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Phylogeny of *Homo* and its Implications for the Taxonomy of the Genus

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ABSTRACT

The genus *Homo* has a moderately high degree of morphological diversity, with about fifteen species proposed. It is debatable whether there could have been several species of *Homo* coexisting and sharing similar ecological niches, especially during the Chibanian (Middle Pleistocene). A thorough systematic evaluation of these 'species' is needed, and a reliable phylogeny with high taxon coverage is critical to such an endeavor. Here we evaluate the potential taxonomic assignments of several *Homo* fossils using a phylogenetic framework based on a large morphological data matrix. The phylogenetic analyses suggest that human evolution was not a gradual process and was not obscured by recurrent gene flow. Several species or clades coexisted. There are at least three distinct and temporally deep clades in later human evolution, and these three clades are all monophyletic groups and can potentially be considered valid species. The African and Asian *Homo erectus*/*Homo ergaster* populations form a paraphyletic group, with Dmanisi not belonging to the other Eurasian *H. erectus* populations. It may be possible to identify these African, Asian, and Dmanisi populations as three distinct species. The Chibanian African and European non-sapiens and non-Neanderthal hominins are a paraphyletic group, representing transitional forms of varying degrees. Although there are many taxonomic names for these hominins, a thorough revision of these names is needed.

Introduction

At the most fundamental level, species is the most basic rank of classification and unit in taxonomy. Unfortunately, because of the complexity of the natural world, "species" has never actually had a generally accepted definition, and moreover the concept of species is constantly changing

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(Mallet et al. 2022). Darwin, for instance, mentioned "species" more than a thousand times in his Origin of Species, but he never provided a clear definition (Darwin 1859). In traditional Darwinism, a species has no clear boundaries and is a systematic borderline case, in which the boundaries between a species, a subspecies, a race, or some other classification unit cannot be clearly and precisely defined. As Dobzhansky once pointed out "… it is impossible to decide whether one is dealing with species or with races" (Dobzhansky 1944: 251). In the Modern Synthesis, a species is defined in sexually reproducing organisms as a group of populations that are reproductively isolated to the extent that the exchange of genes between different species is absent or so slow that genetic differences are not reduced or obscured (Dobzhansky 1937, 1944). This species concept was later popularized as the "Biological Species Concept" (Mayr 1970). Several problems exist with the Biological Species Concept: 1) it is inapplicable to asexual organisms; 2) it ignores the widespread phenomenon of interspecific hybridization; and 3) it does not work well with extinct organisms. Templeton (1989) proposed the Cohesion Species Concept where species is the most inclusive group of all individuals that have the potential for genetic and/or demographic exchangeability. The Cohesion Species Concept extends the Biological Species Concept by including asexual organisms and downplaying the importance of interbreeding in sexually reproducing organisms. According to the Cohesion Species Concept, a species is a population or series of populations that have phenotypic cohesion with genetic or demographic exchangeability. In fact, alternative contemporary species concepts have been proposed based on different properties such as mate recognition, ecological niche, or adaptive zone, unique evolutionary fate, phylogeny, phenetic cluster, and diagnosability. These are just a few examples of the currently more than 25 different species concepts that have been proposed (for example, see De Queiroz 2007; Mallet et al. 2022; Mayden 1997).

For traditional paleontologists and taxonomists, the Biological Species Concept is almost always inapplicable, where morphological differences become of central importance (Bae 2024). This is commonly defined as the Phenetic Species Concept (classification or grouping based completely on overall morphological similarity [De Queiroz 2007; Mallet et al. 2022]). An operational species is usually defined based on detectable or diagnostic morphological gaps between the organisms from certain geographic areas and geological time periods (Simpson 1937, 1945). Quantitative differences in phenetic clusters and qualitative differences in diagnosability are the main basis for species delimitation in the Phenetic Species Concept. Although the Phenetic Species Concept and the practice of phenetic classification were rejected by cladists and those who believed that classifications should be based on phylogeny, paleontologists and traditional taxonomists usually use multiple morphological and genetic characteristics to sort individual specimens into discrete groups, between which there are as few intermediate forms as possible (Mallet et al. 2022). This practice is closely similar to the classification of the Phenetic Species Concept.

For paleoanthropologists, the concepts of species and speciation remain essential for understanding human evolutionary diversification and the origins of novelties within a generalized taxonomic framework that reflects the development of phylogenetic relationships (Harrison 1993; Kimbel and Martin 1993; Kimbel and Rak 1993). In the genomic era, it has been concluded that specific nomenclature should be applied in human paleogenomic publications from an integrative perspective on different species conceptions and delimitation criteria, maintaining congruence with zoological literature. This is evident in the study of the species delimitation of *H. sapiens* and *H. neanderthalensis* (Meneganzin and Bernardi 2023). Recently, Harvati and Reyes-Centeno (2022) reviewed the historical development of the species concept and related theories. They proposed that a major shift in the conceptual and theoretical frameworks of systematics and phylogenetics is critical to understanding the complex and bewildering picture of human evolution during the Middle to Late Pleistocene.

It is now generally accepted that the divergence of the human clade from the chimpanzee clade occurred about 6–8 Ma before present, commonly referred to as the human-ape divergence. Following the appearance of *Sahelanthropus, Orrorin*, and *Ardipithecus*, which are usually regarded as basal hominins, the human clade displays a high degree of diversity. Despite the high diversity, all species of the human clade show evidence of habitual upright walking, which was once considered the key feature defining *Homo* (Mayr 1950). Theodosius Dobzhansky and Franz Weidenreich, two of the proponents of the modern theory of synthetic evolution, once even proposed that hominin evolution took place within a single species, and that it was a divergence of races within this single human species (Dobzhansky 1944; Weidenreich 1943). Although the view that all fossil hominins belong to one species is no longer accepted by most scientists, there are still many different views on how to define the genus *Homo* and the species within the genus (e.g. see Bräuer 2008; Schwartz and Tattersall 2015; Wood and Collard 1999a, b; Zanolli et al. 2022).

Within the widely accepted definition of *Homo*, although the genus exhibits only a moderately high degree of morphological diversity (Antón 2012; Conroy and Pontzer 2012; Harcourt-Smith 2016; Leakey et al. 1964; Prat 2022; Schwartz and Tattersall 2015; Wolpoff 1999; Wood and K. Boyle 2016), there in fact are some fifteen or so species of *Homo* that have been proposed. Commonly seen and widely cited *Homo* species include *Homo habilis*, *Homo erectus*, *Homo ergaster*, *Homo heidelbergensis*, *Homo neanderthalensis*, and *H. sapiens*. In recent years, a few more species have been added to the list: *Homo antecessor*, *Homo floresiensis*, *Homo luzonensis*, *Homo naledi*, *Homo longi*, and *Homo bodoensis* (Reed 2025). Most recently, Bae and Wu (Bae 2024; Bae and Wu 2024) proposed naming Xujiayao and Xuchang *Homo juluensis* informally called Juluren (big-headed man). Although there is still disagreement about the taxonomy of a number of these species, researchers generally agree that several *Homo* species coexisted, particularly during the

Middle Pleistocene (or Chibanian, 770–126 ka) (Bae et al. 2024). For instance, in Africa, fossils from Jebel Irhoud, Morocco, with an age of ~315±34 ka (Hublin et al. 2017) have been proposed to represent the oldest known *H. sapiens*. This late Middle Pleistocene age would mean that early *H. sapiens* were contemporary with *H. naledi*, *H. bodoensis* in Africa (or *H. heidelbergensis* as traditionally used [Stringer 1983] and now more widely used [see Delson and Stringer 2022; Roksandic et al. 2022a, b; Sarmiento and Pickford 2022 for recent discussion]). In western Eurasia, early *H. neanderthalensis* probably coexisted with *H. heidelbergensis* (or *H. bodoensis* as it was suggested recently Roksandic et al. [2022a, b], but see Delson and Stringer [2022]; Sarmiento and Pickford [2022]) and later on in the Pleistocene, with later arriving sapiens.

In eastern Asia, Middle Pleistocene *Homo* is even more diverse. *H. erectus sensu lato* seemingly survived much longer in eastern Asia than in Africa (Rizal et al. 2020; Swisher et al. 1996). As such, *H. erectus* probably overlapped temporally with other hominins in the region. Further, a plethora of late Middle Pleistocene hominins that cannot be easily assigned to *H. erectus* or *H. sapiens* often remain known simply as "mid-Pleistocene *Homo*," "Middle Pleistocene *Homo*," or "archaic *Homo sapiens*"—but these terms are nothing more than waste bin names that carry little-to-no meaning (Bae 2010; Bae et al. 2023; Pope 1992; Wu and Poirier 1995). According to the ICZN (International Commission on Zoological Nomenclature 1999), these names are not taxonomic units and are not clearly defined. No diagnosis or generally accepted characters have ever been used to formalize these grouping names. In Asia, the hominins in concern include Narmada (Hathnora), Dali, Jinniushan, Hualongdong, Xiahe, Penghu, Xujiayao, Maba, Xuchang, Harbinn, and Denisova (Liu et al. 2022). The taxonomy of these Asian Middle Pleistocene hominins remains much debated (Bae 2024; Bae and Wu 2024; Bae et al. 2023; Delson and Stringer 2022; Ni et al. 2021; Roksandic et al. 2022b). In recent years, many paleoanthropologists have either lumped most of these latter fossils into the waste bin of "archaic *Homo sapiens*" (Bräuer 2008) or have suggested that they could be assigned to an all-inclusive *H. heidelbergensis* or something else altogether (Bae and Wu 2024; Bae et al. 2023; Mounier and Caparros 2015; Roksandic et al. 2018; Stringer 2012).

In the case of hominin taxonomy, individual fossil specimens usually show large inter-individual differences, but display ambiguous trends of continuous variation across multiple individuals. When relying strictly on the hominin fossil evidence, it has always been difficult to establish criteria for identifying species of *Homo* (Schwartz and Tattersall 2015; Wood and Collard 1999a, b; Wood and Lonergan 2008). For instance, Wood and Collard (1999a, b) proposed that a group should be defined as a species or monophyletic group whose members occupy a single adaptive zone. They emphasized the importance of the adaptive zone, but argued that the adaptive zone need not be unique nor distinct. Their definition of a species and/or genus obviously assumes a concept of species-as-individuals—species have stable but not essential properties (Brogaard 2004; Ghiselin 1987). In a later review, Wood and Lonergan (2008) presented a summary of Plio-Pleistocene hominin taxa that were organized into evolutionary grades. They did note, however, that in practice, most researchers in hominin taxonomy typically use a phylogenetic or Phenetic Species Concept to define a species, hypothesizing this was the smallest group of individual organisms that can be diagnosed based on shared morphology as preserved in the fossil record (Wood and Lonergan 2008).

Regardless of the species concept used in hominin taxonomic research, modern researchers generally agree that a reliable phylogeny representing the evolutionary relationships among hominin species is always important. Although phylogenetic models have been proposed frequently, actual phylogenetic analyses based on large phenetic data matrices are rare in paleoanthropology. Earlier, we presented a phylogeny of *Homo* at the population level in our report on *Homo longi* (Ni et al. 2021). The phylogenetic tree included 55 OTUs (operational taxonomic units), representing most of the major species or populations that are widely cited in paleoanthropology. The phylogenetic analyses and some conclusions derived from the analyses have been summarized in Ni et al. (2021), but the technical details of the analyses were presented in the supplementary file to that paper (Ni et al. 2021). Further, the potential impact of phylogeny on the taxonomic assignment of *Homo* was not discussed. In order to present the phylogeny of *Homo* more clearly, here we have reorganized the methods and results of our earlier phylogenetic analyses and discuss the correlation between phylogeny and potential taxonomic grouping. We emphasize that a reliable phylogenetic framework is important to understand the natural classification and identification of how many species are actually present within the genus *Homo*.

MATERIALS AND METHODS

MATERIALS

We observed 95 cranial, mandibular, and dental specimens of the genus *Homo* (Supplementary Information [SI] Table 1) in this study. Specimens from the same locality, with similar date range and morphology and that are generally accepted as the same species/population were grouped into one operational taxonomic unit (OTU). Each OTU represents a population or a paleodeme (Gilbert et al. 2003; Howell 1999). After merging, 55 OTUs were used as terminal taxa for phylogenetic and biogeographic analyses. The OTUs cover all major clades or forms of the genus *Homo*, including *H. habilis*, *H. erectus*/*H. ergaster*, *H. heidelbergensis*, *H. bodoensis*, *H. neanderthalensis*, *H. longi* and *H. sapiens* (SI Table 1). Given that *H. juluensis* was only recently proposed (Bae 2024; Bae and Wu 2024), it was not considered a separate OTU in this analysis. For each terminal taxon/specimen, we use the most recently published dating results. For the combined OTUs, the dates for all specimens were used as the age range. The two crania from Yunxian, China, were not included from this study because a reliable

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reconstruction is needed for further phylogenetic analyses. Although one of the two Yunxian crania (Yunxian II) was reconstructed from CT scan data (Vialet et al. 2010), the results still show obvious deformation and cracking. A third hominin cranium was reported from Yunxian recently but has yet to be formally published. *Homo floresiensis* (Brown et al. 2004), *Homo luzonensis* (Détroit et al. 2019), and *H. naledi* were not included in the current analyses. These three species show distinctive combinations of strongly plesiomorphic and apomorphic features (Argue et al. 2017; Détroit et al. 2019; Jungers et al. 2009a; b; Kaifu et al. 2015a; b; Larson et al. 2009). These fossils will be the subject of future phylogenetic analyses.

METHODS: BUILDING DATA MATRICES FOR PHYLOGENETIC ANALYSES

We constructed a phenomic data matrix containing 234 discrete characters and 400 continuous characters scored for 95 cranial, mandibular, and dental specimens of the genus *Homo* (SI Table 1) using MorphoBank (O'Leary and Kaufman 2011). Character state scoring and metric measurements were performed at the specimen level. Most of the discrete characters are widely used and discussed in paleoanthropological research (e.g., Arsuaga et al. 2014; Lordkipanidze et al. 2013; Martínez and Arsuaga 1997; Rightmire 1996; Rightmire et al. 2006; Schwartz and Tattersall 1996a, b, 2000). We have revised the character definitions by providing illustrations in MorphoBank for most characters except those that are clearly or unambiguously defined. The continuous characters include 184 linear measurements, 22 angles, and 194 ratios. The linear and angular measurements were made according to the standards defined by Martin and Saller (1956) and Howells (1973). The ratios are derived from the linear measurements. It has long been recognized that dental characters are not simply discrete. Most of the gross morphology of hominin dentition shows extensive variation. The wide range of variation should be evaluated on a ranked scale. We have therefore ranked the morphological features of the permanent upper and lower dentitions of the *Homo* specimens using the Arizona State University Dental Anthropology System (Turner et al. 1991). This ranking system is widely accepted as a standard (Edgar 2017; Scott and Irish 2017) for studying dental variation in anthropology and has been used to infer hominin phylogenetic relationships (Irish et al. 2013). Discrete character definitions, standard linear and angular measurements, and original scores and measurements are stored in MorphoBank (MorphoBank Project 3385), a publicly available web application and database widely used for large-scale online morphological character standardization and data collection (O'Leary and Kaufman 2011). To date, a total of 1379 media, 9618 labels, and 22042 cell scores have been entered into MorphoBank Project 3385. The final data matrix for parsimony and Bayesian analyses can be downloaded from: https://morphobank.org/index.php/Projects/ProjectDocuments/project_id/3385.

The discrete characters were all equally weighted. Forty-six multi-state characters were set as "ordered" and the rest of them (188 characters) were unordered. When the scored specimens were merged into a terminal taxon, their character states were also merged. The merged multi-state characters were set to polymorphism. It is widely known that linear measurements are allometrically related to body mass. It is also widely known that body mass and cranial capacity, which is closely related to brain size, has a close relationship (e.g., Jerison 1973, 1979; Martin 1990). We used cranial capacity as a proxy for body mass to remove the effect of body size. The linear measurements of the crania and the upper dentitions of a scored specimen were divided by the 1/3rd power of the cranial capacity of this specimen (to keep the same dimension volume is the 3 power of length; cranial capacities listed in SI Table 1). The result can therefore be interpreted as the relative size of this measurement in relation to the body mass of the examined individual. The linear measurements of the mandibles and lower dentitions of a scored specimen were divided by the bi-ramus breadth at the alveolar margin of this specimen. Similarly, the bi-ramus breadth of the mandible was chosen as a reasonable proxy for body mass.

Ratios were calculated as one linear measurement over another linear measurement and multiplied by 100. After removing the effect of body size, linear measurements, ratios, and angle variables were normalized. Given a variable, a value of this variable minus the minimum of the variable, then the result was divided by the difference between the maximum and minimum of this variable among all the scored specimens. After transformation and normalization, all continuous characters have a range between 0 and 1.

In both the parsimony and Bayesian analyses, the morphological characters (both discrete and continuous) were treated as independent data points, and thus no correlations among characters were considered. This follows the most common practice in morphological data analyses. Nevertheless, some characters are likely to be correlated due to their anatomical structure or synergy in function. Here we discuss the potential biases that could be introduced and the further work that needs to be done. Because parsimony and Bayesian analyses assume that characters evolve independently, we consciously avoided redundant and potentially correlated discrete characters when we built the data matrix (Collard and Wood 2007; Lieberman 1995; von Cramon-Taubadel 2014, 2019; Weaver 2018). Normalization of the continuous characters can significantly reduce the potential correlations (correlation analysis indicating Kendall' Tau are low). As parsimony has no explicit model assumption, the consequence of ignoring character correlation is hard to predict. One obvious corollary would be overestimating the number of changes (parsimony length) in the tree and would probably aggravate long-branch attraction. In Bayesian tip-dating analysis, the overestimation of character changes is reflected in the branch lengths, each of which is a product of divergence time and evolutionary rate. With sufficient fossils and relatively accurate ages, the divergence time estimates would be less affected while resulting in accelerated evolutionary rates. The ignorance of character correlation would also include erroneous or overconfident topological inference (Ronquist et al. 2016), although simulation studies have shown that the estimate is relatively robust (Parins-Fukuchi 2018). Some studies also show that when the correlation is low, treating the characters as independent still can produce reliable estimates of topology and time (Álvarez-Carretero et al. 2019; Parins-Fukuchi 2018). The potential correlation between some characters can be considered equivalent to setting a higher weight for characters. If an anatomical feature is represented by more potentially correlated characters than other features, we assume that this anatomical feature is potentially more important for reconstructing evolutionary relationships and should be given higher weight than other features. Further efforts are still needed in model development for morphological characters.

PARSIMONY ANALYSES

Parsimony analyses of the data set, including both discrete and continuous characters scored for the 55 OTUs, were performed using TNT (Tree analysis using New Technology), a parsimony analysis program sponsored by the Willi Hennig Society (Goloboff et al. 2008). We used the parallel version of TNT on one hundred CPU cores and ran 1 million replications in the Institute of Vertebrate Paleontology and Paleoanthropology's (IVPP) supercomputing center. We ran two parallel analyses—with and without backbone constraints. The backbone constraints were set to reflect recent results from paleoproteomic and ancient DNA research (Chen et al. 2019; Prüfer et al. 2014; Reich et al. 2010; Welker et al. 2020): partial backbone constraints were used to force the Xiahe mandible as a sister group to Neanderthals and to force Gran Dolina outside the Neanderthal-Xiahe-sapiens clade. The same parsimony search strategy was used in both the non-constrained and constrained analyses.

In both analyses, the monophyly of sapiens, Neanderthals, and the Harbin-Xiahe-Dali-Jinniushan-Hualongdong clade is supported (Table 1). The consistent presence of the Xiahe mandible, with its inferred Denisovan affinities, in the Harbin clade might indicate that Denisovans are related to this group, but we believe that this is something to be tested further by genetic and morphological research (see also Bae 2024; Wu and Bae 2025). Most of the African and European Chibanian non-sapiens and non-Neanderthal hominins, such as Kabwe (Broken Hill), Bodo, Mauer, Arago, Petralona, and the like (Kabwe-like), were placed in a monophyletic group in the backbone constrained parsimony analysis, while they form a paraphyletic group in the unconstrained analysis. Asian *H. erectus* was grouped in a monophyletic group in the constrained analysis, but to a paraphyletic group in the unconstrained analysis. The most parsimonious trees (Figure 1a) are preferred because they require fewer assumptions and fewer character state changes than the backbone-constrained trees (Figure 1b).

ESTIMATING THE DIVERGENCE TIMES

It is widely believed that to date the species divergence time and evolutionary rate, researchers have to rely on a molecular clock. However, molecular clocks can only be used to reconstruct the evolutionary history of extant species and those only recently extinct with some genetic data still available (such as aDNA and some proteomic data). Further, such clocks have to use fossil data to calibrate the internal nodes of the phylogenetic tree (dos Reis et al. 2016; Ronquist et al. 2016). To estimate the divergence time and evolutionary rate of a relatively completely sampled group that includes most fossil taxa, molecular clock-based methods are of little use (Gavryushkina and Zhang 2020). In recent years, the development of the Bayesian tip-dating method, also known as total-evidence dating, allow evolutionary biologists to simultaneously analyze fossil and recent taxa and incorporate a wide range of sources of dating information into a unified statistical analysis (Gavryushkina et al. 2017; Gavryushkina and Zhang 2020; Ronquist et al. 2012a; 2016; Zhang and Wang 2019; Zhang et al. 2016).

We used the Bayesian tip-dating approach implemented in MrBayes 3.2.7 (Ronquist et al. 2012b) to infer the time tree and evolutionary rates. The method integrates both fossil ages and morphological data in a coherent analysis, while also accounting for their uncertainties. The morphological data (both discrete and continuous characters) are treated as two data partitions. For the discrete data, the Lewis Mk model with variable ascertainment bias correction (Lewis 2001) and gamma rate variation across characters (Yang 1994) (Mkv+Γ) was used for the likelihood calculation. Since MrBayes 3.2.7 cannot handle continuous characters directly and can deal with ordered characters only up to six states, all the continuous characters (400 characters) were discretized into six states. This is done by first dividing the range of 0 and 1 into six equal-length intervals (numbered as 0 to 5) and then converting each trait value into a state according to its interval assignment. The discretized continuous characters were all defined as ordered to fit the nature of gradual change and modelled under Mkv+Γ. The Mkv+Γ model has only one free parameter, the gamma shape (Yang 1994), which was assigned an exponential (1.0) prior by default. The gamma shape models rate variation within each partition, while the evolutionary rate variation among the two data partitions were accounted for using a uniform Dirichlet prior (Zhang et al. 2016). The prior for the time tree was modelled by the fossilized birth-death (FBD) process (Gavryushkina et al. 2014; Heath et al. 2014; Stadler 2010; Zhang et al. 2016). The process is conditioned on the time of the most recent common ancestor (root age) and has hyperparameters of speciation rate, extinction rate, fossil-sampling rate, and extant-sampling probability.

It has long been hypothesized that the origin of the genus *Homo* was related to climatic and environmental shifts around 3.0–2.6 Ma (Alemseged et al. 2020; Robinson et al. 2017). The root age was assigned an offset-exponential prior with a mean age of 3600 kyr and minimum age of 2800 kyr, referring to the potentially oldest fossil of *Homo* sp. (DiMaggio et al. 2015; Villmoare et al. 2015) and the beginning of the Late Pliocene epoch. The ages of the fossil tips were either fixed or given uniform distributions based on the corresponding stratigraphic ranges. The speciation,

TABLE 1. COMPARISON BETWEEN THE MOST PARSIMONIOUS PHYLOGENETIC TREES AND THE BACKBONE CONSTRAINED PHYLOGENETIC TREES.

	Most parsimonious tree	Backbone constrained parsimony tree	Parsimony backbone constrained Bayesian tree
Most parsimonious tree number	25	55	--
Rearrangements examined	3,247,009,993,272	3,207,084,736,601	--
Tree length	2812.68	2818.90	--
Consistency Index	0.26	0.26	--
Retention Index	0.46	0.46	--
Homo sapiens	Monophyletic	Monophyletic	Monophyletic
Neanderthals	Monophyletic	Monophyletic	Monophyletic
Chibanian Kabwe-like hominins	Paraphyletic	Monophyletic	Paraphyletic
Homo erectus/H. ergaster	Paraphyletic	Paraphyletic	Paraphyletic
Sapiens-Harbin monophyly	Supported	Not supported	Supported
Sapiens-Xiahe monophyly	Supported	Not supported	Supported
Neanderthal-Harbin monophyly	Not supported	Supported	Not supported
Neanderthal-Xiahe monophyly	Not supported	Constrained	Not supported
Harbin-Xiahe-Dali-Jinniushan-Hualongdong monophyly	Supported	Supported	Supported
Harbin-Maba-Narmada-Xuchang monophyly	Not supported	Supported	Not supported
Kabwe-like hominins-Harbin monophyly	Not supported	Not supported	Not supported
Kabwe-like hominins-Maba monophyly	Not supported	Not supported	Not supported

extinction, and fossil-sampling rates were reparametrized for convenience (Heath et al. 2014; Zhang et al. 2016). Apart from the time tree, the other key component in the Bayesian tip-dating analysis is the relaxed clock model, which models the evolutionary rate variation along the branches in the tree. We used the white noise (WN) (Lepage et al. 2007) model, in which the branch rates follow independent gamma distributions. As the discrete and continuous characters probably have distinct patterns of change through time, we unlinked the clock variance in these two partitions so that the evolutionary rate varies independently between partitions.

We executed four independent runs and eight chains per run (1 cold and 7 hot chains with temperature 0.05) in the Markov chain Monte Carlo (MCMC) simulation. Each run was executed with 100 million iterations and sampled every 2000 iterations. The first 30% of the samples were discarded as burn-in and the rest from two runs were combined. Good convergence and mixing were diagnosed by an effective sample size (ESS) (Geyer 1992) larger than 200 for all parameters and the average standard deviation of split frequencies (ASDSF) (Ronquist et al. 2012b) smaller than 0.02. The posterior trees were summarized to both 50% majority-rule consensus tree and all-compatible consensus tree. The analysis took about 83 hours using the parallel version of MrBayes in the IVPP's supercomputing center.

The initial Bayesian tip-dating run with no topological constraint was not able to resolve the phylogenetic relationship in the clade containing the African and European Chibanian hominins, Harbin, Maba, Neanderthals, and

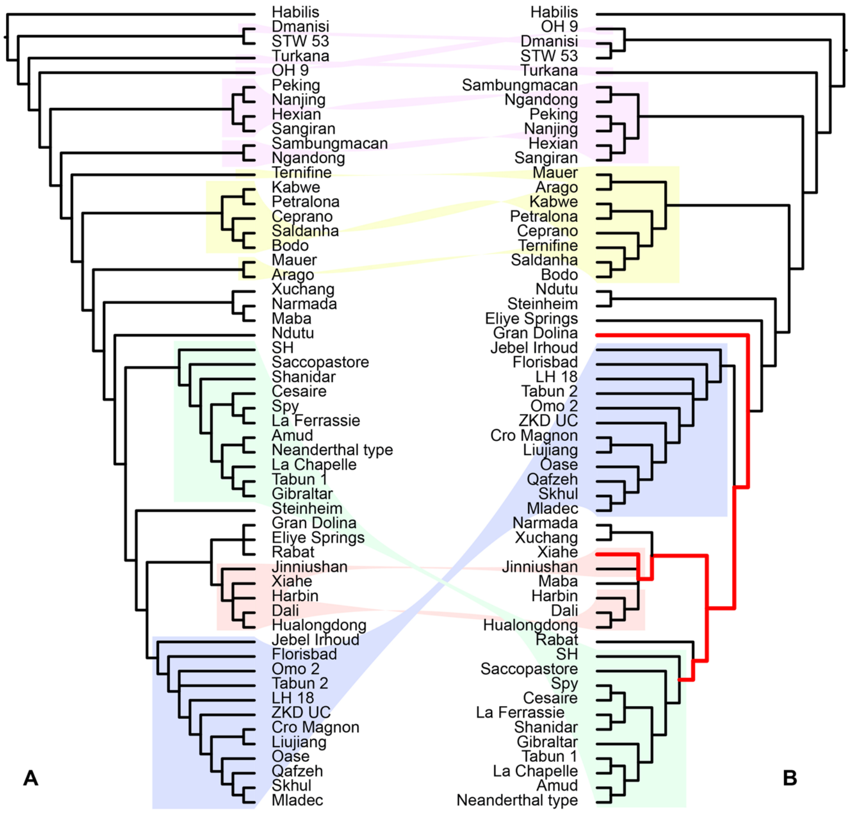

Figure 1. Phylogenetic tree inferred based on parsimony analyses. A) Majority-rule consensus tree of 25 most parsimonious trees. B) Majority-rule consensus trees of 55 most parsimonious backbone-constrained trees. Backbone constraints were used to force Xiahe as the sister group of Neanderthals and Gran Dolina outside of the Neanderthal-sapiens clade, as indicated by red lines. Color shadows indicate the clades discovered in both analyses.

sapiens. We further enforced a few backbone constraints based on the parsimony analysis, which handled the continuous characters directly without discretization (see Figure 1a). Although Bayesian inference and parsimony analysis are two phylogenetic methods based on two different sets of assumptions, previous research has shown that it is possible to link the methods mathematically. When implemented in a maximum likelihood framework, some stochastic models of character change can provide a correspondence between maximum parsimony and maximum likelihood (Farris 1973; Huelsenbeck et al. 2008; Tuffley and Steel 1997). For instance, Huelsenbeck et al. (2008) found that the integrated likelihood is a rescaling of the parsimony score for a tree, and the marginal posterior probability distribution of the length of a branch depends on how the maximum parsimony method reconstructs the characters at the inner nodes of the tree. As a possible consequence of the linear relationship between parsimony scores and probabilities, they also found that trees sampled by the MCMC algorithm are similar to maximum parsimony trees (Huelsenbeck et al. 2008). Inspired by the link between parsimony scores and probability, a method of parsimony-guided tree proposals was first introduced in MrBayes 3.2, and was included in the default set of tree moves (Ronquist et al. 2012b; Zhang et al. 2020). Combining the two methods is a useful strategy for obtaining a more harmonious phylogenetic model. This practice can be viewed as follows: given a limited number of proposed phylogenetic tree models (consistent with the results of parsimony analysis in this particular case), we use Bayesian tip-dating to estimate the divergence time of the internal nodes of these proposed trees.

RESULTS

In the preferred Bayesian tip-dating phylogenetic tree (Figure 2), sapiens and Neanderthals are monophyletic groups. Harbin, Dali, Jinniushan, Xiahe, and Hualongdong form a monophyletic group (Harbin-like group) that is part of the sister group to the monophyletic sapiens group. The monophyly of these groups was also supported by parsimony analyses. Asian *H. erectus* and African and European Kabwe-like hominins are all paraphyletic groups, as suggested by the parsimony analyses. Within the monophyletic sapiens group, the estimated earliest divergence time of the group is between 621.7~886.2 ka, i.e., the Last Common Ancestor (LCA) of sapiens originated around 621.7~886.2 ka. The currently oldest fossil record of sapiens (Jebel Irhoud) is then more than 300,000 years younger than the estimated LCA of sapiens. Within the monophyletic Neanderthal group, the origin of the LCA of this group is estimated to be between 584.2~905.2 ka, close to the estimated origin age of the LCA of sapiens. The oldest known Neanderthal

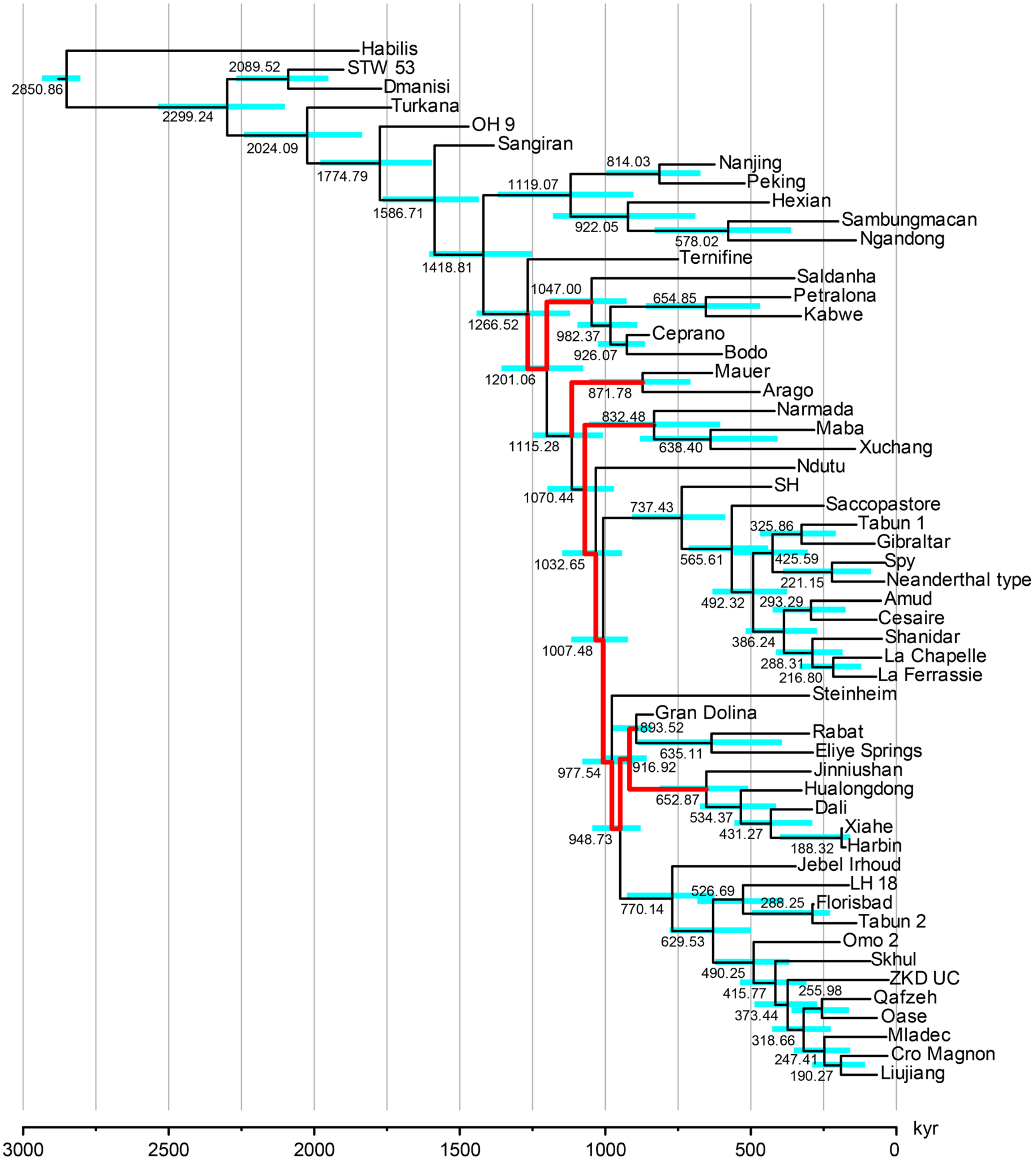

Figure 2. Phylogeny of the 55 selected fossil OTUs from the genus Homo. *This time tree was inferred from the Bayesian tip-dating analysis using MrBayes 3.2.7 and summarized as the all-compatible tree. To reduce the polytomy at some clades, the strict consensus of the most parsimonious trees from the parsimony analysis (Figure 1A) was used as a reference. The branches in red indicate the backbone constraints based on the most parsimonious trees. Branch lengths are proportional to the division age in thousand years. Numbers at the internal nodes are the median ages, and the blue bars indicate the 95% highest posterior density interval of the node ages.*

fossil record, Sima de los Huesos, is approximately 300 ka younger than the estimated LCA. The Harbin-like monophyletic group probably has an LCA between 506.3~810.1 ka. The oldest known fossil record of this group is more than 300 ka younger than the estimated age of origin of its LCA. The Harbin-like group is grouped with the European Gran Dolina and the African Eliye Springs and Rabat fossils. Together, these hominins form a sister clade of sapiens. This sister clade originated around 854.5~996.5 ka and diverged from the sapiens clade around 875.3~1041.4 ka. This estimate suggests that there was a widely distributed (Africa, Europe, and Asia) hominin clade prior to the origin of the sapiens clade. Because this widely distributed hominin clade is a monophyletic group, no hominin fossil in the analysis is closer to the sapiens clade than the other hominins. The Neanderthal clade diverged from the monophyletic sapiens plus Harbin-like clade between 919.2~1113.6 ka. The European Kabwe-like hominins and the Asian

Narmada, Maba, and Xuchang fossils are paraphyletically related. The divergence of these hominins began around 1118~1438.9 ka. According to this analysis, Asian and African *H. erectus*/*H. ergaster* arose around 2097.4~2533.4 ka. The paraphyletic Asian *H. erectus* group diverged from their African relatives between 1431.3~1761.8 ka.

DISCUSSION AND CONCLUSION

Phylogeny is the study of relationships among different organisms and their evolutionary development, while taxonomy is the study of orderly classification of organisms according to their presumed natural relationships. However, synthesizing phylogeny and taxonomy into a coherent system is very challenging (Hinchliff et al. 2015). In terms of paleoanthropology, the challenges come from two additional perspectives: 1) the taxonomic system of fossil hominins continues to be controversial; and 2) phylogenetic analyses that include most hominin fossils remain rare.

To reflect the fact that some recently divergent species, such as *H. neanderthalensis*, *H. longi*, and *H. sapiens*, have maintained their phylogenetic identity over long periods but could have experienced low levels of introgression, the Evolutionary Lineage Species Concept is suggested as the most appropriate concept with which to grapple the diversity of Middle to Late Pleistocene hominins (Harvati and Reyes-Centeno 2022; Stringer 2016). According to this concept, species can be identified in the fossil record as evolutionary lineages that maintain their identity despite small amounts of introgression over significant periods of time. However, identifying evolutionary lineages is difficult without a reliable phylogenetic framework.

Here, we constructed a phylogenetic tree of *Homo* at the population (paleodeme) level using parsimony and Bayesian criteria. Our parsimony and Bayesian tip-dating analyses show quite consistent results. The preferred phylogeny shows a clear branching topology with internal node age estimates. Some recent analyses based on ancient DNA have produced relatively younger estimates of Neanderthal-sapiens divergence dates (Posth et al. 2017). The approach is also tip dating—using ancient DNA sequences as data and their ages serve as tip dates. Although there were abundant molecular sequences in their analysis, it does not necessarily mean that their estimates are more reliable than ours. Theoretical studies have shown that even with infinitely long molecular sequences (or infinitely many morphological characters analogously) so that the branch lengths (distances measured by expected number of substitutions per site) can be inferred without error, the divergence times and evolutionary rates are confounded and rely on the information of fossil ages (or calibration priors) and clock models to get resolved (dos Reis and Yang 2013; Zhu et al. 2015). These analyses based on ancient DNA only included Neanderthals, Denisovans, and sapiens with the oldest being the Sima de los Huesos early Neanderthals (~430 kyr) and lack information that may inform on the divergences near the root of the genus *Homo*. Our study is different in that we included all the major clades of the genus *Homo* (as mentioned above, *H. floresiensis*, *H. luzonensis*, and *H. naledi* were not included), and thus we have more information from fossil ages to inform the divergence times of all the *Homo* clades. Posth and colleagues (2017) also fixed the mutation rate and thus put apparent certainty in the clock model, which might also bias the age estimates. In our study, the clock rate was co-estimated with the divergence times from the tip-dating analysis. The FBD model that we used explicitly models the speciation, extinction, and sampling processes and is more suitable for our data than the coalescent model (Drummond et al. 2005) used by Posth et al. (2017), which is better suited for a single population without population structure.

Based on the phylogenetic tree inferred in this study, we can evaluate the taxonomic units of *Homo*. Both sapiens and Neanderthals are monophyletic groups with deep time divergence from other *Homo* clades; as such, they are well-defined species. No archaic *H. sapiens*, anatomically modern human, or other fuzzily defined terms are needed to describe the intraspecific variation of *H. sapiens*. Further, *H. neanderthalensis* should not be considered a subspecies of *H. sapiens*.

As part of the sister group to the sapiens clade, Harbin-like hominins from Asia form a monophyletic group. Future systematic revision of Dali, Hualongdong, Jinniushan, Xiahe, and Harbin may show that they all belong to one species or alternatively two or more species. As proposed, *H. longi* is an available and valid name. Recently, Xujiayao was proposed as *H. juluensis*, and Xiahe, Xuchang, Penghu, Denisova, and Tam Ngu Hao 2 were included in this species (Bae 2024; Bae and Wu 2024). "*Homo daliensis*" and "*Homo mapaensis*" has been reviewed and identified as unavailable (Bae et al. 2023; Reed 2025). Gran Dolina, Harbin-like, and African Eliye Springs and Rabat form a deeply diverged monophyletic group. Given their deep divergence, Eliye Springs and Rabat may represent a different lineage. However, the two human fossils are incomplete, and comparison of morphology with Gran Dolina and Asian Harbin-like hominins is limited. Eliye Springs also shows pathological deformation (Bräuer et al. 2003). Additionally, the phylogenetic positions of the two fossils in our analyses are unstable. Different search strategies yield different results (as shown in Figure 1a and Figure 1b) and thus it is premature to assign them to an existing or new *Homo* species. Gran Dolina includes a partial facial skull of a juvenile individual and some isolated teeth. It shows weaker supraorbital torii and smaller teeth than Harbin-like hominins. Although they form a monophyletic group, significant morphological differences ensure that they should be assigned to a different species (*H. antecessor*).

The paraphyletically related Chibanian Kabwe-like hominins from Africa and Europe and the Asian Narmada, Maba, and Xuchang fossils show very high morphological differences and a very deep divergence time. They have been suggested to represent several different lineages or species. For example, Xuchang was grouped with Xujiayao and the two were thought to be different from *H. longi* and the African and European Kabwe-like hominins (Bae et al. 2023). In fact, Xujiayao and Xuchang were recently pro-

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posed to represent a new species, *H. juluensis*, a species distinct from *H. longi* (Bae 2024; Bae and Wu 2024). Currently available (but not necessarily valid) taxonomic names for these Middle Pleistocene African and Eurasian hominins include *H. heidelbergensis* Schoetensack, 1908, *H. rhodesiensis* Woodward, 1921, *H. steinheimensis* Berckhemer, 1936, *H. mauritanicus* Arambourg, 1954, *H. saldanensis* Drennan, 1955, *H. palaeohungaricus* Thoma, 1972, *H. bilzingslebenensis* Vlcek, 1978, *H. narmadensis* Sonakia, 1984, *H. reilingensis* Czarnetzki, 1989, *H. antecessor* Bermudez de Castro et al., 1997, *H. cepranensis* Mallegni et al., 2003, *H. longi* Ji and Ni, 2021, *H. bodoensis* Roksandic et al., 2022, and *H. juluensis* Wu and Bae 2025 (Bae 2024; Bae et al. 2023; Reed 2025). Given that overall morphological variation of these Middle Pleistocene hominins is still not very large within the *Homo* clade (Mounier et al. 2009; Rightmire 1998; Stringer 1983), it is unlikely that there could have been so many *Homo* species roughly coexisting that shared similar ecological niches during the Middle Pleistocene. Therefore, a thorough systematic revision of these "species" is needed (Bae 2024; Bae et al. 2023; Reed 2025).

Asian *H. erectus* is well separated from African *H. erectus*/*H. ergaster*. Although they are paraphyletically related, it is reasonable to consider African *H. erectus*/*H. ergaster* as a separate species (an available name is *H. ergaster*; but see Antón and Middleton [2023] for recent in-depth discussion about whether this is an appropriate taxonomic designation). Dmanisi is widely separated from other *H. erectus* or *H. ergaster* fossils and it may represent an early failed branch of *Homo* that dispersed into Eurasia. Given its phylogenetic position and deep divergence from other hominins, Dmanisi should probably be considered as a separate species (the available name is *H. georgicus* [Lordkipanidze et al. 2013], but again, see Anton and Middleton [2023] about how muddled the early *Homo* picture currently is).

In addition to taxonomy or systematics, phylogeny or phylogenetic trees are prominent in all branches of biology, such as comparative analysis, functional evolution, and biogeography. This is because phylogeny is the most direct representation of the principle of common ancestry—the core of evolutionary theory. Although there are many phylogenetic studies of the great apes and humans (such as Caparros and Prat 2021; Collard and Wood 2007; Delson 1985; Parins-Fukuchi et al. 2019; Pugh 2022; Püschel et al. 2021; Strait et al. 2007; Strait et al. 2013; Strait et al. 1997; Wood and Richmond 2000), the lack of tree thinking (Baum 2008, 2009; Baum et al. 2005) can still be considered a problem in paleoanthropology. There are two main erroneous practices—using cluster diagrams of non-evolutionary context as phylogeny, and reading a phylogenetic tree along peaks to form a progressive evolutionary sequence. The latter practice is particularly problematic because it leads to the widespread misconception that human evolution is a linear progression from apes to *H. erectus* to *H. sapiens*. Many paleoanthropologists arrange human fossils by age and interpret the results as evidence of gradual local evolution, ignoring speciation and dispersal events. In addition, the hypothesized existence of "braided streams" during the evolution of the genus *Homo* (e.g., see Stringer 2022) is considered by some to negate normal taxonomic procedures. Our present phylogenetic analysis of *Homo* provides a phylogenetic framework for discussing human evolution in a broader and evolutionary sense. This phylogenetic framework clearly shows that the cladogenesis of *Homo* species is as complex as that of other mammals. Human evolution was not a gradual process leading directly from *H. habilis* to *H. sapiens*, nor one which is obscured by recurrent gene flow (Bae 2024; Bae and Wu 2024; Bae et al. 2023). Several species or lineages coexisted, and we identify at least three clear and temporally deep clades in later human evolution—those of *H. sapiens*, *H. neanderthalensis,* and at least one containing *H. longi* (though *H. juluensis* is now proposed as well). Further revision of the taxonomy of *Homo* based on phylogenetic trees is critical for future progress.

The phylogenetic analyses presented in this study provide an informative and useful framework for the taxonomic classification of *Homo* and for understanding the evolutionary process of the genus. However, this kind of analysis needs significant improvement. Future work should focus on developing new, more complicated models that incorporate genomic and proteomic data with morphological data and include more fossil records to account for greater variation.

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Special Issue: What’s in a Name? Late Middle and Early Late Pleistocene Hominin Systematics

Supplement 1: Phylogeny of *Homo* and its Implications for the Taxonomy of the Genus

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SUPPLEMENT 1
This section contains S-Table 1 and S-References.

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S-Table 1. Specimens used for building OTUs and metrical and discrete character scoring and phylogenetic analyses

OTUs*	Specimens	Age (kyr)	Cranial capacity (ml)	Age Reference	Cranial Capacity Reference
Gran Dolina	*H. antecessor* ATD6-15 ATD6-69 ATD6-96	900-800	1000	Ref.(Moreno et al. 2015)	Ref.(Bermúdez de Castro et al. 1997)
	H. antecessor Dental	900-800		Ref.(Moreno et al. 2015)	
Narmada	*Homo* sp. Narmada	780-236	1155-1421	Ref.(Sonakia and de Lumley 2006)	Ref.(Kennedy et al. 1991)
Eliye Springs	*Homo* sp. Eliye Springs	300-200	1170-1245	Ref.(Klein 2009)	Ref.(Bräuer et al. 2004)
Ndutu	*Homo* sp. Ndutu	350	1100	Ref.(Ash and Gallup 2007; Bailey and Geary 2009)	Ref.(Ash and Gallup 2007; Bailey and Geary 2009)
Jebel Irhoud	*H. sapiens* Irhoud1	349-281	1369-1381	Ref.(Hublin et al. 2017)	Ref.(Neubauer et al. 2018)
	H. sapiens Irhoud2	349-281	1467-1473	Ref.(Hublin et al. 2017)	Ref.(Neubauer et al. 2018)
Florisbad	*H. sapiens* Florisbad	294-224	1280	Ref.(Grün et al. 1996)	Ref.(Bailey and Geary 2009; De Miguel and Henneberg 2001)
Omo 2	*H. sapiens* Omo II	195	1487-1495	Ref.(Neubauer et al. 2018)	Ref.(Neubauer et al. 2018)
LH 18	*H. sapiens* LH18	150-120	1232-1242	Ref.(Neubauer et al. 2018)	Ref.(Neubauer et al. 2018)
Skhul	*H. sapiens* Skhul V	115	1362-1364	Ref.(Neubauer et al. 2018)	Ref.(Neubauer et al. 2018)
	H. sapiens Skhul IX	115	1400-1587.33	Ref.(Neubauer et al. 2018)	Ref.(Bailey and Geary 2009; Holloway et al. 2004)
Qafzeh	*H. sapiens* Qafzeh IX	115	1492-1502	Ref.(Neubauer et al. 2018)	Ref.(Neubauer et al. 2018)
Mladec	*H. sapiens* Mladec I	35	1606	Ref.(Neubauer et al. 2018)	Ref.(Holloway et al. 2004)
	H. sapiens Mladec II	35	1390	Ref.(Neubauer et al. 2018)	Ref.(Holloway et al. 2004)
	H. sapiens Mladec V	35	1500-1650	Ref.(Neubauer et al. 2018)	Ref.(Bailey and Geary 2009; Holloway et al. 2004)
	H. sapiens Mladec VI	35		Ref.(Neubauer et al. 2018)	
Cro-Magnon	*H. sapiens* Cro-Magnon I	31	1573-1575	Ref.(Neubauer et al. 2018)	Ref.(Neubauer et al. 2018)
	H. sapiens Cro-	31		Ref.(Neubauer et al.	

	Magnon II			2018)	
	H. sapiens Cro-Magnon III	31	1781-1845	Ref.(Neubauer et al. 2018)	Ref.(Neubauer et al. 2018)
Oase	*H. sapiens* Oase1	41.47-39.41		Ref.(Rougier et al. 2007)	
	H. sapiens Oase2	41.47-39.41	1400-1500	Ref.(Rougier et al. 2007)	This research
ZKD UC	*H. sapiens* Upper Cave 101	27	1500	Ref.(Liu et al. 2014)	Ref.(Liu et al. 2014)
	H. sapiens Upper Cave 103	27	1290-1300	Ref.(Liu et al. 2014)	Ref.; Ref.(Holloway et al. 2004)
Liujiang	*H. sapiens* Liujiang	67	1567	Ref.(Liu et al. 2014)	Ref.(Liu et al. 2014)
SH	*H. neanderthalensis* SH4	430	1360	Ref.(Poza-Rey et al. 2019)	Ref.(Arsuaga et al. 2014)
	H. neanderthalensis SH5	430	1092	Ref.(Poza-Rey et al. 2019)	Ref.(Arsuaga et al. 2014)
Tabun 1	*H. neanderthalensis* Tabun C1	122-100	1270.5-1271	Ref.(Bailey and Geary 2009)	Ref.(Bailey and Geary 2009; Holloway et al. 2004)
Tabun 2	*H. sapiens* Tabun C2	122-100		Ref.(Bailey and Geary 2009)	
Spy	*H. neanderthalensis* spy ii	40	1278-1296	Ref.(Neubauer et al. 2018)	Ref.(Neubauer et al. 2018)
	H. neanderthalensis Spy II	40	1524-1538	Ref.(Neubauer et al. 2018)	Ref.(Neubauer et al. 2018)
Gibraltar	*H. neanderthalensis* Gibraltar1 (=Forbes' Quarry 1)	75	1209-1217	Ref.(Neubauer et al. 2018)	Ref.(Neubauer et al. 2018)
Amud	*H. neanderthalensis* Amud	53	1731-1763	Ref.(Neubauer et al. 2018)	Ref.(Neubauer et al. 2018)
La Chapelle	*H. neanderthalensis* La Chapelle aux Saints	52	1487-1493	Ref.(Neubauer et al. 2018)	Ref.(Neubauer et al. 2018)
La Ferrassie	*H. neanderthalensis* La Ferrassie1	70	1638-1648	Ref.(Neubauer et al. 2018)	Ref.(Neubauer et al. 2018)
Shanidar	*H. neanderthalensis* Shanidar1	50	1650	Ref.(Ash and Gallup 2007; Bailey and Geary 2009)	Ref.(Ash and Gallup 2007; Bailey and Geary 2009)
	H. neanderthalensis Shanidar5	50	1550	Ref.(Ash and Gallup 2007; Bailey and Geary 2009)	Ref.(Ash and Gallup 2007; Bailey and Geary 2009)
Césaire	*H. neanderthalensis* St Césaire	41.95-40.66		Hublin et al., 2012(Hublin et al. 2012)	
Saccopastore	*H. neanderthalensis*	250	1234.3	Ref.(Ash and Gallup	Ref.(Ash and Gallup 2007; Bailey

	Saccopastore I			2007; Bailey and Geary 2009)	and Geary 2009)
	H. neanderthalensis Saccopastore II	250	1295	Ref.(Ash and Gallup 2007; Bailey and Geary 2009)	Ref.(Ash and Gallup 2007; Bailey and Geary 2009)
Neanderthal type	Neanderthal 1	42	1337.8	Ref.(Ash and Gallup 2007; Bailey and Geary 2009)	Ref.(Ash and Gallup 2007; Bailey and Geary 2009)
Xiahe	*Homo* sp. Xiahe	155-164.5		Chen et al., 2019(Chen et al. 2019)	
Dali	*Homo* sp. Dali	267.7-258.3	1120	Sun et al., 2017(Sun et al. 2017)	Wu and Athreya, 2013(Wu and Athreya 2013)
Hualongdong	*Homo* sp. Hualongdong	331-275	1150	Ref.(Wu et al. 2019)	Ref.(Wu et al. 2019)
Harbin	*Homo* sp. Harbin	225-221	1400	This research	This research
Jinniushan	*Homo* sp. Jinniushan	310-200	1390	Ref.(Liu et al. 2014)	Ref.(Liu et al. 2014)
Maba	*Homo* sp. Maba	278-230	1300	Ref.(Shen et al. 2014)	Ref.(Wu and Bruner 2016)
Xuchang	*Homo juluensis* Xuchang	125-105	1800	Ref.(Li et al. 2017)	Ref.(Li et al. 2017)
Mauer	*H. heidelbergensis* Mauer 1	649-569		Ref.(Wagner et al. 2010)	
Arago	*H. heidelbergensis* Arago XXI XLVII	469-407	1138.667-1166	Ref.(Falguères et al. 2015)	Ref.(Bailey and Geary 2009; Holloway et al. 2004)
	H. heidelbergensis Arago XIII	469-407		Ref.(Falguères et al. 2015)	
	H. heidelbergensis Arago II	469-407		Ref.(Falguères et al. 2015)	
Kabwe	*H. heidelbergensis* Broken Hill	324-274	1249	Ref.(Grün et al. 2020)	Ref.(Neubauer et al. 2018)
Petralona	*H. heidelbergensis* Petralona1	400-150	1160-1164	Ref.(Neubauer et al. 2018)	Ref.(Neubauer et al. 2018)
Ceprano	*H. heidelbergensis* Ceprano	850-400	1185	Ref.(Ash and Gallup 2007; Bailey and Geary 2009)	Ref.(Ash and Gallup 2007; Bailey and Geary 2009)
Steinheim	*H. heidelbergensis* Steinheim S11	300	1111.192	Ref.(Ash and Gallup 2007; Bailey and Geary 2009)	Ref.(Ash and Gallup 2007; Bailey and Geary 2009)
Saldanha	*H. heidelbergensis* Saldanha (=Elandsfontein)	500-350	1216.667	Ref.(Ash and Gallup 2007; Bailey and Geary 2009)	Ref.(Ash and Gallup 2007; Bailey and Geary 2009)
Bodo	*H. bodoensis* Bodo	600	1200-1325	Ref.(Ash and Gallup 2007; Bailey and Geary 2009)	Ref.(Conroy et al. 2000)
Ternifine	*H. heidelbergensis*	750		Ref.(De Miguel and	

	Ternifine1			Henneberg 2001)	
	H. heidelbergensis Ternifine2	750		Ref.(De Miguel and Henneberg 2001)	
	H. heidelbergensis Ternifine3	750		Ref.(De Miguel and Henneberg 2001)	
	H. heidelbergensis Ternifine4	750	1300	Ref.(De Miguel and Henneberg 2001)	Ref.(Ash and Gallup 2007; Bailey and Geary 2009; De Miguel and Henneberg 2001)
Peking	*H. erectus* Peking X	580-280	1225	Ref.(Chen and Zhou 2009; Liu et al. 2014)	Ref.(Liu et al. 2014)
	H. erectus Peking XII	580-280	1030	Ref.(Chen and Zhou 2009; Liu et al. 2014)	Ref.(Liu et al. 2014)
	H. erectus Peking XIII	580-280		Ref.(Chen and Zhou 2009; Liu et al. 2014)	
	H. erectus Peking LII	580-280		Ref.(Chen and Zhou 2009; Liu et al. 2014)	
	H. erectus Peking RC1996	580-280	1030	Ref.(Chen and Zhou 2009; Liu et al. 2014)	Ref.(Liu et al. 2014)
Nanjing	*H. erectus* Nanjing1	620-580	876	Ref.(Liu et al. 2014)	Ref.(Liu et al. 2014)
Hexian	*H. erectus* Hexian	437-387	1025	Cui and Wu, 2015(Cui and Wu 2015)	Ref.(Liu et al. 2014)
Sambungmacan	*H. erectus* Sambungmacan1	200		Ref.(Neubauer et al. 2018)	
	H. erectus Sambungmacan3	200	898-906	Ref.(Neubauer et al. 2018)	Ref.(Neubauer et al. 2018)
Sangiran	*H. erectus* Sangiran2	1500-1300	789-797	Ref.(Neubauer et al. 2018)	Ref.(Neubauer et al. 2018)
	H. erectus Sangiran17	1500-1300	1020	Ref.(Neubauer et al. 2018)	Ref.(Ash and Gallup 2007; Bailey and Geary 2009)
Ngandong	*H. erectus* Ngandong 7	117-108	1013	Ref.(Rizal et al. 2020)	Ref.(Holloway et al. 2004)
	H. erectus Ngandong 9	117-108		Ref.(Rizal et al. 2020)	
	H. erectus Ngandong 12	117-108	1127	Ref.(Rizal et al. 2020)	Ref.(Holloway et al. 2004)
Dmanisi	*H. erectus* Dmanisi 211 2282	1770	650	Ref.(Lordkipanidze et al. 2013)	Ref.(Lordkipanidze et al. 2013)
	H. erectus Dmanisi 2280	1770	730	Ref.(Lordkipanidze et al. 2013)	Ref.(Lordkipanidze et al. 2013)
	H. erectus Dmanisi 2700 2735	1770	601	Ref.(Lordkipanidze et al. 2013)	Ref.(Lordkipanidze et al. 2013)
	H. erectus Dmanisi 4500 2600	1770	546	Ref.(Lordkipanidze et al. 2013)	Ref.(Lordkipanidze et al. 2013)
Rabat	*Homo* sp. Rabat	300		Ref.(Neuville and	

				Ruhlmann 1942; Oujaa et al. 2017)	
STW53	*Homo* sp. STW53	1900	570	Ref.(Ash and Gallup 2007; Bailey and Geary 2009)	Ref.(Ash and Gallup 2007; Bailey and Geary 2009)
OH 9	*H. erectus* OH9	1470	1009-1017	Ref.(Neubauer et al. 2018)	Ref.(Neubauer et al. 2018)
Turkana	*H. erectus* Turkana	1535	846-854	Ref.(Neubauer et al. 2018)	Ref.(Neubauer et al. 2018)
	H. erectus ER 3733	1780	876-880	Ref.(Neubauer et al. 2018)	Ref.(Neubauer et al. 2018)
	H. erectus ER 3883	1570	837-839	Ref.(Neubauer et al. 2018)	Ref.(Neubauer et al. 2018)
Habilis	*H. habilis* OH24	1800	597	Ref.(Ash and Gallup 2007; Bailey and Geary 2009)	Ref.(Ash and Gallup 2007; Bailey and Geary 2009)
	H. habilis OH7	1780		Ref.(Ash and Gallup 2007; Bailey and Geary 2009)	Ref.(Ash and Gallup 2007; Bailey and Geary 2009)
	H. habilis ER1805	1850	616	Ref.(Ash and Gallup 2007; Bailey and Geary 2009)	Ref.(Ash and Gallup 2007; Bailey and Geary 2009)

* OTUs: operational taxonomy units.

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