

Dental evidence on the hominin dispersals during the Pleistocene

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A common assumption in the evolutionary scenario of the first Eurasian hominin populations is that they all had an African origin. This assumption also seems to apply for the Early and Middle Pleistocene populations, whose presence in Europe has been largely explained by a discontinuous flow of African emigrant waves. Only recently, some voices have speculated about the possibility of Asia being a center of speciation. However, no hard evidence has been presented to support this hypothesis. We present evidence from the most complete and up-to-date analysis of the hominin permanent dentition from Africa and Eurasia. The results show important morphological differences between the hominins found in both continents during the Pleistocene, suggesting that their evolutionary courses were relatively independent. We propose that the genetic impact of Asia in the colonization of Europe during the Early and Middle Pleistocene was stronger than that of Africa.

Eurasia | teeth

The question about the origin and fate of Early and Middle Pleistocene hominins found in Eurasia remains unsolved. Overall, the fossil evidence has been interpreted as supportive of an “out of Africa” origin, and early Asian hominins have been often interpreted as evolutionary “dead ends” (1–4). In this context, it has been commonly suggested that the origin of Middle Pleistocene populations of Europe lay in the arrival of African emigrants who evolved in Europe toward the Neanderthal lineage (4–8). If this hypothesis is correct, and Africa is the main cradle of the Eurasian populations, then we should expect to find an African influence or a discontinuity in the morphological pattern of the European Pleistocene populations. To test this hypothesis, we analyzed the crown morphology of >5,000 permanent teeth assigned to a number of hominin species from the genus *Australopithecus* and *Homo* (Table 1), which covers the majority of the hominin fossil record available from the late Pliocene and Pleistocene [Table 1 and supporting information (SI) Text]. Because of their high component of genetic expression, teeth are considered the “safe box” of the genetic code, so with teeth more than with any other skeletal part, the phenetic proximity/distance can be read as genetic proximity/distance (9–12). The present study represents the most complete study of the hominin fossil dental record to our knowledge at present, including both a phenetic and a cladistic approach.

Results

As can be seen in Fig. 1, the dendrogram obtained by phenetic analysis consists of three main branches. One of them identifies the similarities among the species found in the Eurasian continent, clustering *Homo erectus* (ERE) with *Homo heidelbergensis* (HEI), *Homo neanderthalensis* (NEA), and the Sima de los Huesos (SH) hominins. SH and NEA show the highest similarities (rescaled distance <1). A second branch groups the African species, *Homo habilis* (HAB) being the closest group to the

species of the genus *Australopithecus*: *Australopithecus afarensis* (AFA) and *Australopithecus africanus* (AFR). In a third branch can be found the species *Homo sapiens* (SAP), relatively equidistant between the two broader groupings.

From the cladistic analysis carried out in this study, two cladograms were obtained with the only difference that one of them shows no resolution for the relationship between HEI, SH hominins, NEA, and SAP. Fig. 2 shows the cladogram that resolves this relationship and thus, the most informative of them (consistency index = 0.76; retention index = 0.88). AFA, AFR, and HAB are excluded from a large clade that groups the remaining hominin species. *Homo georgicus* (GEO) is the sister group of a large clade that contains all of the later *Homo* species. In this clade, a bifurcation is produced: one branch clusters *Homo ergaster* (ERG) and the hominins found in the Middle Pleistocene of North Africa (MPA), whereas in the other we can find ERE as the closest sister group of the fossils found in the Eurasian continent during the Pleistocene. *Homo antecessor* (ANT) is the closest group to the Middle and Upper Pleistocene species. HEI, NEA, and SH hominins form a sister clade of SAP.

Both the phenetic and cladistic analyses provide consistent results, with the only differences regarding the position of SAP. With both analyses, dental evidence allows us to define two main groups: in one, we can find the Eurasian fossil hominins (ERE, ANT, HEI, and NEA), and in the other, we have the fossils that have been found in Africa (AFA, AFR, HAB, ERG, and MPA) with SAP and GEO having a particular position with respect to the two broader groups that will be explored below. A consideration of dental morphological variability emphasizes that anterior and posterior dentitions have followed different ontogenetic trajectories. The anterior dentitions of the hominin groups found in the Eurasian continent are generally characterized by their “morphological robusticity” with high frequencies of “mass additive traits” (term from Irish; ref. 10), such as shovel shape, cingular derivatives, mesial canine ridge, and strong labial convexity. Although these traits are not exclusive to these groups, the high frequencies of their most pronounced grades are typical of HEI and NEA and can be traced back to ERE (13–15) and ANT populations, which also show incipient degrees

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Abbreviations: ERE, *Homo erectus*; HEI, *Homo heidelbergensis*; NEA, *Homo neanderthalensis*; SH, Sima de los Huesos; HAB, *Homo habilis*; AFA, *Australopithecus afarensis*; AFR, *Australopithecus africanus*; SAP, *Homo sapiens*; GEO, *Homo georgicus*; ERG, *Homo ergaster*; MPA, Middle Pleistocene of North Africa; ANT, *Homo antecessor*; ASUDAS, Arizona State University Dental Anthropology System.

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Table 1. Populations studied and sample size (only one antimer per individual)

Group	N	Site
AFA	163	Laetoli, Hadar, Fejej, Maka
AFR	83	Sterkfontein, Makapansgat, Gladysvale
HAB	50	Olduvai Gorge, Koobi Fora
GEO	24	Dmanisi*
ERG	36	Olduvai Gorge, Koobi Fora
MPA	31	Rabat, Tighenif*
ERE	130	Sangiran Dome*, Trinil*, Zhoukoudian
ANT	25	Atapuerca-Gran Dolina (TD6)*
HEI†	53	Mauer*, Arago*, Mountmarin*, Pontnewydd, Steinheim
SH‡	323	Atapuerca-SH*
NEA	391	Saccopastore*, Monte Circeo*, Le Moustier, Saint Cesaire, Cabezo Gordo, Zafarraya, l'Hortus*, Krapina, Sidrón, Kebara, Tabun, Vindija, Kulna 1, Pinilla del Valle*, Engis II, La Quina*, Shanidar, Gibraltar (Devil's Tower), Petit-Puymoyen, Fondo Cattie
SAP	1,684	San Nicolás*, Brassempouy, Wad, Almonda, Mladec, Abri Pataud Trou Magritte, Dolni Vestonice*, Pavlov*, Caldeirao, Skhul, Predmostí

See *SI Text* for a detailed list.

*Original fossils. The rest of the examined material belong to the cast collections held at American Museum of Natural History of New York and the Teeth High Resolution Casts Collection of the Universitat de Barcelona.

†Although some authors assign to HEI the European and African Middle Pleistocene hominins (such as those from Bodo and Kabwe), we have used this denomination to refer exclusively to the European fossils.

‡Because this article focuses on the understanding of the evolutionary scenario of the European Pleistocene populations, we have preferred to analyze the fossils from the Atapuerca-SH site, which represent >90% of the hominin fossil record worldwide for the Middle Pleistocene, separately from the rest of the European Middle Pleistocene specimens, to precisely assess their position in the evolutionary tree.

of triangular shovel shape (14, 15) (Fig. 2 and *SI Fig. 4*). This morphological pattern could be related to the tendency for the relative expansion of the anterior dentition observed in the Middle Pleistocene populations (16). In the posterior dentition, Eurasian fossils display qualitative traits derived from dental reduction: loss of cusps in upper and lower molars, increasing frequencies of groove-patterns different from the “*Dryopithecus*” pattern, and simplification of the occlusal surfaces. The morphological pattern of the posterior dentition in the Eurasian “complex” could be related to the tendency of Middle Pleistocene populations to reduce their posterior dentition (16, 17), a trajectory that could be traced back to the ERE populations, where some dentognathic reduction processes, although less pronounced than in later *Homo* populations, have been described (18). The Dmanisi hominins (GEO), despite the fact that they have been found outside of Africa, are morphologically closer to the Pliocene and Pleistocene African specimens than to the Eurasian fossils. However, despite their primitive dentition (*SI Fig. 5*), the molar series display a decreasing size sequence (M1 > M2 > M3) and certain talonid reduction in their lower fourth premolars and relatively small bucco-lingual dimensions in their lower incisors when compared with African specimens (e.g., OH7, OH13, or OH16) (19) that could be pointing to the root of the reduction processes ascertained in the Eurasian groups. In addition, the posterior dentitions of Eurasians groups

include a typical combination (although not for all specimens) of a deep anterior fovea with continuous midtrigonid crest, and transverse crest in the lower premolars typical of NEA and HEI (14, 20), but also ascertained in ANT and ERE in variable percentages (14, 15, 18). In addition, the particular morphology of the upper first molar (14, 21) and lower fourth premolar (20) in ANT, HEI, SH, and NEA emphasizes the links between the Early and Middle Pleistocene populations in Europe (*SI Fig. 6*).

The anterior dentitions of the hominins found in Africa tend to show shovel shape in lower degrees of expression with an absence of pronounced labial convexity. In their posterior dentition we find that the transverse crest is commonly absent in lower fourth premolars, and in lower molars the continuous midtrigonid crest is absent and there are only low frequencies of deep molar anterior fovea (14). In these features, SAP would overlap with the African fossils. The fossils of the Africa continent are also characterized by high frequencies of accessory cusps in molars and premolars (10, 11, 22, 23). The particular “intermediate” position of SAP in the phenetic tree may be because of its combination of primitive and derived traits,

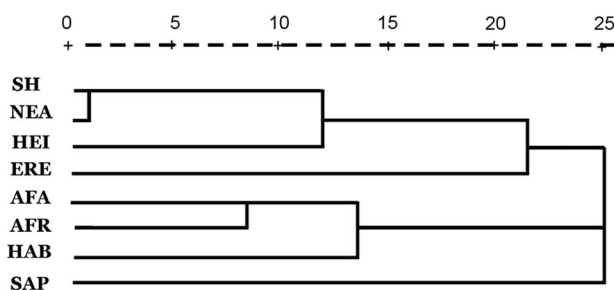


Fig. 1. Dendrogram obtained from phenetic analysis of the dental evidence.

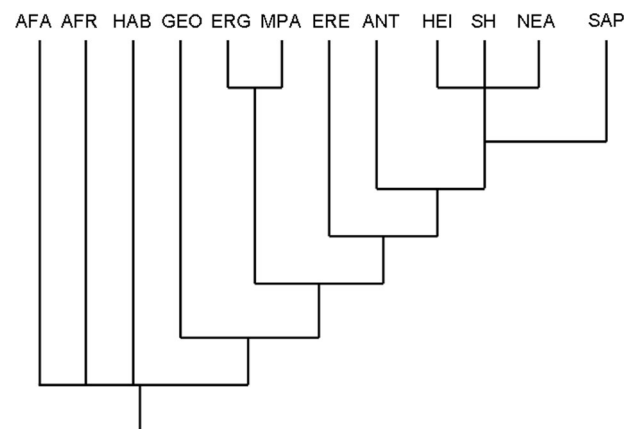


Fig. 2. Cladogram obtained from analysis of the dental evidence.

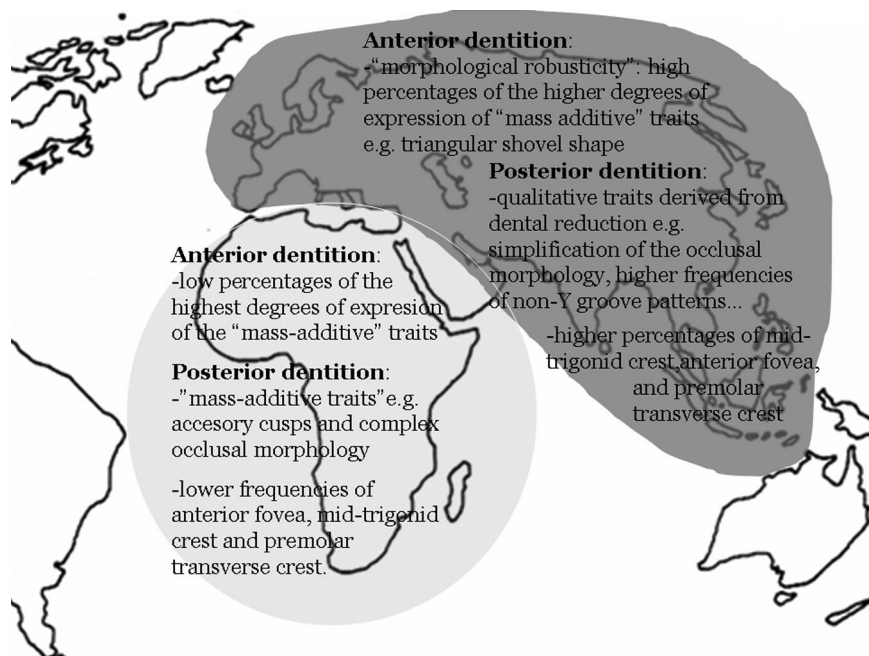


Fig. 3. Schematic diagram illustrating the general characteristics of the hominins found in the Eurasian continent from the Early Pleistocene until the appearance of the Neandertals (light gray shading) and in the African continent from the Plio-Pleistocene to the Middle Pleistocene (dark gray shading).

because the phenetic analysis gives the same weight to all of the recorded traits regardless of their polarity. SAP appears to be a very heterogeneous and derived species with the development of three autapomorphies (SI Text, SI Table 2, and SI Fig. 7). It is interesting to highlight that many of the dental traits characterizing the Eurasian group would be primitive with respect to SAP (14, 24), although this species would have in common with the Eurasian complex the morphological traits derived from the posterior teeth reduction (Fig. 3). The cladistic approach emphasizes the evolutionary weight of these features so SAP is closer to the Eurasian fossils than to the African fossils.

Discussion

If the population of the Eurasian continent during the Early and Middle Pleistocene was mainly the result of several out-of-Africa incursions, we should have found African influences in the morphology of the Eurasian populations. However, the continuity of the “Eurasian dental pattern” from the Early Pleistocene until the appearance of the Upper Pleistocene Neandertals suggests that the evolutionary courses of the Eurasian and the African continents were relatively independent for a long period and that the impact of Asia in the colonization of Europe was stronger than that of Africa. This finding does not necessarily imply that there was not genetic flow between continents, but emphasizes that this interchange could have been both ways (25, 26). Around 1 Ma, hominins appear to have dispersed into temperate latitudes as far north as 40–45° N (27–29), not only from Africa, but also within Eurasia (29–31). These populations were probably descendants of an ancient out-of-Africa exodus, rather than a later one at the end of the Early Pleistocene (30). In addition, a recent study on the European Lower Pleistocene hominin populations has revealed a possible Eurasian origin for these groups (32). Furthermore, it has been pointed out that during the Middle Pleistocene there was hardly any faunal exchange between East Africa and the Levant (33) and that the desert between the Sahara and Arabia was an important barrier at that time (26), therefore contributing to the isolation of both continents. With the exception of the SAP out-of-Africa dispersion based mainly on genetic data (2), the history of human

populations in Eurasia may not have been the result of a few high-impact replacement waves of dispersals from Africa, but a much more complex puzzle of dispersals and contacts among populations within and outside continents. In the light of these results, we propose that Asia has played an important role in the colonization of Europe, and that future studies on this issue are obliged to pay serious attention to the “unknown” continent.

Materials and Methods

A detailed list of the included material can be found in SI Text. Although both antimeres (when present) were analyzed, we have followed the unilateral count method, including the antimeres with the highest degree of expression for each trait in case of asymmetry (9). For the phenetic analysis, 51 dental traits were recorded, resulting in 142 categories of expression (SI Table 3). These traits cover the dental variability of the anterior vs. posterior dentitions and the maxillary vs. mandibular dentitions in a balanced way. This is important for a complete appreciation of the whole dentition and an assessment of possible different trajectories for the anterior and posterior dentitions variation. To calculate the similarity between groups we used the relative frequency for each category of expression of each morphological trait and performed a hierarchical cluster analysis based on the χ^2 distance (SPSS 12.0). Hierarchical clusters identify relatively homogenous groups based on selected characteristics by using an algorithm that starts with each variable in a separate cluster and combines clusters until only one is left. This clustering is based on a criterion of phenetic distance. χ^2 distances are considered an appropriate measure of dissimilarity for frequency-count data. The proximity matrix of the χ^2 distances obtained between each pair of hominin groups is shown in SI Table 4. Smaller values for this distance means that the groups are similar, so the distance of one group with itself would be zero. Finally, a dendrogram with the average linkage between groups algorithm was obtained. The average linkage algorithm is considered the one with the lowest chaining effect, that is, the tendency to form small clusters with many nonlinked elements (groups formed by only one element), so we consider it as the most appropriate and high-resolution method to apply (34). The small number of

elements (N) of some tooth classes for the GEO, ERG, and ANT groups prevent their inclusion in this analysis, but their phylogenetic position was later assessed through the cladistic analysis. Unless specified in [SI Table 5](#), the definition and degrees of expression of the morphological traits can be found in the Arizona State University Dental Anthropology System (ASUDAS) classification (9). The ASUDAS was developed to cover dental variability in modern populations, but it fails to cover the full variability of the genus *Homo* when Pleistocene fossils are included. This system does not include some features that are important for characterizing some groups (e.g., the symmetrical contour of lower third premolars in SAP), neither does it cover the full observed range of expression of the analyzed traits (e.g., the maximum labial convexity of incisors registered in the ASUDAS plaques is below the labial convexity degree usually observed in Neanderthals) (14) (see [SI Text](#)).

Contrary to phenetics, not all of the morphological traits in cladistics have the same weight, and thus, we have carried out a rigorous preselection excluding those traits that are highly homoplastic and/or variable within populations. The features we recorded are not included in the ASUDAS classification but they are important in characterizing some groups and therefore, potentially useful for assessing their phylogenetic relationships (ref. 15 and [SI Text](#)). As a result, we have obtained a list of nine dental traits: shovel shape in upper lateral incisors, upper canines shape, lower canines shape, cingulum expression in lower canines and premolars, midtrigonid crest in M1 and/or M2, the absence of C5 in M1 and/or M2, upper first molar shape, lower third premolar shape, and lower fourth premolar shape. Again, there is a balance between the anterior and posterior dentition traits and between maxillary and mandibular dentition traits. The definition, polarity, character states, and distribution in the fossil record can be found in [SI Text](#). We generated a cladogram through the branch and bound method. The cla-

dogram is a tree-like diagram that shows evolutionary relationships among the groups, so any two branch tips sharing the same immediate node are most closely related. The branch and bound method is an algorithmic technique that finds the optimal solution by keeping the best solution found so far. If a partial solution cannot improve on the best, it is abandoned. We have used the *Australopithecus* outgroup and followed parsimony and the specifications of the type of trait (ordered/nonordered) (MacClade/PAUP 4.0) (see [SI Text](#)).

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