through the gingiva (Smith, 1991a) or above the alveolus (Hillson, 1996). Recent reviews point towards variation in tooth emergence among geographically diverse modern humans (Guatelli-Steinberg, 2009). However, several phases of tooth emergence are generally identified among modern humans: I: deciduous teeth (0.0 to 2.0 years), II: first molar, first incisor, second incisor (6.0 to 8.0 years), III: canine, third premolar, fourth premolar, and second molar (10.0 to 12.0 years), IV: third molar (age > 18.0 years) (Smith, 1991a). As noted by Smith (1991a), there remain several gaps in these events, specifically between 3.0 and 6.0 years, 8.0 and 10.0 years, and 12.0 and 18.0 years. These gaps may confound attempts at estimating age-at-death in human fossils or skeletal remains with precision if tooth emergence is the primary method used to estimate age-at-death. Given the variation reported in tooth emergence it remains important to accurately report the relative phases of this process in association with tooth formation to gain a better perspective on global variation in these patterns and report on a more precise method to estimate age-at-death using tooth emergence within a population-specific context.

Furthermore, studies of tooth emergence suggest that this process is influenced by systemic stressors and may provide evidence for the cost of physiological adjustment to varied environments. Differences in ages of tooth emergence between wild and captive chimpanzees are observed and may reflect variation in stress between the two samples (Zihlman et al., 2004; Smith et al., 2013). Significantly delayed tooth emergence in chimpanzees who died at younger ages suggests that stressors involved in this process may also be linked to mortality (Smith and Boesch, 2010). Coefficients of variation are significantly greater for tooth emergence compared to tooth formation in a sample of individuals from the Fels Longitudinal Growth Study suggesting that environmental stressors may have a greater influence on the emergence compared to formation of teeth (Lewis and Garn, 1960; Garn et al., 1973). Differences in tooth emergence are also reported in association with familial social status in South America: individuals from higher socioeconomic statuses experienced earlier emergence of deciduous teeth (Alvarez, 1995; Alvarez et al., 1988). These results suggest that the emergence of teeth, while genetically buffered, may record evidence for the energetic costs

of maintaining physiological homeostasis.

Skeletal maturation is measured using a variety of methods including epiphyseal and apophyseal union. Epiphyseal union occurs when primary and secondary centers of ossification fuse following the cessation of cellular activity in a growth plate, while apophyseal fusion occurs at the site of tendinous insertions and include the iliac crest, femoral trochanters, and superior and inferior surfaces of each vertebral body (Scheuer and Black, 2000). Cartilaginous growth plates are found in reptiles and mammals (Hall, 2005). In mammals the growth plate is a highly organized structure and includes four activity zones: hypertrophy, proliferation, calcification, and ossification. The growth plate separates the diaphyses and epiphyses of growing bones and it is in this region that modeling of new bone occurs—as mentioned, chondroblasts produce a cartilaginous template which is broken down by osteoclasts and reengineered through ossification by osteoblasts (Martin et al., 2001). Following epiphyseal union, growth of the bone in question stops. Each bone has distinct centers of ossification and experiences epiphyseal fusion at predictable stages of life history (Scheuer and Black, 2000; Baker et al., 2005).

However, independence between formation of teeth and fusion of skeletal elements is noted (Cheverud, 1981). This difference is associated with the relative impact of environmental factors on skeletal maturation, specifically fusion of epiphyseal or apophyseal joints—samples from lower socioeconomic statuses or environmentally impoverished regions experience delays in epiphyseal and apophyseal fusion (Frisancho et al., 1970a, 1970b; Albert and Greene, 1999; Meijerman et al., 2007; Cardoso, 2008a, 2008b). One study of skeletal maturation recently argued that these indicators may be more sensitive to the costs of systemic stress burdens than longitudinal growth (Conceição and Cardoso, 2011). Therefore, analysis of relative skeletal maturation also clarifies variation in the relative cost of maintaining physiological homeostasis within particular environments.

Stress in relation to the life course has been explored among hunter-gatherers from the Cis-Baikal region. A comparatively high frequency of linear enamel hypoplasia has been documented among samples from this region, though these experiences were not related to early mortality (Lieverse et al., 2007). Evidence for growth disruption in body mass and femoral length have also been reported (Temple et al., 2014) and are consistent with indicators of body size variation in adults from this region (Stock et al., 2010). The largest residuals for growth in body size were found at ages associated with the cessation of weaning (i.e., Waters-Rist et al., 2011), suggesting that the transition to an adult diet may have instantiated physiological and psycho-social stress (Temple et al., 2014). The Cis-Baikal population relied heavily on terrestrial and aquatic mammals as well as lacustrine fish, all of which were available in seasonal cycles (Scharlotta et al., 2016; Weber et al., 2016a; Weber and Bettinger, 2010). This dietary pattern may have increased risk of growth disruption during cycles of diminished returns.

The goal of this study is to document variation in ages of skeletal and dental maturation, evidence for growth disruption in this process, and interpret patterns of variation within an environmental and developmental context.

2. Materials

The skeletal growth samples utilized by this study are drawn from two distinct phases of occupation in the Cis-Baikal region. The first phase is associated with the Early Neolithic Kitoi culture. Early Neolithic (EN) Kitoi cultures date between 7560 and 6600 BP (Weber et al., 2020). EN Kitoi cemeteries are geographically concentrated along the southwestern tributary of the Angara River and Southwest Baikal micro-region. Kitoi populations were biological descendants of ancient Mesolithic, or possibly, Paleolithic inhabitants of the Baikal region and have elevated frequencies of haplogroups D, F, and U5a (Moodel et al., 2010). These haplogroups help distinguish the Kitoi from the Late Neolithic / Early Bronze Age samples (see below) as well as modern Indigenous

inhabitants of the region. The sublineage of haplogroup F found in the Kitoi populations are also observed at high levels in modern Kets indicating the possibility of close affinity between these two groups (Schurr et al., 2010). The use of nuclear DNA analysis will help further resolve these questions. The EN sample was recovered from two sites, Lokomotiv and Shamanka II, located along the banks of the Angara River in the city of Irkutsk and the southern tip of Lake Baikal respectively (Fig. 1). Radiocarbon dating of human skeletal remains from these sites has been completed for 59 skeletons from the Lokomotiv site and 36 skeletons from the Shamanka II site (Weber et al., 2010, Weber et al., 2016a, 2016b). These cemeteries date between 7470 and 6750 BP (Weber et al., 2016a, 2016b). Sample sizes for the Lokomotiv and

Shamanka II sites are listed in Table 1.

Late Neolithic (LN) mortuary traditions in the Cis-Baikal region are known as Isakovo, while those dated to the Early Bronze Age are associated with Glazkovo culture. Isakovo dates between 6060 and 4410 BP in the Southern Baikal and Angara River geographic regions, while Glazkovo dates between 4970 and 3470 BP (Weber et al., 2020). Genetic discontinuity has been found between the EN Kitoi and LN Isakovo samples, with the LN sample having a different sublineage of haplogroup F than the EN groups, and possessing the U5a haplogroup suggesting close relationships with Uralic and indigenous people from the Altai region (Schurr et al., 2010). Of further importance is the noted lack of haplogroups H–K, T, V, and X indicating little relatedness to the

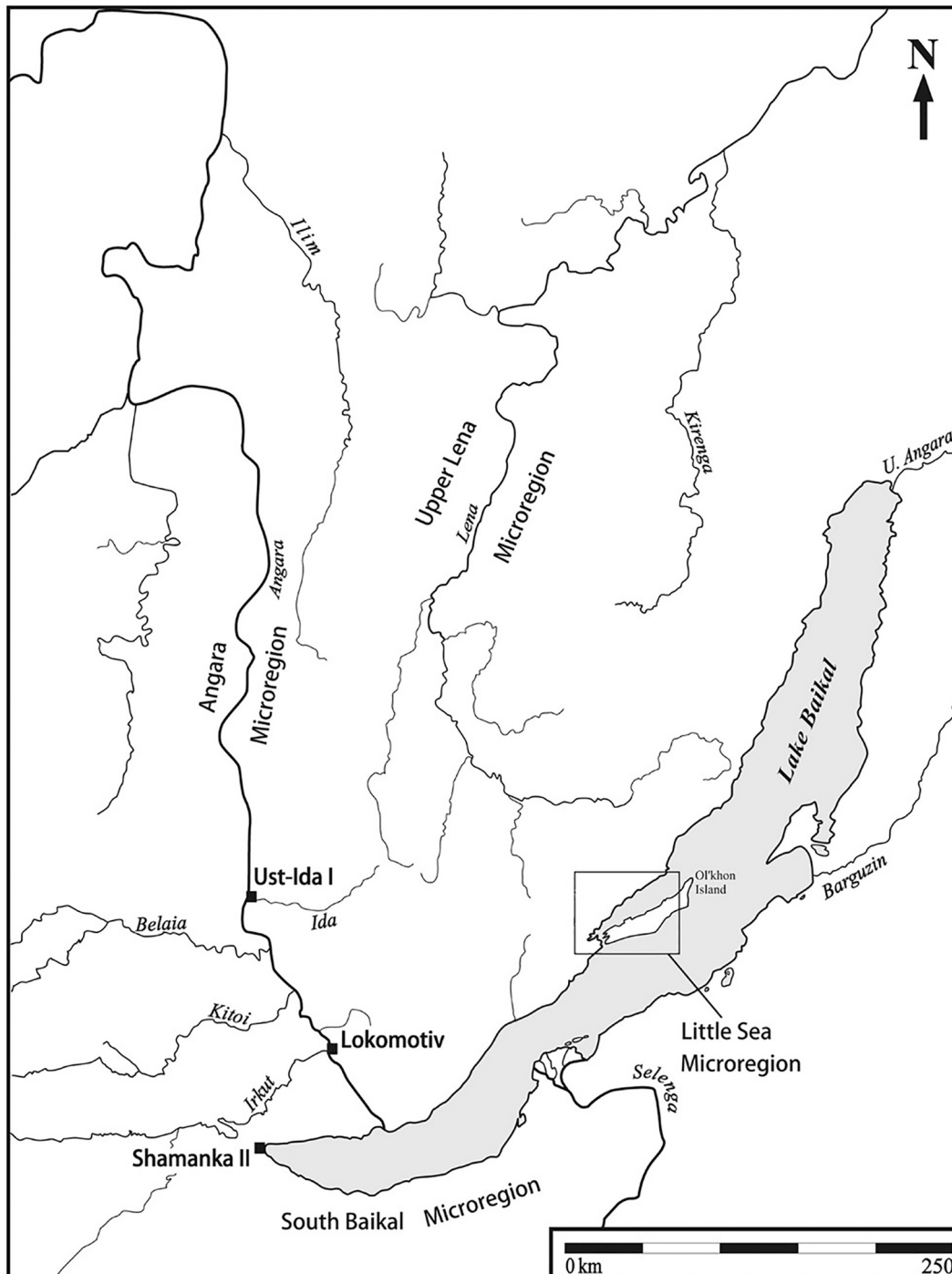


Fig. 1. Map indicating the location of sites included in this study.

Table 1
Sample sizes for each observation by site.

	Ust Ida I	Shamanka II	Lokomotiv	Total
	Late Neolithic	Early Neolithic	Early Neolithic	
	Isakovo	Kitoi	Kitoi	
Tooth Formation	27	19	13	59
Tooth Emergence	23	18	9	50
Mandible	26	15	14	59
Proximal Humerus	25	19	13	57
Humeral Trochlea	25	18	10	53
Medial Humerus	26	19	9	54
Radial Head	21	17	8	46
Distal Radius	21	16	8	45
Proximal Ulna	20	17	9	46
Distal Ulna	21	17	7	45
Femoral Head	27	19	9	55
Greater Trochanter	26	19	9	54
Distal Femur	26	19	9	54
Proximal Tibia	27	19	8	54
Distal Tibia	27	19	8	54
C1 anterior arch	5	12	4	21
C1 posterior arch	17	12	4	33
C2 ce ^a -na ^b	13	11	5	29
C2 na-na	18	10	5	33
C3-C7 ce-na	19	18	5	43
C3-C7 na-na	21	18	5	42
C3-C7 rings ^c	19	17	5	41
T1-T12 ce-na	21	17	4	42
T1-T12 na-na	21	18	4	43
T1-T12 rings	20	16	4	40
L1-L5 ce-na	21	16	3	40
L1-L5 na-na	19	18	3	32
L1-L5 rings	19	17	3	37

^a Vertebral centrum.

^b neural arches.

^c apophyseal rings.

Western Eurasian populations associated with the EN Kitoi people. The LN sample was recovered from one cemetery, Ust'-Ida I, located along the Angara River approximately 100 km north of Irkutsk (Fig. 1). Radiocarbon dates have been obtained for 64 individuals from the Ust'-Ida I site (Weber et al., 2010; Weber et al., 2016a, 2016b). The samples from Ust'-Ida I that are included in this study are associated with the Isakovo culture. One pre-adult grave at the site is identified as Kitoi and five other pre-adults date to a Glazkovo cultural occupation. These six individuals were removed from the analysis. The Isakovo component of the Ust'-Ida I site dates between 5420 and 5180 BP (Weber et al., 2016a, 2016b). Sample sizes for the Isakovo occupation of Ust'-Ida I included in this work are listed in Table 1.

3. Methods

Age-at-death was estimated using tooth formation due to the limited impact of environment on this process and repeated independent confirmation of accuracy between studies (Smith, 1991; AlQhatani et al., 2010). The sample sizes for individuals with observable tooth formation stages are listed in Table 1 by site. Mandibles and maxillae were radiographed using the NOMAD Pro Hand-Held X-ray System (Aribex, Provo, Utah) and Dr. Suni Plus Intraoral Digital Light Sensor (SUNI Medical Imaging Inc., San Jose, California). Formation stages of teeth were recorded using standard qualitative methods derived for deciduous and permanent teeth (Liversidge and Molleson, 2004; AlQhatani et al., 2010). Formation stages were compared to standards that provide estimates of age for the deciduous (Liversidge and Molleson, 2004) and permanent (AlQhatani et al., 2010) dentition. A minimum of one tooth was observed in each individual. Where multiple teeth were observed, the average age estimated from all available teeth was utilized. Utilizing these averages as an estimate of chronological age is acceptable as the correlation coefficient ($r = 0.801$) and slope ($b =$

0.9048) indicate a relatively high degree of intraobserver agreement for age estimations derived from the formation stages of multiple teeth from the same individual (Fig. 2). Furthermore, because there is some variability in the formation stages of different teeth relative to age, utilizing the average of these estimates provides a more accurate estimation of age (Smith, 1991a).

Phases of tooth emergence were recorded using standard protocols (Hillson, 1996). Where the occlusal most point of a tooth crown had not emerged beyond the alveolus, the tooth was recorded as NE—not emerged. Once the most occlusal point of a tooth crown was observed beyond the alveolus, the tooth was recorded as AE—alveolar emergence. Finally, teeth emerged into occlusion were recorded as EO—emerged into occlusion. These stages were compared to age-at-death estimates that were established on the basis of tooth formation.

Epiphyseal and apophyseal fusion were recorded according to two stages: fused (i.e., ossified, though fusion lines may remain) or unfused. It should be noted that multiple phases of fusion are possible to record in immature skeletal remains (Buikstra and Ubelaker, 1994). However, previous studies avoided dividing the level of fusion in skeletal growth samples into these smaller categories because of problems in element preservation as well as standardizing the presence and absence of fusion lines in the absence of radiographic analysis (Sciulli, 2007). Because the number of individuals with evidence for fusion was small, these samples were divided into maturity phases based on ages estimated using tooth formation stages. Nine maturity phases were utilized for these samples. Maturity phases include GP1 (0.1–0.9 years), GP2 (1.0–1.9 years), GP3 (2.0–3.9 years), GP4 (4.0–5.9 years), GP5 (6.0–7.9 years), GP6 (8.0–9.9 years), GP7 (10.0–12.9 years), GP8 (13.0–16.9 years), and GP9 (17.0–22.0 years).

Fisher's exact tests were used to compare the relative number of individuals with fused and unfused elements as well as emerged and non-emerged teeth between age ranges. This method tests the null hypothesis that no differences in the relative number of individuals with fused and unfused elements or emerged and non-emerged teeth will be found between successive age groups. Elevated degrees of heterogeneity will result in no significant differences between samples. Heterogeneity is defined by relative equivalency in the proportions of fused and unfused or emerged and un-emerged specimens in an age group or maturity phase.

4. Results

4.1. Dental maturity

Tooth emergence patterns are listed in Fig. 3. Light gray bars indicate ages where a mixture of teeth are emerged into occlusion, emerged beyond the alveolus, and not emerged. Dark gray bars are associated with ages where the tooth in question has emerged into occlusion for 100% individuals within the cohort. The order of full mandibular tooth emergence among the Cis-Baikal hunter-gatherers is as follows: di1/di2, dc, dm1, dm2, M1, I1, I2, C, PM3, PM4, M2, M3. Little heterogeneity in the relationship between tooth emergence and ages based on tooth formation were found. For all individuals, the first and second deciduous incisors erupted into occlusion during the first year of life. For two tooth types (dc and dm2), full eruption in all individuals occurred within 1.0 year of the first individual having one of these tooth crowns emerged beyond the alveolus. For five tooth types (dm1, I2, C, PM3, PM4, and M1), full emergence in all individuals occurred within 2.0 years of the first individual having one of these tooth crowns emerged beyond the alveolus. For two tooth types (I1 and M2), full emergence occurred within 3.0 years of the first individual having one of these tooth crowns emerged beyond the alveolus. There are approximately three years between the full emergence of the deciduous dentition and that of the first permanent molar (M1), approximately two years between the full emergence of the anterior and posterior permanent dentition, and approximately four years between the emergence of the posterior

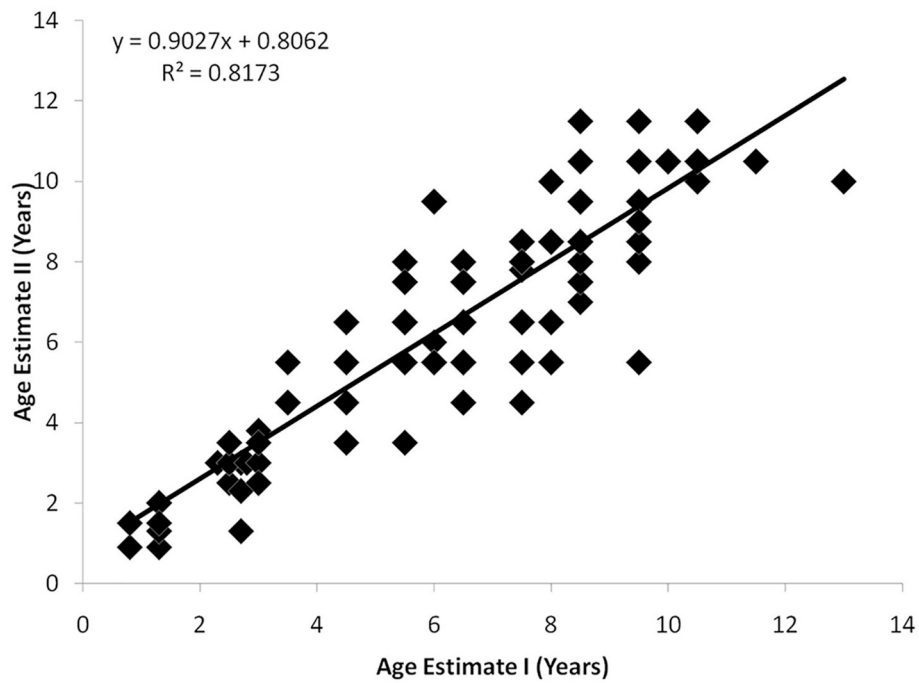


Fig. 2. Reduced major axis regression analysis of age estimates using tooth formation standards in individuals with two teeth.

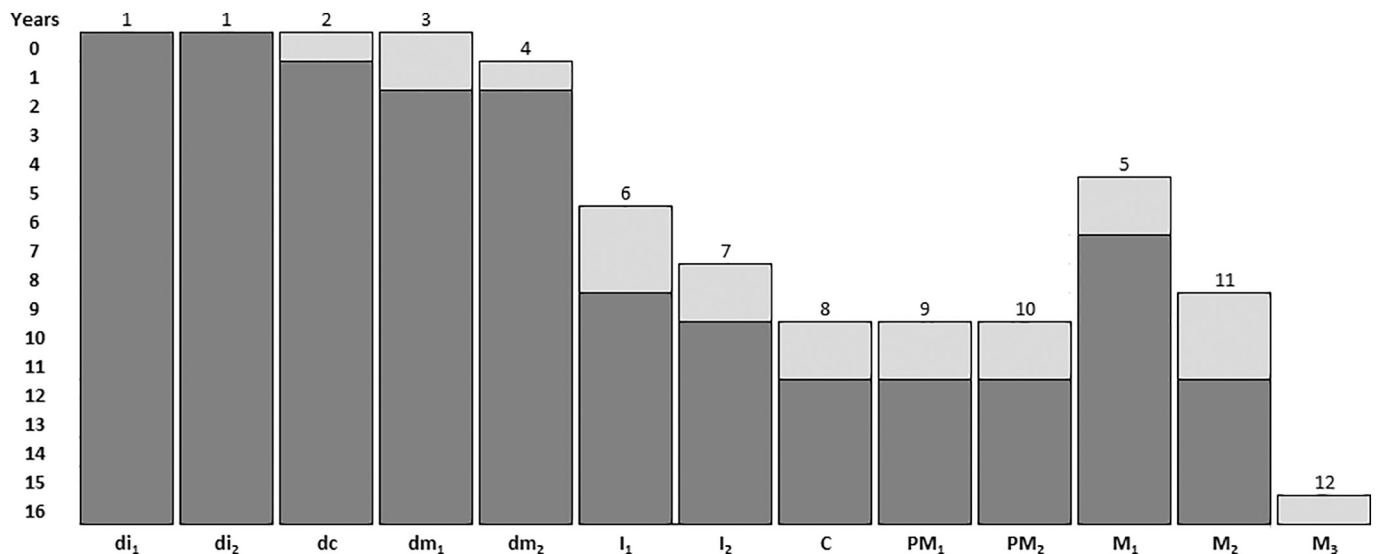


Fig. 3. Patterns of tooth emergence in the Cis-Baikal samples. Light gray bars indicate ages where a mixture of teeth are emerged into occlusion, emerged beyond the alveolus, and not emerged. Dark gray bars are associated with ages where the tooth in question has emerged into occlusion for 100% individuals within the cohort. The number above each bar indicates the ordering of tooth emergence for each tooth type.

dentition, particularly M2, and the third molar.

4.2. Skeletal maturity

Table 2 lists the proportion of individuals with fused and unfused skeletal elements in each age group. Dark gray outlines are used to indicate where statistically significant ($P \leq 0.05$) differences between the proportion of individuals with fused relative to unfused elements are found. In many cases, the process of fusion begins at an earlier stage in ontogeny than the point where statistical significance was attained. The point where fusion begins is outlined in light gray. This is likely due to smaller sample sizes in some age groups. These light gray outlines are used to alert the reader to the onset of fusion for the element in question.

The mandibular symphysis fused at the earliest point in ontogeny (GP1), followed by the vertebral elements. Within the vertebral elements, neural arch fusion occurred earliest for each vertebral section, though statistical significance was not reached due to attenuated sample sizes. Neural arch fusion was followed by neurocentral fusion in each vertebral section, and finally, the apophyseal (annular) rings of each vertebral element. In terms of the appendages, the medial epicondyle of the humerus and proximal ulna (GP 8) fused first and were followed by all other epiphyseal elements in the latest age group (GP9).

Table 2

Percentages of individuals in each age group where fusion could be observed. Light gray shading is used to indicate the onset of fusion, while dark gray shading is used to indicate that a statistically significantly greater proportion of individuals has experienced fusion than in previous age groups. Sample sizes are listed in parentheses within each cell.

	GP 1	GP 2	GP 3	GP 4	GP 5	GP 6	GP 7	GP 8	GP 9
Age (Years)	0.0–0.9	1.0–1.9	2.0–3.9	4.0–5.9	6.0–7.9	8.0–9.9	10.0–12.9	13.0–16.9	17.0–22.0
Mandibular Symphysis	100.0 (1)	100.0 (6)	100.0 (11)	100.0 (6)	100.0 (11)	100.0 (8)	100.0 (8)	100.00 (4)	100.0 (4)
Proximal Humerus	0.0 (1)	0.0 (5)	0.0 (8)	0.0 (3)	0.0 (12)	0.0 (7)	0.0 (8)	0.0 (4)	100.0 (9)
Humeral Trochlea	0.0 (1)	0.0 (5)	0.0 (8)	0.0 (3)	0.0 (11)	0.0 (6)	0.0 (6)	25.0 (4)	100.0 (9)
Humeral Medial	0.0 (1)	0.0 (4)	0.0 (7)	0.0 (3)	0.0 (8)	0.0 (6)	0.0 (6)	50.0 (3)	100.0 (10)
Radial Head	0.0 (1)	0.0 (4)	0.0 (7)	0.0 (3)	0.0 (8)	0.0 (6)	0.0 (6)	0.0 (3)	100.0 (8)
Distal Radius	0.0 (1)	0.0 (3)	0.0 (7)	0.0 (3)	0.0 (8)	0.0 (6)	0.0 (6)	0.0 (3)	100.0 (8)
Proximal Ulna	0.0 (1)	0.0 (4)	0.0 (8)	0.0 (3)	0.0 (7)	0.0 (5)	16.7 (5)	66.7 (3)	100.0 (10)
Distal Ulna	0.0 (1)	0.0 (4)	0.0 (8)	0.0 (3)	0.0 (7)	0.0 (5)	0.0 (5)	0.0 (3)	87.5 (9)
Femoral Head	–	0.0 (5)	0.0 (9)	0.0 (3)	0.0 (10)	0.0 (7)	0.0 (8)	0.0 (3)	100.0 (10)
Femoral Trochanter	–	0.0 (5)	0.0 (9)	0.0 (3)	0.0 (10)	0.0 (7)	0.0 (8)	0.0 (3)	100.0 (9)
Distal Femur	–	0.0 (5)	0.0 (9)	0.0 (3)	0.0 (10)	0.0 (7)	0.0 (8)	0.0 (3)	77.7 (9)
Proximal Tibia	0.0 (1)	0.0 (6)	0.0 (7)	0.0 (3)	0.0 (9)	0.0 (7)	0.0 (8)	0.0 (3)	88.8 (10)
Distal Tibia	0.0 (1)	0.0 (6)	0.0 (8)	0.0 (3)	0.0 (9)	0.0 (7)	0.0 (8)	0.0 (3)	100.0 (9)
Cervical 1 anterior arch	–	0.0 (3)	0.0 (2)	–	100.0 (2)	100.0 (2)	100.0 (2)	100.0 (4)	100.0 (6)
Cervical 1 posterior arch	–	80.0 (2)	100.0 (5)	100.0 (1)	100.0 (5)	100.0 (3)	100.0 (7)	100.0 (4)	100.0 (6)
Cervical 2 ce ^a -na ^b	–	0.0 (2)	0.0 (2)	0.0 (5)	100.0 (5)	100.0 (4)	100.0 (6)	100.0 (4)	100.0 (6)
Cervical 2 na-na	–	0.0 (2)	100.0 (2)	100.0 (1)	100.0 (7)	100.0 (4)	100.0 (6)	100.0 (4)	100.0 (7)
Cervical 3–7 ce-na	0.0 (1)	0.0 (5)	0.0 (6)	66.7 (3)	100.0 (6)	100.0 (5)	100.0 (6)	100.0 (4)	100.0 (7)
Cervical 3–7 na-na	0.0 (1)	71.4 (7)	100.0 (6)	100.0 (3)	100.0 (6)	100.0 (5)	100.0 (6)	100.0 (4)	100.0 (6)
Cervical 3–7 rings ^c	0.0 (1)	0.0 (4)	0.0 (6)	0.0 (2)	0.0 (6)	0.0 (5)	0.0 (6)	0.0 (4)	100.0 (7)
Thoracic 1–12 ce-na	0.0 (1)	0.0 (4)	0.0 (6)	50.0 (2)	100.0 (6)	100.0 (5)	100.0 (6)	100.0 (4)	100.0 (8)
Thoracic 1–T12 na-na	0.0 (1)	40.0 (5)	83.3 (6)	100.0 (2)	100.0 (6)	100.0 (5)	100.0 (6)	100.0 (4)	100.0 (8)
Thoracic 1–12 rings	0.0 (1)	0.0 (3)	0.0 (6)	0.0 (2)	0.0 (6)	0.0 (5)	20.0 (5)	100.0 (4)	100.0 (8)
Lumbar 1–5 ce-na	0.0 (1)	0.0 (4)	0.0 (5)	50.0 (2)	100.0 (6)	100.0 (5)	100.0 (6)	100.0 (3)	100.0 (8)
Lumbar 1–5 na-na	0.0 (1)	40.0 (5)	66.7 (6)	66.7 (6)	100.0 (2)	100.0 (6)	100.0 (5)	100.0 (3)	100.0 (8)
Lumbar 1–5 rings	0.0 (1)	0.0 (3)	0.0 (5)	0.0 (2)	0.0 (5)	0.0 (5)	0.0 (5)	0.0 (3)	100.0 (8)

^a Vertebral centrum.

^b neural arches.

^c apophyseal rings.

5. Discussion

5.1. Dental maturity

Residuals associated with the two ages estimated from tooth formation increase over the lifespan, and especially after four years of age (Fig. 2). Collations of tooth formation stages for first, second, and third molars document a successive, nearly three-fold increase in standard deviation for age-at-attainment in later forming teeth (Hillson, 2014). Similar results were observed at the Shamanka II cemetery (Scharlotta et al., 2018). Initiation stages ages for the second and third molar were delayed relative to the first suggesting greater variation in the formation patterns of later forming teeth. These results are consistent with observations by this study that suggest increasing differences in dental age estimated from multiple teeth at later ages of development. However, it remains important to note that standard deviations between dental age and chronological age reduce markedly when averages from multiple teeth are used (Smith, 1991) suggesting that there exists a strong correspondence between dental age and chronological age (Garn et al., 1960).

The order of tooth emergence (Fig. 3) is consistent with previously reported studies (Ubelaker, 1989; Smith, 1991; Hillson, 1996; Sciulli, 2007). In addition, little time elapsed between age groups where some individuals expressed alveolar emergence of a particular tooth and all individuals having this tooth emerged into full occlusion. This suggests relatively low heterogeneity in tooth emergence among hunter-gatherers from Cis-Baikal. The samples sizes used by this study are small in comparison to those reported by previous analysis of tooth emergence (Smith, 1991; Sciulli, 2007). Smaller samples produce lower heterogeneity by virtue of the fact that it is much easier to move from a context of mixed emergence (those with both emerged and un-emerged teeth) to 100% emergence (Smith, 1991). As a result, some degree of caution in interpreting these findings is necessary, though consistency between these results and those reported by other studies suggest

genetic constraint in ages and sequencing of tooth emergence.

Elevated heritability for ages at tooth emergence is reported (Garn et al., 1960, 1965, 1973; Townsend et al., 2009). Elevated heritability for tooth emergence reflects highly conserved, coordinated patterns of gene expression. Tooth emergence begins when a series of mechanical forces move the tooth along the emergence pathway (Nanci, 2008; Marks and Schroeder, 1996; Wise, 2009; Proffit and Frazier-Bowers, 2009). Experimental studies suggest that cellular proliferation and vasodilation at the root apex may be responsible for these forces during the initial stages of tooth emergence, while pressure within the periodontal ligament at the post-emergent stages may be implicated (Proffit and Frazier-Bowers, 2009). During this process, the basal and coronal portions of the dental follicle control the expression of gene families that respectively stimulate osteoclastogenesis and bone formation along the emergence pathway (Marks and Cahill, 1987). The gene families within the dental follicle are expressed at different times, with the gene families that are initially expressed governing bone (and root of un-emerged deciduous tooth) resorption (CSF-1, EMAP-II, MCP-1, SFRP-1*), and the gene families that are secondarily expressed governing the formation of bone around a tooth root within the alveolar crypt (OPG, RANKL, VEGF, TNF- α) (Marks et al., 1983; Wise and Fan, 1989; Cielinski et al., 1994; Liu and Wise, 2007; Wise and Shaomian, 2003; Yao et al., 2006). The interdental septum separates each tooth crypt, allowing the process to occur independently in each tooth (Nanci, 2008).

These findings do not downplay the importance of environmental influences on tooth emergence. In fact, recent work emphasizes that tooth emergence may be delayed in response to environmental challenges to physiological homeostasis (Zihlman et al., 2004; Cardoso, 2007; Smith and Boesch, 2010; Conceição and Cardoso, 2011; Oziegbé et al., 2013; Smith et al., 2013), though these delays are significantly reduced when compared with skeletal maturation (Cardoso, 2007; Conceição and Cardoso, 2011). Tooth formation from the Cis-Baikal region do in fact suggest delayed initiation in dentin formation for the second and third molar (Scharlotta et al., 2018). This difference is not

attributed to variation in stress, but instead, genetic variation in the timing of tooth formation and subsequent emergence in this population. Given these observations, it remains unlikely that tooth emergence among the Cis-Baikal hunter-gatherers was offset by systemic stress to an appreciable degree. The observed patterns of tooth emergence in these samples are instead associated with the interactions of regulatory genes and the timing of cellular differentiation and tooth formation.

Sequences of tooth emergence reported here have “lag times” of several years between different sets of teeth: three years between the full emergence of the deciduous dentition and first permanent molar, two years between the emergence of the anterior and posterior permanent dentition, and four years between the full emergence of the second and third molars. This finding is consistent with previous studies reporting similar “lag times” between the emergence of these tooth categories (Smith, 1991). The results suggest that estimating age-at-death in human skeletal remains using only tooth emergence provides wide ranges that may not offer the type of precision required for studies of growth and development. Gaps in the emergence of tooth groups may produce difficulty in estimating ages between 2.0 and 5.5 years, 7.0 and 10.0 years, and 12.0 and 15.5 years. As a result, age-at-death profiles recorded for immature skeletal samples should rely on a combination of tooth emergence and formation. Tooth formation provides a substantially more precise method by which to estimate age-at-death in immature remains because the process is continuous, rather than incremental (Smith, 1991; Hillson, 1996), and as suggested by the results of this and other studies (Smith, 1991; Sciulli, 2007; Cardoso, 2007), there is a high degree of agreement when ages are estimated using multiple teeth from the same individual.

5.2. Skeletal maturity

Fusion of primary and secondary centers of ossification is age-dependent and a useful indicator of age-at-death in human skeletal remains. In human populations caution is exercised in estimating age-at-death using this method because fusion is sometimes delayed due to nutritional stress. The results of this study suggest a fairly uniform distribution of fusion within the samples from Cis-Baikal. Where statistical significance was not found in the first group to express fusion, many still had greater than 65% of all individuals with fused elements. Two exceptions to this pattern are the neural arches of cervical and thoracic vertebrae. Therefore, some caution should be exercised when utilizing these two vertebral segments in estimating age-at-death among skeletal samples from Cis-Baikal.

In terms of skeletal maturity, the earliest observed element to fuse was the mandibular symphysis. This result was unsurprising as previous studies note that this element fuses during the first year of life (Scheuer and Black, 2000; Schaefer et al., 2009) and is found to be fused on 100% of all cases at the earliest stage of ontogeny in prehistoric skeletal samples (Sciulli, 2007). Fusion of the vertebral elements follow the most consistent pattern of fusion for children and juveniles. The posterior neural arches of the first cervical vertebra fuse in GP4, while anterior arch fusion occurs in GP5. In the general cervical vertebrae category, neural arch fusion begins in GP4, while neurocentral fusion occurs in GP5. For the thoracic and lumbar vertebrae, neural arch fusion begins in GP4, and neurocentral fusion in GP5. Appendicular epiphyses and vertebral apophyseal (annular) rings are the last elements to fuse. The cervical and lumbar vertebrae experience apophyseal union in GP9, while the thoracic elements experience fusion in GP8. This result may be useful in narrowing age estimates among middle and older adolescents, as GP8 corresponds with an age range of 13.0 to 16.9 years, while GP9 corresponds with an age range of 17.0 to 22.0 years.

Fusion of the vertebral neural arch and centrum are mostly consistent with expectations that suggest dimensions of the neural canal are associated with early life experiences (Clark et al., 1986; Clark, 1988; Watts, 2011, 2013, 2015; Newman and Gowland, 2015). Of particular interest is the finding that the neural arch fuses to the vertebral body

around 4.0 years of age and that transverse diameter remains consistent from this point to adulthood (Watts, 2013). Similarly, fusion of the neural arch begins around 1.0–2.0 years for the cervical vertebrae, and 2.0–4.0 years of age for the thoracic and lumbar vertebrae, suggesting that anterior-posterior diameter of the neural canal may reflect growth at the very earliest stages of ontogeny. Recent studies, however, demonstrate continued growth between these landmarks until approximately 15–17 years of age (Watts, 2013). These results are consistent with the argument that vertebral neural canal diameters are formed in the early life environment and that these measurements should be used as a barometer for early life stress. In particular, these results confirm that the anterior-posterior diameter tracks growth in infancy, while the transverse diameter tracks growth between late infancy and early childhood. Some caution should be exercised in evaluating anterior-posterior diameters as this dimension continues expansion following fusion. Measurements of vertebral neural canal have not been collected in the Cis-Baikal samples and represent a new way that early life stress may be explored in high resolution chronological context among these samples.

Results regarding ages for fusion of the annular rings differ slightly from previous studies. Annular rings of the cervical and lumbar vertebrae begin fusion after 17.0 years of age in the Cis-Baikal sample. Annular ring fusion of cervical and lumbar vertebral bodies occurs between 14 and 21 years of age for males and females in an early 20th century sample from Portugal (Cardoso and Ríos, 2011). This difference may be associated with underlying differences in skeletal maturation between the two populations, or it may reflect sampling protocols and age estimation methods. The sample from Portugal is part of a collection where chronological age is known, whereas age at death was estimated using stages of tooth formation in the Cis-Baikal sample. In addition, the sample from Portugal has a substantially larger number of individuals ($n = 104$) between 9.0 and 30.0 years of age. As a result, it is possible that the earliest stages of fusion for the annular rings are not represented in the Cis-Baikal sample, and that the process is skewed towards older ages. Results from Cis-Baikal, however, are consistent with those reported by Buikstra et al. (1984): annular ring fusion of cervical vertebral bodies in a sample of early 20th century black and white Americans begins between 17 and 25 years of age. Fusion of thoracic annular rings begins around 14.0 years in the sample from Portugal (Cardoso and Ríos, 2011), and this follows observations from Cis-Baikal, where the earliest fusion occurs between 10.0 and 12.9 years of age. These results differ from previous studies of white and black Americans where annular ring fusion of thoracic vertebrae begins at older ages (17–18 years) (McKern and Stewart, 1957; Albert and Maples, 1995).

In terms of epiphyseal union, the medial humeral epicondyle and proximal ulna (olecranon) may be used to identify early and middle stage adolescents as a significant proportion of individuals in GP8 (13.0 to 16.9 years) experience fusion of these elements. Among the other epiphyses, all other structures fuse at 100% prevalence in GP9 (17.0 to 22.0 years). Results for epiphyseal fusion are consistent with previous bioarchaeological studies that found the medial humeral epicondyle and proximal ulna were among the first epiphyseal segments to fuse and may help differentiate between early and middle stages of adolescence (Sciulli, 2007; Cardoso, 2008b).

There exists a slight delay in the earliest stages of fusion in lower limb bones between this study and those previously reported. Femoral and tibial epiphyses and apophyses do not begin fusion until GP9 (17.0–22 years) in the Cis-Baikal sample. By contrast, fusion of femoral and tibial epiphyses and apophyses begin between 14 and 15 years of age in samples from early 20th century Portugal (Cardoso, 2008a). Previous studies report delays between 0.5 and 2.0 years when skeletal maturation is compared between individuals from lower and higher socioeconomic status, though these delays are less pronounced when compared to skeletal growth, and are most apparent prior to adolescence (Dreizen et al., 1967; Frisancho et al., 1970a, 1970b). Epiphyses and apophyses associated with the lower limb begin ossification prior to

adolescence (Scheuer and Black, 2000). As such, it is possible that stress during this time period disrupted ossification of these elements and resulted in delayed fusion. However, it is also important to point out that because these earlier studies (i.e., Sciulli, 2007; Cardoso, 2008a) had larger sample sizes, the fusion of epiphyses were subdivided by fusion stage rather than consolidated into the single stage used in this study, specifically with regard to the epiphyses of the proximal femur and tibia. However, the percentages of individuals with fused proximal femora and tibiae in this intermediate category remain small (fused <20%) compared to those in the final stage of development. It, therefore, is less likely that these delays are associated with methods for recording stages of ossification.

One final point to consider is that the Cis-Baikal sample includes individuals of unknown sex. Differences in skeletal maturation are near universally noted with earlier fusion ages reported for females compared to males (e.g., Albert and Maples, 1995; Buikstra and Ubelaker, 1994; Cardoso, 2008a, 2008b; Scheuer and Black, 2000). Combining the samples from Cis-Baikal, therefore, creates an unknown source of error as it is not possible to be certain that the 2–3 years delay in lower limb fusion results from male bias. That said, systemic stress must also be considered as a potential causative agent for the pattern of delayed skeletal maturity observed in the lower limb.

Studies comparing chronological age to ages estimated using tooth formation, long bone growth, and epiphyseal fusion consistently found evidence for delayed skeletal growth and maturation in groups with lower socioeconomic status, and the differences were significantly greater in skeletal compared to dental elements (Cardoso, 2007; Conceição and Cardoso, 2011). Skeletal and dental indicators of growth disruption show no relationship to mortality in the samples from Cis-Baikal (Lieverse et al., 2007; Temple et al., 2014). However, disruptions to skeletal growth were found in these samples and concentrated in the lower limb (Temple et al., 2014). *cis*-Baikal hunter-gatherers participated in a hunting economy where resources such as terrestrial and aquatic mammals as well as lacustrine fish were exploited (Katzenberg et al., 2010; Weber et al., 2016a, 2016b). Exploitation of these resources followed seasonal cycles, and disruptions to these cycles in association with climatic perturbation was likely (Weber and Bettinger, 2010). Differences in adaptive strategies characterize the Early and Late Neolithic samples included in this study: greater homogeneity in dietary patterns combined with cultural heterogeneity is found during later phases of the Early Neolithic (Scharlotta et al., 2016; Weber and Bettinger, 2010). Greater heterogeneity in dietary strategy and homogeneity in cultural expression is found in Late Neolithic samples (Weber and Bettinger, 2010). While increasing dietary homogeneity in the Early Neolithic sample likely increased precarity to environmental stressors, seasonality may have introduced stress in both samples and resulted in disruption of elemental fusion in the lower limb.

It remains important to point out that the preadult samples in this study represent a non-surviving cohort. It is possible that elemental fusion was delayed in this non-surviving sample, and that individuals who lived beyond 22.0 years experienced elemental fusion at an earlier age. It is, therefore, more prudent to conclude that seasonal stress appears to have slightly delayed fusion of some skeletal elements among individuals who did not survive past early adulthood, though the general trend still supports a pattern of relative homogeneity in elemental fusion in this non-surviving cohort of the population.

6. Conclusions

This study compared the relative dental and skeletal rates of maturation to ages estimated using developmental phases of teeth. The study found little heterogeneity between ages of tooth formation and emergence. This result is potentially rooted in small sample sizes. Findings also point towards a highly conserved process that is rooted in control over gene expression by the dental follicle. This finding does not argue against environmental influence on tooth emergence. Instead, it

suggests that variation in tooth emergence was limited among the Cis-Baikal hunter-gatherers and likely not driven by the need to maintain homeostasis during physiological disruption. Relatively low degrees of heterogeneity in the fusion of skeletal elements were found, and the ordering of fusion follows previously reported studies. Fusion of vertebral elements are consistent with previously reported data sets and suggest that measurements of the vertebral neural canal capture growth and maturation in the early life environment. Ages for fusion in the upper limb match earlier work and suggest that maturation in these elements may be used to estimate age at death. Slight delays in fusion of the lower limb are found. While it is not possible to rule out sex bias or sample size as contributing factors, it is also likely that stress experiences may have contributed to this pattern of delayed maturation in this non-surviving cohort.

Author statement

All authors equally contributed, and no specific credit allocation is requested.

Declaration of Competing Interest

The authors of this manuscript have no conflict of interest to declare.

Acknowledgements

We thank Rick Schulting for comments on an earlier draft. We thank Andrea Hiob for logistical support. DHT thanks Sam lo Presto for comments and references regarding vertebral neural canal growth. We are grateful to the editor and anonymous reviewers for providing comments that greatly improved this research.

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