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Maja Seselj

Lyle W. Konigsberg

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A different interpretation of dental development stages in Xujiayao 1 Middle-to-Late Pleistocene *Homo*

Keywords: Dental development; Pleistocene *Homo*; Age estimation; Fels Longitudinal Study

1. Introduction

Xing et al. (2019) recently suggested a modern human-like pattern of dental development in the Middle to Late Pleistocene *Homo* juvenile specimen from the site of Xujiayao, in northern China. The fossil, Xujiayao 1, consists of a partial left maxilla with preserved I¹ and C¹–M²; none of the teeth have completed crown and root formation. Of particular interest is the argument put forth by Xing et al. (2019) that, for its chronological age, Xujiayao 1 exhibits stages of dental development that are comparable to recent modern human children of similar age. During the Middle to Late Pleistocene we find the earliest fossil evidence of derived craniodental morphologies and tempo (i.e., acceleration or deceleration; in this case, deceleration) of dental development associated with modern humans, mostly in Africa and the Levant (e.g., McCown and Keith, 1939; White et al., 2003; McDougall et al., 2005; Smith et al., 2007; Aubert et al., 2012; Hublin et al., 2017; Richter et al., 2017; Hershkovitz et al., 2018). At the same time, in East Asia there is a diversity of fossils whose phylogenetic relationships to later taxa, such as modern humans, Neanderthals and Denisovans, are unclear (Xiao et al., 2002; Wu and Athreya, 2013; Xing et al., 2015, 2019; Martínón-Torres et al., 2017; Xing et al., 2019). A Middle to Late Pleistocene fossil from northern China that potentially possesses stages of dental development similar to recent modern human children of comparable age (Xing et al., 2019) is therefore both unexpected and exciting, especially since the Xujiayao hominins appear to exhibit a mosaic of ancestral morphological features seen in *Homo erectus* and derived features observed in Neanderthals and recent modern humans (Xing et al., 2015).

Xing et al. (2019) proposed that many aspects of dental development in Xujiayao 1 fall within the recent modern human range of variation. The authors determined the periodicity, number and distribution of perikymata, crown formation and initiation times, root extension rates, and age at M¹ eruption in Xujiayao 1, and evaluated its stages of dental development across teeth and in comparison with recent modern human children. For many of these traits, the authors asserted that the teeth of Xujiayao 1 fall within the recent modern human range of variation, or just outside of the range for recent modern human but within the range of variation seen in fossil *Homo sapiens*. They argued these ontogenetic similarities include a close agreement of the estimated ‘dental age’ of 6.62 years for Xujiayao 1 and its chronological age estimate of 6.51 years. A dental age refers to the estimate of the likely chronological age of a specimen obtained using dental development stages to draw comparisons with reference samples, in this case a sample of recent modern human children.

We would like to offer a point of correction and a different interpretation of the estimated dental age of Xujiayao 1 relative to its age-at-death. Xing et al. (2019) used the 14-stage dental development scoring system of Moorrees, Fanning and Hunt (MFH; Moorrees et al., 1963), and the associated chronological age values, to produce a dental age estimate of 6.62 years. MFH assessed the development of incisors from intraoral radiographs of patients from the Forsyth Dental Infirmary, whereas the canine and postcanine dentition was assessed from oblique mandibular radiographs from the Fels Longitudinal Study (Moorrees et al., 1963). Since the MFH publication only presented their results in graphical format, Xing et al. (2019) used age values estimated from the graphs in the MFH publication by Shackelford et al. (2012) to obtain a dental age estimate. They concluded that “the Xujiayao juvenile dentition does not form at an accelerated schedule relative to that of modern humans” (Xing et al., 2019: 6). This interpretation, however, hinges on the age estimation function described by Shackelford et al. (2012) to determine the fossil’s dental age, and on the accuracy and

appropriateness of the MFH age data for age estimation purposes, which has also been put into question (Liversidge, 2003, 2009; Liversidge et al., 2010; Šešelj et al., 2019).

2. Results and discussion

2.1. Dental age estimates using Shackelford et al. (2012) data

Firstly, we would like to clarify that Xing et al.'s (2019) use of the term 'median attainment age' (Xing et al., 2019: Table 2) for the dental age data derived from Shackelford et al. (2012) in fact refers to estimates of age given stage, and not ages of attainment. The so-called 'age given stage' (also referred to as 'age within a stage', or 'age for stage') refers to the likely age based on the distribution of chronological ages for a given stage of dental development (Smith, 1991, Liversidge, 2011). The 'age of attainment' (or 'average age entering a stage') refers to the chronological age at which it is estimated that at least half of the reference sample has entered a particular stage of dental development, and by definition precedes the average 'age given stage' (Liversidge, 2003, 2011).

The data presented by Xing et al. (2019: Table 2) stem from the maximum likelihood estimate of log-scale, conception-corrected, age conditional on tooth stage. It appears the authors have reached their estimates by exponentiating values from Table 6 of Shackelford et al. (2012) and subtracting 0.75 years. Their value of 6.62 years comes from an approximate method given in Shackelford et al. (2012) that makes use of Shackelford et al.'s (2012: Tables 5 and 6), whereby one divides the sum of the products of precisions with their associated means by the sum of the precisions. However, following those steps we obtain the value of 6.52 years. This value is also obtained using the maximum likelihood estimation assuming conditional independence among the teeth (Figs. 1a and 2; Table 1). Regardless of this minor difference in the estimated dental age, those estimates should be referred to as estimates of

age given stage (i.e., the likely chronological age based on stages of dental development), not ages of attainment.

2.2. Issues with using Moorrees et al. (1963) reference values for age estimation

More importantly, using the age estimates based on MFH reference values in the first place is not without its challenges. Comparing the accuracy and precision of different age estimation methods, Liversidge and colleagues have noted that the ages based on the Moorrees et al. (1963) study are unusually young relative to other recent modern human samples (Liversidge, 2009; Liversidge et al., 2010). Shortly after Xing et al. (2019) published their analysis of Xujiayao 1 using the MFH reference values from Shackelford et al. (2012), Šešelj et al. (2019) published a new set of reference values for estimating age from dental development using permanent canine and postcanine mandibular dentition based on over 6,000 longitudinal radiographs from 590 participants in the Fels Longitudinal Study (FLS). The participants in the study are Midwesterners largely of European ancestry, and the radiographs were taken between 1929 and 1984. That dataset thus likely includes most, if not all, of the Fels Longitudinal Study participants on whose oblique jaw radiographs Moorrees et al. (1963) based their age estimation values for canine and postcanine teeth. The FLS-based reference age values, estimated using transition analysis, are for the most part not a good match for the MFH values. In particular, the MFH reference values tend to produce increasingly younger age estimates across root formation stages, up to a year or two younger than the estimates obtained by Šešelj et al. (2019) on a much larger sample of that same participant population. They concurred with the assessment of Liversidge et al. (2010) that MFH values should not be used for the purposes of age estimation. The unusually young MFH-based reference ages, therefore, could make the stages of dental development of a fossil look comparable to chronologically younger recent modern human children than would a different reference sample.

Using the FLS-based reference ages instead of the MFH reference ages to assess the stages of dental development exhibited by Xujiayao 1, the age given stage estimates for canine and postcanine teeth are consistently higher (Figs. 1b and 3; Table 1) than those estimated by Xing et al. (2019), or by us using the Shackelford et al.'s (2012) age values (Figs. 1a and 2; Table 1). Using the FLS data, we estimate the maximum likelihood age given stage of Xujiayao 1 to be 7.72 years, with the 95% highest posterior density (HPD) interval ranging from 6.52 to 9.13 years of age (Fig. 1b; Table 1). The chronological age estimate of 6.51 ± 0.13 years reported for Xujiayao 1 based on dental microstructure, and the age given stage estimate of 6.52 years based on MFH, thus fall at the lower bound of the 95% HPD interval. This suggests that the stages of dental development exhibited by Xujiayao 1 are unusual and decidedly on the accelerated end of the range of variation for ages at which modern human children from the FLS sample would be in the observed dental stages.

The FLS-based age given stage estimates for Xujiayao 1 are also close to the mean age within stage values of a recent clinical sample from London (Table 1), consisting of Londoners of European and Bangladeshi ancestry (Liversidge, 2009). The estimates in Table 1 using Liversidge's (2009) results use her probit analyses to find the maximum likelihood age for each tooth given its developmental stage. The final age is found assuming conditional independence, while the 95% HPD is found using the within tooth variance (again, assuming conditional independence) plus the between tooth variance (see Shackelford et al. 2012 for this method). Because Liversidge (2009) used probit on the raw scale of age, rather than the log scale, the estimated values are means rather than medians.

It is important to note that the recent modern human reference values for the development of permanent teeth mentioned here (e.g., Moorrees et al., 1963, Liversidge, 2009; Shackelford et al., 2012, Šešelj et al., 2019) are based on mandibular, and not maxillary, dentition. Mandibular teeth often form at a slightly more accelerated pace than maxillary teeth, and thus it is possible that this introduces an additional degree of error when estimating age given stage for maxillary teeth using mandibular teeth as

a reference, producing slightly younger age given stage estimates. However, maxillary reference samples are generally not available (with the exception of Anderson et al., 1976, but see Šešelj et al., 2019, for concerns regarding that study). Since all comparisons were based on mandibular teeth as a reference, this issue does not explain the difference between our dental age estimates for Xujiayao 1 compared to the values presented by Xing et al. (2019). Additionally, the differences in timing between maxillary and mandibular teeth are relatively small (e.g., a few weeks to a few months), and thus cannot explain the magnitude of difference we present here, which is further based on comparisons drawn with two different reference samples.

3. Conclusions

In sum, though many aspects of dental development in Xujiayao 1 may well be within the range of variation of recent modern humans, we find that the stages of its dental development given its chronological age appear to be accelerated compared to average recent modern human values observed in the FLS sample and an unrelated, ethnically diverse clinical sample of London children (Liversidge, 2009). Relative to recent modern human children of comparable stages of dental development, the chronological age of Xujiayao 1 of 6.51 years falls on the lower bound of the 95% HPD interval (i.e., the accelerated end) for the FLS sample, well below the median of 7.72 years, and within, though towards the lower end, of the 95% HPD interval for the London sample, below the mean of 7.3 years. Jointly, this strongly suggests that the tempo of dental development in Xujiayao 1 was accelerated compared to recent modern human children of comparable chronological age.

However, this discrepancy is not necessarily surprising in a Middle to Late Pleistocene hominin that displays a mosaic of ancestral and derived features in its dental morphology (Xing et al., 2015). Moreover, we do not know enough about the range of variation in the tempo of dental development among early *H. sapiens*, and there is also considerable variation, both individual and at the population

level, in this aspect of dental development among living *H. sapiens*. Thus, at the present time there is no well-established criterion that requires a fossil member of our genus, more than a hundred thousand years old, to exhibit stages of dental development typical for its recent modern human age peers. Based on the complex and mosaic pattern of evolution in other aspects of our craniodental and postcranial morphology, it stands to reason that the pattern and tempo of dental development in *H. sapiens* likely evolved in a similarly gradual and mosaic fashion until demonstrated otherwise.

In fact, the somewhat older dental age we propose for the Xujiayao 1 specimen can also help reconcile its 6.51 years age-at-death estimate based on dental microstructure with observations by Xing et al. (2019) that certain aspects of its dental development appear to be accelerated relative to recent modern human children of comparable chronological age. Xing et al. (2019) noted that the crown formation times in C^1 , P^4 , M^1 and M^2 of Xujiayao 1 fall just above the recent modern human range of variation, and that root extension rates of its I^1 and M^1 are quite accelerated and fall outside of the modern human range of variation, exceeding even those reported for the Jebel Irhoud 3 juvenile (Smith et al., 2007). In conjunction with our dental age estimate for this fossil, we get a more complete picture of the mosaic nature of dental development in Xujiayao 1 compared to recent modern human children. More subadult fossils from the Middle to Late Pleistocene are needed to ascertain whether the somewhat accelerated dental development in Xujiayao 1 is an example of individual variation, or in fact representative of a central tendency in Middle to Late Pleistocene *Homo* in general, or this population in particular.

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Figure captions

Figure 1. A) The probabilities for age given stage for Xujiayao 1 using the age reference data from Shackelford et al. (2012). B) The probabilities for age given stage for Xujiayao 1 canine and postcanine teeth using the age reference data from Šešelj et al. (2019). Dashed line is chronological age from Xing et al. (2019). All ages in years.

Figure 2. Posterior distribution of age given dental stages and an uninformative prior (using MFH parameters). The solid curve gives the distribution assuming conditional independence of dental stages (given age). The dashed curve adds the between tooth variance from the median age estimates per tooth. The thin vertical line gives our estimate from Table 1, while the thin vertical dashed line gives the estimate from Xing et al. (2019). The gray region represents the 95 highest posterior density for the age estimate from total tooth variation.

Figure 3. Posterior distribution of age for Xujiayao 1 across all teeth using the Šešelj et al. (2019) age reference values. Curves, vertical lines, and shading are as in Figure 2.

Xujiayao juvenile (MFH)

Xujiayao juvenile (FLS)

Xujiayao juvenile (MFH)

Xujiayao juvenile (FLS)

Table 1

Comparisons of different age estimates given tooth formation stages for the Xujiayao juvenile based on different modern human reference samples. All ages in years.

MFH tooth stages for Xujiayao fossil <i>Homo</i> (Xing et al., 2019: Table 1)	Xing et al. (2019) 'median attainment age' ^a based on Shackelford et al. (2012)	Maximum likelihood estimate of median age given stage from Shackelford et al. (2012)	Mean age within a stage based on Liversidge (2009)	Seselj et al. (2019) FLS-based median age estimate for age given stage ^b
I ¹ = root 1/2	7.25	7.25	6.27	—
C ¹ = root 1/4	6.51	6.50	7.53	8.46
P ³ = root initiation	6.19	6.19	7.54	7.60
P ⁴ = root initiation	7.17	7.18	8.02	8.15
M ¹ = root 3/4	5.59	5.59	7.38	7.28
M ² = crown complete	6.61	6.61	7.85	7.35
Across all teeth	6.62	6.52	7.30	7.72
			(95% HPD ^e 5.93–8.67)	(95% HPD ^e 6.52–9.13)

Abbreviations: MFH = Moorrees, Fanning, and Hunt (Moorrees et al., 1963); FLS = Fels Longitudinal Study; HPD = highest posterior density interval.

^a These are actually maximum likelihood estimates of log-scale conception corrected age given stage based on Shackelford et al. (2012: Tables 5 and 6), not ages of attainment as reported by Xing et al. (2019).

^b Based on the combined sex sample values, given that the sex of Xujiayao 1 is unknown.