

Early and Middle Pleistocene hominins from Atapuerca (Spain) Show Differences in dental developmental patterns

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Abstract

The patterns of dental development in fossil hominins have been classically analyzed considering teeth as independent units. However, a recent Bayesian statistical approach considers them as forming a developmental module. This approach has been employed to analyze Upper Pleistocene hominins, but never to earlier populations. Here we show its application to five hominins from Gran Dolina (*Homo antecessor*, Lower Pleistocene) and Sima de los Huesos (Middle Pleistocene) archaeological sites, both placed in the Atapuerca complex (Burgos, Spain). Our results show an advanced development of the third molars in both populations in respect with *Homo sapiens*, although the Sima de los Huesos hominins differentiates from *H. sapiens* and *H. antecessor* in their relatively advanced development of the second molar. The relationship between I1/M1 in both hominin populations is present in modern humans, so Neandertals appeared to be unique in this feature. Together with lateral enamel formation times, these evidences point to a shortening of the ontogenetic development in the hominins from Gran Dolina and Sima de los Huesos.

Introduction

Dental development studies in hominins have been focused on the absolute timing of enamel and dentine formation, and/or the pattern of dental maturation (1–4). However, both approaches, time and timing, are indissoluble when reconstructing dental development in fossil hominins, as they offer complimentary views to have an overall picture of the maturation process.

A relatively novel statistical approach to evaluate the pattern of dental development is based on the Bayesian statistical theorem (5). A brief summary of this method, further explained in methods, is that it considers every tooth of the mineralization sequence of an individual dentition as a dependent unit, which grow within a developmental module. Ultimately, a probability is obtained for a particular sequence to be present within modern human variation.

This approach has been recently applied to Neandertals (6, 7), to an Upper Paleolithic specimen from La Madeleine (8), and to the Lagar Velho individual (9). Remarkably, both

Neandertals and the Lagar Velho specimen presented a relative dental development not present in modern human variation, whereas La Madeleine individual did have a dental maturation encompassed in the variation of our species. Interestingly, this statistical approach has never been applied to hominins older than Neandertals. Here, we present the study of the relative dental development of five hominins from two European Lower and Middle Pleistocene populations uncovered in two archaeopaleontological sites from Sierra de Atapuerca (Burgos, Spain). This study complements the one published in this same journal issue about the absolute timing of enamel formation.

The two archaeological sites from Atapuerca are Gran Dolina and Sima de los Huesos. Unit 6 of the Gran Dolina site (~0.9-0.8 Ma) contains more than 160 human fossils representing at least 8 individuals attributed to the species *Homo antecessor* (10–13). The second site is Sima de los Huesos (~0.43 Ma), which contains more than 6500 human fossils ascribed to at least 28 individuals whose taxonomical attribution is still under discussion, although genetic and morphological data strongly suggest that these hominins are likely Neandertal ancestors (14).

Previous studies attempted to evaluate the pattern of dental maturation from these two fossil populations by treating tooth types as independent units. The information offered by the study of three hominins from the Gran Dolina site (15, 16) denotes an advance in the M3 calcification. However, hominin XVIII from the Sima de los Huesos site (Fig. 1) displayed a developmental delay of the lower and upper canines and an advanced development of the lower second molars and especially upper and lower third molars (17). Here we applied the Bayesian approach to the pattern of dental development of two hominins from the Sima de los Huesos site (XVIII and XXV) and three hominins of *H. antecessor* from the Gran Dolina-TD6 site (H1, H3, H11) by treating teeth as dependent units. We have studied both upper and lower dentition, including when present, deciduous teeth.

Results

The mineralization stages of the teeth from *H. antecessor* and Sima de los Huesos hominins are displayed in Table 1. Specimen H11 of *H. antecessor* is the youngest individual of the TD6 sample, as it has their teeth in an earlier stage of development compared to H1 and H3. It is followed by the H3 hominin and lately by H1, which is the eldest hominin out of the three specimens. Both Sima de los Huesos hominins (specimens XVIII and XXV) have their incisors and first molars completely formed, whereas premolars and second and third molars are still under development. Among them, hominin XVIII is slightly younger than XXV, as their developing teeth are in an earlier mineralization stage compared to XXV. In fact, the canine's roots of the XVIII hominin were still forming when this specimen died.

The average and distribution of probabilities of these fossil specimens to have their dental mineralization sequences within modern human variation is shown in Table 2. The hominin H11 of *H. antecessor* has the highest probabilities, either incorporating or excluding deciduous teeth, to have their sequence within modern humans, with values above 0.95 (Fig. 2). The other TD6 hominins have lower probabilities than H11. In the case of H1, who

is represented by lower and upper dentitions, their probabilities when the M3 is excluded are between 0.73 and 0.83, respectively. However, when the M3 is incorporated in the analysis, the probability of the upper dentition decreases down to 0.60, whereas the probability of the lower dentition is barely altered. The probability of the upper dentition sequence of the H3 specimen when the M3 is excluded is encompassed within modern humans, with a value of 0.85. However, when the M3 is included, the probability is not found in modern humans, so that its probability is 0. Concerning Sima de los Huesos hominins XVIII and XXV (Fig. 3), their probabilities of the upper and lower dentitions when the M3 is included in the calculations are 0, meaning that neither modern human in our reference sample has that particular sequence of mineralization. Interestingly, when M3 is removed, their probabilities increase. In this case, depending on the reference sample, their probabilities of the lower dentition are above 0.80 using the Bordeaux sample, and below 0.25 using the Burgos reference sample. Upper dentition of the XVIII hominin has an average probability of 0.41

Discussion and conclusion

The Bayesian statistical approach has never been applied to fossil populations older than Neandertals. In this regard, we bring here two extinct hominin populations from the European Lower and Middle Pleistocene sites of Atapuerca (Spain) where this statistical procedure has been applied.

The mineralization sequences of hominin H1 of *H. antecessor* have high probabilities to be found in modern human variation. However the sequences of this hominin show that incisors, canines, premolars and M1s are at stage H (Table 1), indicating that we cannot evaluate whether differences exist or not between anterior and posterior teeth. So their high probabilities come from the relative development of the second and third molars, which are still forming. On the other hand, the mineralization sequence of the hominin H11 of the same population, which has the permanent dentition from the I1 to the M1, including the two deciduous molars, is very likely to be present within modern humans. However, as this specimen does not preserve the M2 and M3, the comparison between anterior-posterior dichotomy remains incomplete. Finally, H3 of *H. antecessor* does present anterior and posterior teeth that are still forming. In this case, the probabilities vary from 0 to 0.85 depending on the inclusion or exclusion of the M3, respectively. Overall, *H. antecessor* dental development follows modern human patterns when looking only at anterior or posterior teeth (when M1 is excluded). When both areas are compared, the M3 is advanced in its formation in respect with modern humans, and the relative development of the I1/M1 fits with modern human expectations, which confirm previous observations (16, 18).

Concerning the hominins from the Sima de los Huesos site, clear differences appear between the modern human sample employed and the presence of the M3 in the analyses. In all cases, when the M3 is included, the mineralization sequences are not present within the modern human sample, denoting that this tooth is advanced in its development in respect with our species, just in the same way as it occurs in *H. antecessor*. When the M3 is removed, the probabilities vary depending on the reference sample of modern humans.

Mandibular third molars are highly variable in their timing of maturation in modern humans (19). They have as well the highest frequency of polymorphism, malposition, impactation and agenesis (20–23). It has been proven that a statistical difference exists in the delay of M3 formation between children from London (White and Bangladeshi) and Cape Town (Cape Coloured) compared to Black South Africans (19). This delay also occurs when a French-Canadian population is compared to Black South Africans, not only in the third molar formation, but also in the second molar (24). The delay of molar formation in non-Black Africans compared to Black Africans might be the responsible of finding different probabilities in the Sima de los Huesos lower dentition to be their mineralization sequences included in modern human variation. On the one hand, the sample from University of Bordeaux includes Black Africans from the Ivory Coast, whereas the sample from University of Burgos does not include any Black Africans. As a result, the advanced lower molar developmental sequences of Sima de los Huesos might be present within the Black African children of the Bordeaux sample, consequently increasing their probabilities to be included in the modern human variation in respect with the Burgos sample.

Importantly, it is expected to have different probabilities for a single sequence to belong to modern humans. This is due to the extreme variability of the polymorphic *H. sapiens* species, which ultimately might bias the results depending on the population origin. For instance, tooth eruption ages in *H. sapiens* pygmies are advanced in respect with any other modern human population (25). However, their life history variables remain within the expected variation of modern humans (25), whereas some differences in their somatic growth have been documented (26).

The relationship I1/M1 cannot be assessed directly in Sima de los Huesos, as the two hominins have both teeth completely formed (stage H). However, the fact that their probabilities are not zero when the M3 is removed, in some cases having high probabilities depending on the reference sample, allow us to hypothesize that the relation I1/M1 was included in modern human and *H. antecessor* populations.

It has been observed in a sample of American whites that the formation of maxillary M3s was slightly advanced over their mandibular counterparts (27). However, this pattern is not shared neither in Sima de los Huesos hominins nor in *H. antecessor*. Hominin H1 of the Gran Dolina-TD6 site has both M3s at the same stage of mineralization (C), whereas the maxillary M3 of the hominin XVIII from Sima de los Huesos is delayed in its formation respect to the mandibular one (B and C, respectively).

Particularly interesting is the comparison between the lower dental mineralization sequences of the hominin H1 of *H. antecessor* and the hominin XXV of Sima de los Huesos. They both have stages H-G for the first and second molars, respectively (Table 1). Differences between these two hominins emerge when premolars and third molars are considered. Premolars in the hominin XXV from Sima de los Huesos are developmentally delayed compared to hominin H1 of *H. antecessor* (stages F-F and H-H, respectively). By contrast, the third molar is developmentally advanced in XXV with respect to H1 from TD6 (stages D and C, respectively). French-Canadian, Native American and Black African modern human samples do not display differences in their relative premolar calcification

(24), so differences observed in both Pleistocene hominins could be explained by a taxonomic signal.

As the Burgos sample was employed in the calculations of the probabilities in *H. antecessor* and hominins from Sima de los Huesos when the M3 is removed, the fact that the Lower Pleistocene population has more probabilities than the Middle Pleistocene one indicates that the M2 is advanced in its development in Sima de los Huesos in respect with the Gran Dolina-TD6 population. This evidence was previously postulated for the XVIII specimen (17), but has now been confirmed and expanded with the inclusion of the hominin XXV.

Second and third molars are basically the ones that make our specimens less likely to be included within modern human variation. In all cases, by removing M3s and some M2s the probabilities increase. The mineralization stages of our fossil M3s are expected to be found within the age ranges of our modern human samples, which ranges from 2 to 16 years. The wide age distribution of our modern human sample could not bias younger hominins to have more probability to be included in the modern human variation in respect with elder ones. On the contrary, these fossil individuals did have advanced molar development in respect with our species.

Following the Bayesian statistical approach, Neandertals display probability values that exclude them from belonging to modern humans, as shown in the Roc de Marsal (28) and the Cova del Gegant (7) specimens. In both cases, the probability is zero, which means that their mineralization sequences are not present in the modern human reference samples employed. The Lagar Velho 1 child, a potential hybrid specimen between Neandertals and anatomically modern humans, with an age of ~24.5 ka B.P. (29), presents a dental maturational pattern not represented in the modern human variation (9). Interestingly, the Neandertal specimen Spy VI, represented only by four deciduous teeth (lower i1, i2, c; and upper i1), shows a Bayesian probability above 0.75 to belong to modern humans (30). It is remarkable that the chronological relationships between anterior and posterior teeth were found to be responsible for differences in extinct hominins (4). This explains why Neandertals that preserves both types of teeth and the Lagar Velho specimen have a pattern of dental development not present in modern humans, whereas Spy VI, only represented by anterior dentition, has high probabilities. In contrast, La Madeleine Upper Paleolithic child (LM4), a fully anatomically modern human child with an age of $10,190 \pm 100$ years (31), shows comparatively higher probabilities of belonging to modern humans, (32). In particular, LM4 presents 30% of probabilities superior to 0.75 and 70% comprised between 0.25 and 0.75.

The Roc de Marsal child presents a stage of mineralization of the first molar relatively advanced in respect with the comparatively delayed maturational levels of their incisors (28). Bearing in mind that the relation I1/M1 in *H. antecessor*, and very likely in the Sima de los Huesos hominins, is within modern human variation, this asynchrony in the Neandertals I1/M1 could be interpreted as exclusive of *H. neanderthalensis*. Therefore, this feature might become key to differentiate Upper Pleistocene Neandertals from their ancestors of the European Middle Pleistocene.

Different methods have been developed to estimate chronological ages based on dental ages in modern humans (33–35). The accuracy of these methods in predicting chronological ages was lately tested using other modern humans samples (36–38). The accuracy varied with sex, age and origin (36, 37), although the most accurate and robust method was the one proposed by Demirjian et al. (1973) (36, 38). However, the pattern of dental development should not be employed to assess chronological age or age-at-death in extinct hominins. It is utterly imperative to incorporate the timing of dental tissue formation and therefore, to complement the information given by the pattern of dental development. For instance, the calcification stages of the I1/M1 in *Paranthropus* were seen as typical of modern humans, stating that this genus presented an elongated period of growth (39). However, their enamel formation times were shown to be closer to *Australopithecus* and other African apes, and distant from *H. sapiens* (1). This led to the interpretation of homoplasy of the I1/M1 calcification in later *Homo* and *Paranthropus*, rather than evidence of shared ancestry (40).

In a paper published by Modesto-Mata et al. in this same journal and issue, lateral enamel formation times of the whole dentition in both *H. antecessor* and Sima de los Huesos hominins were shown to be a ~27% shorter than modern humans. Despite the high probability of some dental mineralization sequences of *H. antecessor* and Sima de los Huesos to be within modern human variation, the fact the both populations display an advanced molar development and a more rapid enamel formation times, makes them to be clearly separated from *H. sapiens*.

These evidences shed some light on the growth processes in *H. antecessor* and Sima de los Huesos hominins. As a working hypothesis, our results agree with the fact that both Pleistocene populations had a shorter period of growth and an advanced ontogenetic development. However, more data is needed to firmly support or reject this hypothesis, as accurate estimations of times and rates of root formation, as well as estimating cuspal enamel formation times.

Summing up, both *H. antecessor* and Sima de los Huesos hominins have an advanced development of the M3 when they are compared with *H. sapiens*. However, Sima de los Huesos appears to have an advanced development of the M2 in respect with *H. antecessor* and modern humans. When anterior and posterior dentitions of *H. antecessor* are compared independently with modern humans, they present high probabilities to be found within their variation; however, when both anterior and posterior teeth are compared synchronously, their probabilities decreases, indicating some misalignment between the developing anterior and posterior dentitions with modern humans.

Material and methods

Material

Two hominins from Sima de los Huesos (XVIII and XXV) and three from *H. antecessor* (H1, H3 and H11) have been analyzed (Table S1 and Table S2, respectively). The hominin XVIII preserves the complete permanent dentition (32 teeth) and the four deciduous second

molars. The hominin XXV preserves the complete permanent lower dentition (18 teeth) and the two deciduous second molars. The teeth of the TD6 hominins, together with SH specimens and their mineralization stages can be seen in Table 1.

Modern human reference samples

The developmental sequences obtained for fossil individuals were compared to two samples of modern human children of both sexes and diverse geographic and temporal periods: one from the University of Burgos (Spain) and other from University of Bordeaux (France).

Training sample from University of Bordeaux is composed by 2387 children (1346 girls and 1041 boys) aged 2 to 16 years. Their geographic origin is Southern France, Iran and Ivory Coast (see (5) for further details). This reference sample is based on cross-sectional standardized panoramic radiographs of the teeth, and children selected were clinically free of anomalies in tooth number, size or shape. Only lower teeth were scored.

This sample from University of Burgos was drawn from three sources. The first subset was derived from the data included in the Electronic Encyclopedia on Maxillo-Facial, Dental and Skeletal Development CD-ROM (41). These data come from a longitudinal study of Montreal French-Canadian children conducted in the 1960s and 1970s. A subset of girls ($n = 40$) and boys ($n = 40$) aged from 6 to 10 years was selected. The second subset consists of cross-sectional standardized orthopantomographs of 516 Spanish children (254 females and 262 males) aged between 4 and 16 years. In order to cover a wide dental development variability, these two subsets were treated as a pooled sample. The last subset is a sample of 75 children from a Medieval archaeological population excavated from the Dominican Monastery of San Pablo (42) that are now housed at the Laboratory of Human Evolution at the University of Burgos. This sample was used to compare the development of fossil individuals with mixed dentition.

Bayesian statistical approach

The assessment of the degree of similarity or difference between dental developmental sequence in the *H. antecessor* / Sima de los Huesos hominins and that of modern humans was performed following a Bayesian statistical approach (5, 43), which provides a probability that the developmental pattern in a fossil individual could be found within a modern human population.

The underlying hypothesis is that any mineralization sequence represents a developmental module. This sequence is composed of its hierarchical units, which shows varying degrees of interaction. In consequence, teeth are considered as statistically dependent units in the Bayes's rule of conditional probability.

The interactions between teeth can be measured by decomposing the original mineralization sequence in two subsequences with no elements in common. We can construct so many combinations as number of teeth present in the sequence. Every combination has a Bayesian conditional probability, which ranges from 0 to 1. For instance, 254 different combinations can be traced with 8 teeth, 126 combinations with 7 teeth, 62

with 6 teeth, etc. Just to illustrate how any combination should be read, let's use I_1 if $I_2CP_3P_4M_1$ as an example. This combination is read as follows: the conditional probability of observing, in the training sample, the I_1 at its rating in the sequence to be tested when the other teeth, considered as a hierarchical unit, are observed at the ratings seen in the same sequence.

If the conditional probabilities are equal or higher to 0.75, the combination is considered to be likely present in modern humans. By contrast, if its value is equal or lower to 0.25, it is unlikely. Lastly, probabilities comprised between 0.25 and 0.75 can be considered as randomly distributed and therefore non-informative (5). A final mean probability for each specimen has been calculated as the average of all the conditional probabilities of their different combinations.

Scoring of the mineralization stages

To establish the developmental stages of permanent dentition of fossil and modern individuals were scored following the system developed by Demirjian et al. (33), while temporal dentition were scored based on the system established by Liversidge and Molleson (44). Tooth mineralization stages were assigned by three co-authors (RG-G, YQ, MM-M).

When establishing the mineralization stages of the TD6 hominin H11, which corresponds with the fossil ATD6-112 (16), a new undocumented tooth has been recorded. This new tooth in the TD6 fossil hypodigm is the lower right fourth premolar of the ATD6-112 mandible. This tooth is only represented by the initiation formation of the cuspal enamel of the buccal cusp (Fig. S1). Its mesiodistal diameter measures ~3.4 mm.

Tables and figures

| Site | Specimen | Position | I1 | I2 | C | P3 | P4 | M1 | M2 | M3 | dm1 | dm2 |
|------|----------|----------|----|----|---|----|----|----|----|----|-----|-----|
| TD6 | H1 | Lower | - | H | H | H | H | H | G | C | - | - |
| TD6 | H1 | Upper | - | - | H | H | - | H | G | C | - | - |
| TD6 | H3 | Upper | - | G | F | E | E | H | D | B | - | - |
| TD6 | H11 | Lower | D | D | C | B | A | E | - | - | H2 | H1 |
| SH | XVIII | Lower | H | H | F | E | E | H | E | C | - | brk |
| SH | XVIII | Upper | H | H | F | E | E | H | E | B | - | brk |
| SH | XXV | Lower | H | H | H | F | F | H | G | D | - | brk |

Table 1: Mineralization stages of *H. antecessor* (TD6) and Sima de los Huesos (SH) teeth following stages defined by Demirjian et al. (1973) for permanent dentition and Liversidge and Molleson (2004) for deciduous dentition. They were employed in the bayesian statistical approach to discern whether their sequences belong or not to SAP.

| Site | Hominin | Ref. | Pos. | M3 | dm | p(mean) | p(sd) | %p < .25 | .25 < %p < .75 | %p > .75 |
|------|---------|------|------|----|----|---------|-------|----------|----------------|----------|
|------|---------|------|------|----|----|---------|-------|----------|----------------|----------|

| | | | | | | | | | | |
|-----|-------|-----|---|-----|-----|-------|-------|---------|--------|--------|
| TD6 | H1 | UBU | L | Yes | - | 0.735 | 0.140 | 0.000 | 57.143 | 42.857 |
| TD6 | H1 | UBU | L | No | - | 0.730 | 0.242 | 6.452 | 24.194 | 69.355 |
| TD6 | H1 | UBU | U | No | - | 0.834 | 0.178 | 0.000 | 50.000 | 50.000 |
| TD6 | H1 | UBU | U | Yes | - | 0.596 | 0.108 | 0.000 | 90.000 | 10.000 |
| TD6 | H3 | UBU | U | Yes | - | 0.000 | 0.000 | 100.000 | 0.000 | 0.000 |
| TD6 | H3 | UBU | U | No | - | 0.854 | 0.122 | 0.000 | 17.742 | 82.258 |
| TD6 | H11 | UBU | L | - | No | 0.955 | 0.075 | 0.000 | 3.226 | 96.774 |
| TD6 | H11 | UBU | L | - | Yes | 0.962 | 0.064 | 0.000 | 3.150 | 96.850 |
| SH | XVIII | UBU | L | No | - | 0.248 | 0.255 | 63.492 | 30.159 | 6.349 |
| SH | XVIII | BOR | L | No | - | 0.843 | 0.183 | 1.587 | 21.429 | 76.984 |
| SH | XVIII | UBU | U | No | - | 0.419 | 0.369 | 48.413 | 25.397 | 26.190 |
| SH | XXV | UBU | L | No | - | 0.145 | 0.235 | 84.921 | 9.524 | 5.556 |
| SH | XXV | BOR | L | No | - | 0.829 | 0.200 | 3.175 | 26.190 | 70.635 |
| SH | XVIII | UBU | U | Yes | - | 0.000 | 0.000 | 100.000 | 0.000 | 0.000 |
| SH | XVIII | UBU | L | Yes | - | 0.000 | 0.000 | 100.000 | 0.000 | 0.000 |
| SH | XXV | UBU | L | Yes | - | 0.000 | 0.000 | 100.000 | 0.000 | 0.000 |

Table 2: Mean Bayesian probabilities of the Gran Dolina (TD6) specimens (H1, H3, H11) and Sima de los Huesos (SH) hominins (XVIII, XXV) to have their dental mineralization sequences within modern human variation. Mean probabilities [p(mean)] and standard deviations [p(sd)] are shown. Percentage of combinations displaying values of probability below 0.25 (%p < .25), above 0.75 (%p > 0.75) and between both values (0.25 < %p < .75). Two reference modern human samples (Ref.) are included: University of Bordeaux (BOR) and University of Burgos (UBU). M3 and dm represent the inclusion (Yes) or the exclusion (No) of the M3 and deciduous molars, respectively, in the calculations of the mean bayesian probabilities. Position is lower (L) and upper (U).



Fig. 1: Buccal views of the complete dentition of the Sima de los Huesos hominin XVIII. Top row: upper dentition; bottom row: lower dentition. dm2s are placed below the root of their respective P4s. Top left: upper right M3; bottom right: lower left M3. Scale bar = 1 cm.

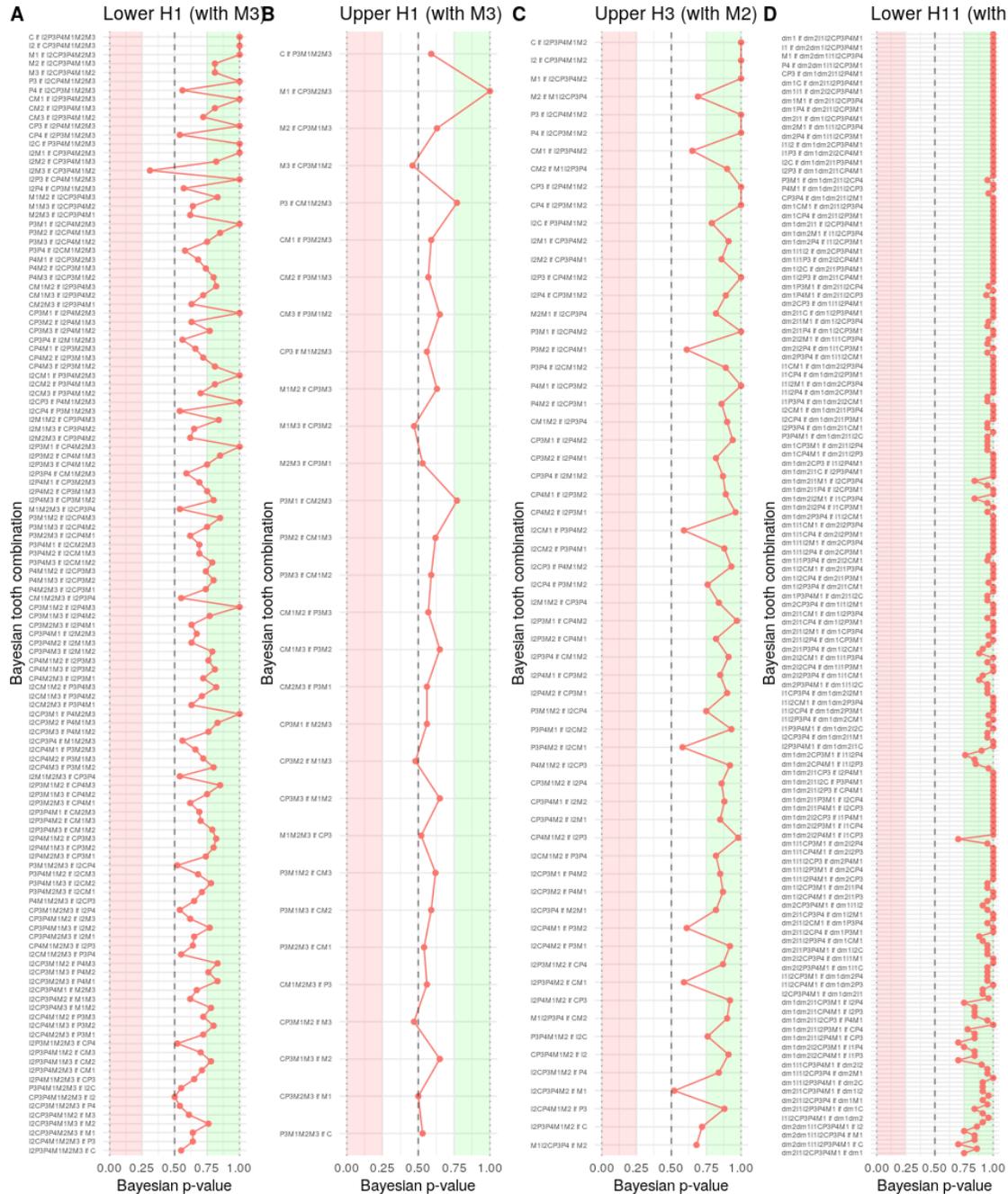


Fig. 2: Bayesian probabilities of the *H. antecessor* dental sequences to belong to modern humans. Three hominins are depicted: H1, H3, H11. A: lower dentition of H1; B: upper dentition of H1; C) upper dentition of H3. D) lower dentition of H11, where only odd combinations are shown. Shaded green bar: probabilities equal or higher to 0.75; shaded

red bar: probabilities equal or lower to 0.25. Red lines and dots: probabilities calculated by using the modern human reference sample from the University of Burgos.

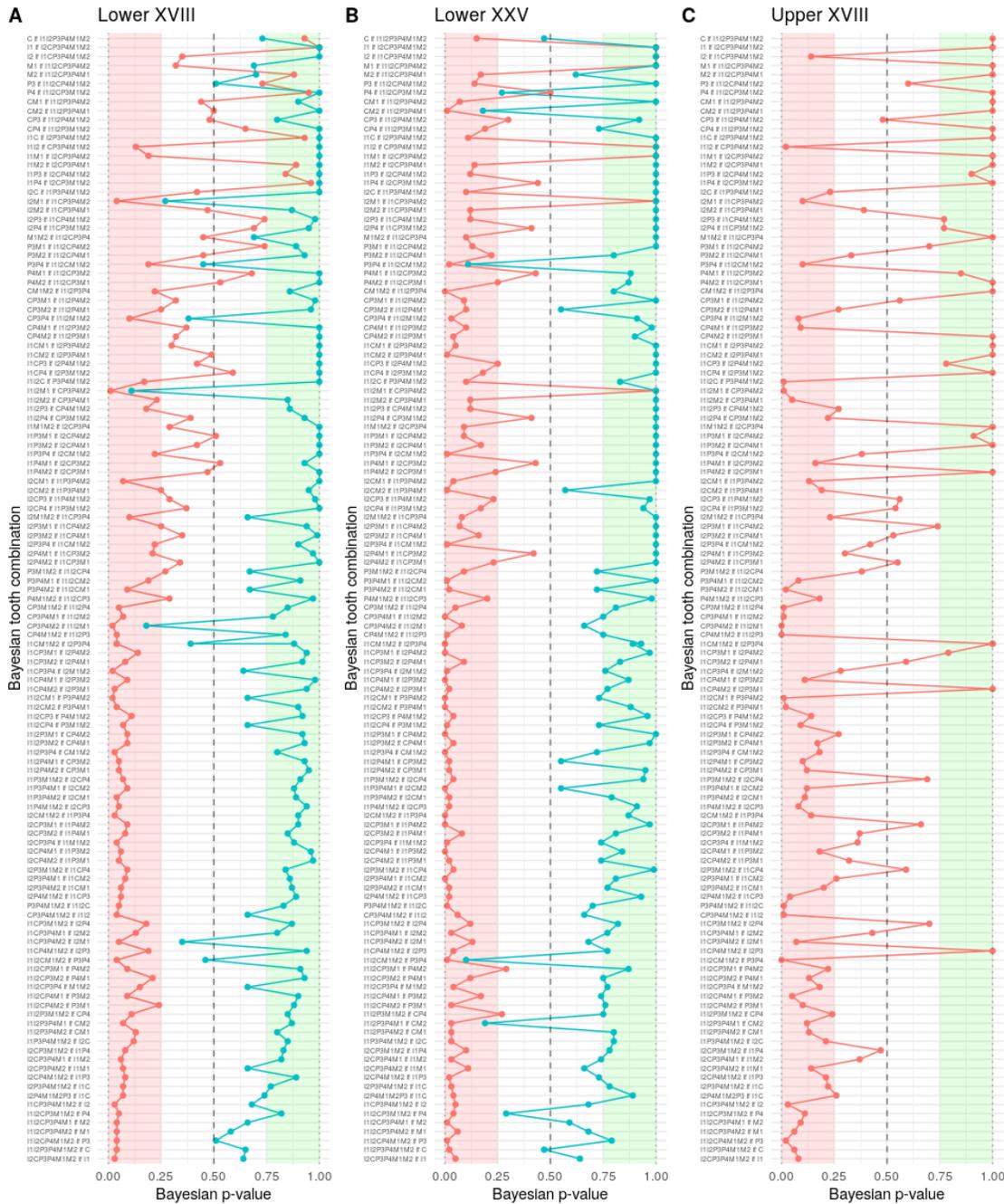


Fig. 3: Bayesian probabilities of the Sima de los Huesos (SH) dental sequences to belong to modern humans. Two hominins are represented: XVIII and XXV. In both hominins, M3 has not been included in the calculation of the Bayesian probabilities. A) lower dentition of hominin XVIII; B) lower dentition of hominin XXV; C) upper dentition of hominin XVIII. Shaded green bar: probabilities equal or higher to 0.75; shaded red bar: probabilities equal or lower to 0.25. Red lines and dots: probabilities calculated by using

Table S2: *Homo antecessor* (TD6) teeth employed in the calculations of the Bayesian probabilities of belonging to modern humans. Three hominins from TD6 have been analyzed: H1, H3 and H11. Position (U = upper; L = lower); side (L = left; R = right).

Supplementary figures

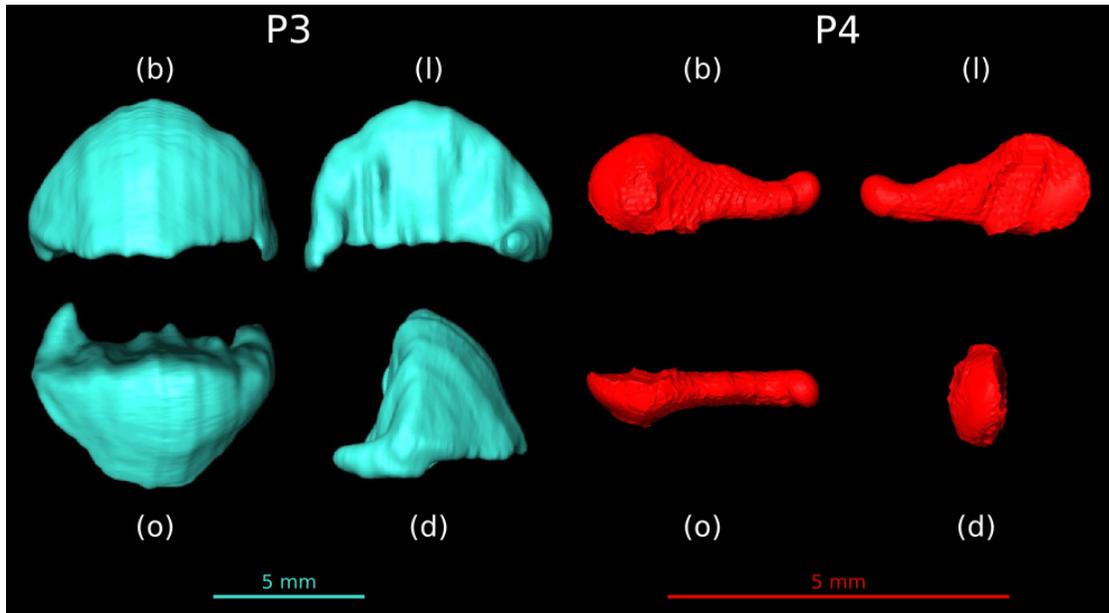


Fig. S1: Microcomputerized axial tomographies of the two right lower premolars of the hominin 11 *H. antecessor*. (b) buccal; (o) occlusal; (l) lingual; (d) distal. Two scales: 5 mm.

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