A reevaluation of the phylogenetic tree for the genus Homo: a reclassification based on contemporary evidence

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TC 660H/TC 359T
Plan II Honors Program
The University of Texas at Austin

12/6/2020

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ABSTRACT

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There is considerable variation in the proposed taxonomic and phylogenetic hypotheses for the genus Homo. This is due to the limitations of the hominin fossil record; morphological data are the most available, as genetic material is less likely to be preserved over large timescales and varying environments. The taxonomic hypotheses fall into two broad categories: lumping taxonomies tend to incorporate many fossil groups into one species, and splitting taxonomies tend to split discovered populations into numerous species. The availability of information on the morphology and genetics of different archaic human species continues to change as data extraction and processing techniques improve, and new species definitions also develop to accommodate evolution in different contexts. This then influences the validity of different taxonomic hypotheses, as well as the phylogenies that incorporate them. Here I evaluated the genetic, morphometric, and probabilistic analyses that have been conducted for different fossils in the genus Homo, and proposed a phylogeny and taxonomy that are most consistent with recent fossil discoveries and advances in the field of evolutionary biology. I analyzed the different fossil specimens that are attributed to H. habilis, H. erectus, and H. sapiens under the most conservative taxonomic hypothesis, and proceeded to reclassify fossils in order to achieve consistency with the current data. I classify H. rudolfensis as a subspecies of H. habilis, and have placed H. antecessor and H. ergaster as subspecies of H. erectus. The rest of the species in the proposed phylogeny are H. floresiensis, H. luzonensis, H. naledi, H. heidelbergensis, H. neanderthalensis, H. denisova, and H.sapiens. H. naledi is classified as a descendent of H. erectus, as the H. erectus-H. naledi pairwise comparisons showed the least divergence for the majority of craniodental traits studied. H. floresiensis and H. luzonensis have also been placed as descendants of H. erectus, due to similarities in dental surface and cranial size trends. Additionally, H. heidelbergensis is designated as the last common ancestor for Neanderthals, Denisovans, and modern humans, owing to trends across several fossils suggesting a relatively large-brained and variable population that descended from H. erectus and spread into Europe. I also discussed the limitations of this phylogeny and potential for reclassification as more fossil data are collected.

Acknowledgements

I would like to thank my thesis supervisor, Dr. Howard Ochman, and my second reader, Dr. Justin Havird, for all their support and feedback during the course of writing this thesis. Additionally I would like to thank the Plan 2 Honors program for providing this valuable learning opportunity.

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Part One: Introduction

Background and Current Situation

In evolutionary biology, a species is most commonly defined as a population of organisms that can interbreed, and two species are separated by their inability to produce viable offspring that is not infertile or does not, upon reproduction, lead to hybrid breakdown (Lagache et al., 2013). This definition is known as the biological species concept (Lagache et al., 2013). Other species concepts include the recognition species concept, the evolutionary species concept, the phylogenetic species concept, and more (Balakrishnan, 2005; Lagache et al., 2013). The recognition species concept defines a species as the population of organisms wherein the individuals recognize one another as mates (Balakrishnan, 2005). The phylogenetic species concept, in contrast, defines a species as the smallest monophyletic group that is identified by shared derived characteristics (Balakrishnan, 2005).

These species concepts generally rely on the analysis of genetic data, and the ability to directly observe populations of different organisms in order to procure empirical evidence (Balakrishnan, 2005; Lagache et al., 2013). The genetic species concept, for example, distinguishes between different species on the basis of genetic isolation, and under this concept populations that are not reproductively isolated but are genetically incompatible are also considered separate species (Baker & Bradley, 2006). The application and testing of this concept would naturally involve the ability to observe naturally existing populations and record both genetic information and information about reproductive behaviors. The identification of different species can therefore be subject to significant uncertainty in contexts where the genetic data of organisms, and the ability to directly observe phenotypic

and behavioral patterns, are not available. One of these contexts is the study and analysis of fossil records.

The evolutionary relationships between different species, which are an example of taxa, can be represented in the form of a phylogenetic tree (Choudhuri, 2014). The phylogenetic tree is a visual representation of evolutionary relationships between taxonomic units such as different species (as well as different populations, families, orders, etc.), and consists of two elements: nodes and branches (Choudhuri, 2014). The nodes represent the taxonomic unit, and the branches represent the length of the duration of the evolutionary relationship between two nodes; the tree is usually rooted, or represented against an axis of time (Choudhuri, 2014). The nodes at the very end of the branch, or terminal nodes, represent operational taxonomic units (Choudhuri, 2014). The operational taxonomic units represent the objects that are being compared, which can range from specific species to genes to populations at higher taxa (Choudhuri, 2014). The internal nodes are referred to as hypothetical taxonomic units, and these are used to represent the last common ancestor of the nodes that arise from these points (Choudhuri, 2014). Descendents that originate from the same node are referred to as sister groups (Choudhuri, 2014). In the context of the hominin evolution, the hominin phylogenetic tree represents the evolutionary relationships between hominin species (Choudhuri, 2014). Within the tribe of Hominini is the genus *Homo*, which includes the anatomically modern human, or *Homo sapiens* (McNulty, 2016).

The construction of phylogenetic trees for hominins, and by extension the genus *Homo*, is usually dependent on the information that can be extracted from fossils and the surroundings they were found in (Llamas et al., 2017). This process is made more difficult by the fact that the fossil record is not continuous and can only be recovered in fragments (Llamas et al., 2017). The fossils themselves are often not whole, and therefore the full range of the morphological characteristics of the species of a specific fossil cannot be

determined either (Llamas et al., 2017). It usually takes many fossils from different parts of the skeleton in order to determine a significant amount of the morphological characteristics of a hominin species (Llamas et al., 2017). Although the role of genetic evidence from fossils has advanced significantly and continues to do so, genetic dating techniques, such as through molecular clocks, are rarely used for samples that are significantly older than 50,000 to 80,000 years (Moorjani et al., 2016). The data that are most often used in making inferences about the hominin evolutionary tree include the morphological characteristics of fossils, dating estimates, comparisons with other fossils, and geographical factors such as the environment in which the fossils were found (Wood & Lonergan, 2008). The hominin phylogenetic trees can therefore be constructed in many different ways due to the lack of definite observations and the dearth of DNA information, and species groupings are determined through inference (Moorjani et al., 2016;Wood & Lonergan, 2008).

Due to gaps in the fossil record, and the resulting gaps in the morphological data available for observation about any hominin individual or population, there are a number of taxonomic hypotheses that are put forth by scientists in the field (Wood & Lonergan, 2008). These hypotheses range from taking a speciose approach, which increases the number of species classified, to taking a relatively more inclusive approach that groups many more fossils under the same species classifications (Wood & Lonergan, 2008). In the formulation of these different taxonomic hypotheses, the taxa are often grouped into grades (Wood & Lonergan, 2008). Grades are used to indicate adaptive zones, in a manner analogous to the determination of clades (Wood & Lonergan, 2008). Hominin species in the same grade are hypothesized to have eaten the same kinds of foods, had similar methods of locomotion, and shared the same kind of posture (Wood & Lonergan, 2008). The main difference between clades and grades is that clades also represent information on the evolutionary relationships between the taxa within them, while grades are only concerned with the

outcomes of the evolutionary history of these populations, rather than the process that generates these outcomes (Wood & Lonergan, 2008).

Biochronological dating is often used to determine the age of hominin fossils (Wood & Lonergan, 2008). This is done by using the known dating estimates of fossils from the same layer as the one in which the hominin fossils were found (Wood & Lonergan, 2008). Dental morphology is also commonly used to make inferences about hominin fossils due to the longer survival of teeth and enamel compared to other bones (Wood & Lonergan, 2008). Other larger bones, such as the femur, are often fragmented and difficult to make morphological determinations about (Wood & Lonergan, 2008). The morphological information alone is not used to classify a fossil as belonging to a specific species; a combination of morphological information from cranial and postcranial bone pieces and fragments must often be pieced together in order to infer the information that would then help determine the species classification of the fossil (Wood & Lonergan, 2008). The inferences made from morphological data include inferences about the diet of the individual, whether the locomotion was arboreal or bipedal, the size of the brain relative to the size of the body, and levels of sexual dimorphism in the population (Wood & Lonergan, 2008). The lack of genetic dating ability for fossils older than 50,000 years necessitates that these inferences be made based on the limited morphological and geographical data available (Moorjani et al., 2016; Wood & Lonergan, 2008).

Additionally, these gaps in the fossil record add a base level of uncertainty to the species classifications that are determined. As only the fossils that survived long enough can be used for inference, individuals and populations that did not leave behind surviving fossils are invisible, and it is possible that there have been hominin species in the past that we have yet to discover, or that we will never know of.

Examples of fossil reclassification in the genus *Homo*

The limited data available at the time of discovery and classification of hominin fossils has meant that, upon the advent of new technologies, dating techniques, and additional fossil discoveries, the species classifications of fossils have been revised and remain open to future revision as well. Apart from the classifications of specific fossils, the origins of species are also revised based on newer data and the outcomes of different dating methods (Argue et al., 2017; Sutikna et al., 2016).

For example, the phylogenetic status of *Homo floresiensis* has been the subject of some debate (Sutikna et al., 2016). The fossils of this hominin species were discovered in Late Pleistocene sediment deposits in Liang Bua, on the island for Flores in Indonesia, from 2001 to 2004 (Sutikna et al., 2016). There are three hypotheses as to its origin: that it is derived from *Homo erectus*, that is it descended from a *Homo* lineage in Africa such as *Homo habilis*, and that it is actually *Homo sapiens* with some pathological condition that affects its size (Argue et al., 2017). The roles of newer dating methods and reanalyses of the information available for dating are significant in cases like these (Sutikna et al., 2016). The deposits containing *Homo floresiensis*, based on the extinct fauna and stone artefacts they also contained, were dated to between 12,000 and 95,000 years ago (Sutikna et al., 2016). This method of dating suggested that *H. floresiensis* continued living after encountering *Homo sapiens* (Sutikna et al., 2016). More recent analyses of the stratigraphic data available suggest that the deposits themselves are 60,000 to 100,000 years old, while the stone artefacts can be dated even older, from 50,000 to 190,000 years in age (Sutikna et al., 2016). The new methods include the dating of sediment samples using infrared stimulated luminescence as well as thermoluminescence dating, which then give age estimates of 65,000 and 71,000 years (Sutikna et al., 2016). Further samples from different deposits that contained *Homo floresiensis* fossils at the site, yield age estimates of 90,000 to 128,000

years (Sutikna et al., 2016). Additionally,the dating of the ulnae of *Homo floresiensis* using uranium-thorium dating yielded minimum age estimates 66,000 to 87,000 years, adding support to the hypothesis that *Homo floresiensis* was older than the first round of dating suggested (Sutikna et al., 2016).

These older ages that were estimated in newer dating analyses have implications for the placement of *Homo floresiensis* in the hominin phylogenetic tree, as the question of whether *Homo floresiensis* lived after 50,000 years ago and continued to live after encountering modern humans is opened up once again (Sutikna et al., 2016).

Another example of a hominin fossil that has been inferred to belong to different species depending on the criteria used to classify it is the ‘Little Foot’ fossil (Clarke, n.d.). The scientist who found it inferred that this fossil was from a completely new species within Australopithecus, called Australopithecus prometheus (Clarke, n.d.). The fossil is also known as StW 573, and it is a near-complete skeleton that was found in Sterkfontein, South Africa from 1994 to 1998 (Clarke, n.d.). The species Australopithecus prometheus has been argued to have existed based on two fossils discovered before StW 573: fossils from Makapansgat and Sterkfontein Member Four (Clarke, n.d.). The proponents of the view that this fossil also belongs to Australopithecus prometheus use morphological comparisons between StW 573 and fossils classified as belonging to Australopithecus africanus and Australopithecus afarensis to substantiate their classification (Clarke, n.d.). They compare, among other characteristics, cranial size, the overall size and width of the muzzle, and the size and shape of the nasal aperture, nasal skeleton, and dental as well as postcranial morphology (Clarke, n.d.). The current view, which is that StW 573 belongs to A. africanus, is based on the fact that the earlier classifications for the fossils from Makapangsat and Sterkfontein Member Four as A. prometheus were changed, and these fossils were instead reclassified as A. africanus (Clarke, n.d.). Since those earlier discoveries were reclassified to

A. africanus, the present classification of StW 573 is also A. africanus, and the variations in different morphological characteristics are viewed as within the parameters for natural variation within a population (Clarke, n.d.). The debate about StW 573's true origins remains ongoing, however (Clarke, n.d.).

The case for reevaluation of the phylogenetic tree for the genus *Homo*

Both of these examples show how the same fossil data can be reinterpreted to support different phylogenetic relationships. Species classifications have the potential to change even faster given the rate of new discoveries about fossils, ancient hominin genetics, and speciation processes. Different methods of analyzing the same morphology can also expose flaws in the reasoning for previous classifications.

One brief illustration of how fossils that were discovered and classified in the past still have the potential to be reclassified and yield new information or contribute to a new understanding of the fossil's lineage would be the dating of the skull from Broken Hill by Grun et al. (Grün et al., 2020). In this study the skull, which had previously been dated at about 500,000 years ago, was reanalyzed and dated to be about 299,000 years old (Grün et al., 2020). The skull was first classified as *Homo rhodesiensis*, and is now classified as *Homo heidelbergensis* (Grün et al., 2020). The new dating estimate lends support to the idea that there were multiple hominin lineages that lived contemporaneously in Africa during the late Middle Pleistocene (Grün et al., 2020). The researchers used uranium-series dating, and so this age can be considered a minimum estimate (Grün et al., 2020). This provides an example of how reevaluations of existing fossils can yield different results, and how these results then affect the current understanding of the hominin evolutionary tree and its relationships.

Additionally, there have been vast improvements in the ability to use available genetic information and formulate accurate genetic dating methods (Llamas et al., 2017). Some hominin species that have been genetically sequenced include Neanderthals and Denisovans, as the fossils contained relatively large amounts of endogenous DNA (Llamas et al., 2017). Recent findings that some bones have more endogenous DNA than others, such as the petrous portion of the temporal bone, and the cementum of teeth, also help improve the possibility of genetic analysis of fossils (Llamas et al., 2017). Even when the probability of finding endogenous DNA is poor, DNA amplification techniques that specifically target ancient DNA fractions of the overall sample can help hone in on the genetic information that is available and make full use of it (Llamas et al., 2017). These advances in genetic analysis can help supplement the morphological data available from hominin fossils, and have the potential to tip the scale towards one side of a classification debate. Genetic information from ancient hominins, such as the epigenome, may potentially reveal gene regulatory patterns that can reveal interactions between the hominin environment and their biology, which is valuable information when trying to classify a fossil and place a hominin species in evolutionary history (Llamas et al., 2017).

Advances in dating techniques also have the potential to unearth more information about the existing fossil record. Genetic dating methods, making use of constant recombination rates, have been tested to date specimens up to 50,000 years old (Llamas et al., 2017). While this does not significantly impact the problem of hominin fossil dating, it provides an example of the rate at which genetic research is progressing (Moorjani et al., 2016). Additionally, the use of different combinations of existing dating techniques, such as uranium-series dating and electron spin resonance dating, can allow for better estimates of the age of the fossil under analysis (Guo et al., 2019). A review of the present evidence for and against the classification of a hominin fossil as a certain species has the potential to result in a changed

phylogenetic tree. Since morphological evidence has gaps of its own, and the rate at which new information is unearthed is relatively fast, a review of the hominin phylogenetic tree will help keep the understanding of ancient human evolutionary relationships as current and rigorous as possible.

The Thesis Question

How does a reevaluation of the phylogenetic tree of the genus *Homo* in light of the current evidence affect the species classifications, and what relationship between the various species best reflects the available data?

Overview of the methods

This paper will proceed to answer the thesis question by conducting a literature review, with special attention to the most recent developments in dating methods, fossil dating and morphological study, fossil discoveries and reclassifications, and techniques that optimize the use of available genetic information. Additionally, the literature will also be analyzed in order to compare different methods of interpreting the information available from the fossil record, as well as the different methods available for constructing phylogenetic trees. Past examples of how fossils were reclassified as different species, as well as examples of how different species were either split into more species or clumped together, will also be considered in order to determine the threshold for considering two specimens to belong to two different species. The literature on current speciation models and how the current conception of speciation can be adapted to ancient hominin species will be reviewed as it contributes to a more nuanced understanding of which information is most relevant when looking for evidence (or information that can be used for the inference) of speciation in the hominin fossil record.

There are many different kinds of data that may potentially be collected from a fossil in order to analyze it. Morphological characteristics, any endogenous genetic data, and the age

of the fossil as estimated by various dating methods are all potential indicators of which species a fossil belongs to. Additionally, data on the variation that is considered expected for a population, as well as the variation in sexual dimorphism across different hominin species, is also useful in determining which characteristic differences are indicative of speciation. The ability to compare different aspects of a fossil to the aspects of the other fossils in the record can help place the fossil in the most accurate location on the phylogenetic tree. Gaps in the fossil record can also be of significance, as they can be indicative of events and environmental changes that were unfavorable for the preservation of fossils. Recognition of the gaps in the information available about a specific fossil can also help prevent errors in analysis and classification, and can contribute to the analysis of the validity of the current species classification of a specimen.

The phylogenetic tree of the genus *Homo* will be reviewed by evaluating the subspecies of three taxa in *Homo*: *Homo erectus*, *Homo habilis*, and *Homo sapiens*. This is due to the fact that, under the 'lumping' approach, the smallest number of species possible in the phylogenetic tree is three, and this is achieved by making H. *erectus*, H. *habilis*, and H. *sapiens* inclusive of all other proposed species in *Homo* (Wood & Lonergan, 2008). A review of H. *erectus*, for example, will involve going through each of the subspecies that are classified as separate hominin species under the 'splitter approach', and reviewing the evidence in order to evaluate whether they are truly a subspecies, as under the 'lumper' approach, or a separate species. This method will ensure that all the hypothesized hominin species are reviewed, and after the three case studies the new suggested phylogeny for the genus *Homo* will be constructed and described.

Part 2: Dating Methods

There are a number of dating techniques that can be used to determine the age of a particular fossil. They fall into two broad categories: relative and absolute. Various combinations of methods may be used depending on the available evidence and the quality of the fossil itself. Due to the nature of the hominin fossil record and the gaps in data, many methods are used to more accurately estimate the timelines for different species (Brumm et al., 2016;Douka et al., 2019;Jensen-Seaman & Hooper-Boyd, 2013).

Relative Dating

Relative dating methods involve the ordering of geological formations and fossil clusters that are found near or with the target fossil, and using the relative order of events to estimate the fossil's age ("Dating Rocks and Fossils," 2013). The estimated ages of matter from around the fossil's excavation site can then also be used to place the fossil's numerical age, especially when used in combination with one or more absolute dating techniques ("Dating Rocks and Fossils," 2013). Relative dating is often used to order geological events and accurately place the fossil in the timescale of those events ("Dating Rocks and Fossils," 2013). Methods considered to be relative include obsidian hydration and the dating of stratigraphic units based on the law of superposition (Munyikwa, 2018). Since these methods can be used even if the target fossil is not well-preserved, relative dating techniques are often used in combination with absolute dating in order to better ascertain where and when the species of the fossil existed ("Dating Rocks and Fossils," 2013).

The law of superposition states that the oldest layer of rock in rock formations will be at the bottom ("Dating Rocks and Fossils," 2013; Munyikwa, 2018). This allows for a placement of the age of the fossil depending on which layer it is found in, and also allows for the supposition that a fossil cannot be older than its rock layer (Munyikwa, 2018). The dating of animal fossils found alongside the target fossil can also aid in dating the rock layer of the fossil and placing its age;

the principle of faunal succession, which holds that different fossil species appear and disappear in the same order, can be used to identify the temporal overlap of two different species' existence, and thereby place in time the formation of the rock layer in which they are both found ("Dating Rocks and Fossils," 2013). The set of fossil species from different strata (rock layers) can then be compared to order them, and the estimates of when the different animals went extinct provide an estimate of the age of the target fossil ("Dating Rocks and Fossils," 2013;Sullivan et al., 2020).

Obsidian hydration refers to the dating of obsidian found in archaeological sites in order to estimate the age of the site. The method estimates the age of the volcanic glass by measuring the depth of the water that has diffused into it over time. The depth measurements can be combined with estimates of diffusion rates (which are influenced by the glass type and environmental conditions) to place the age of fossils and sites (Anovitz & Fayek, 2018; Munyikwa, 2018). This method is generally less reliable than other dating techniques, although its accuracy has been improved in recent years (Anovitz & Fayek, 2018).

Absolute Dating

Absolute dating methods provide more direct estimates of the fossil's age, and are therefore more accurate and yield more information about a fossil's history ("Dating Rocks and Fossils," 2013). Absolute dating methods can be used not only to order events, but also provide direct numerical estimates of specimen ages ("Dating Rocks and Fossils," 2013). Because of this they are usually used in combination with relative methods, and can be used to date fossils of other species, rock layers, etc. and indirectly estimate the target fossil's age, especially in cases where the fossil is not well-preserved ("Dating Rocks and Fossils," 2013;Gaur, 2020) Absolute dating techniques can be broadly divided into radiometric and non-radiometric methods (Gaur, 2020). Radiometric methods are based on rates of radioactive decay of different radioactive elements (Gaur, 2020).

Radiometric Dating

Carbon-14 Dating

Carbon-14 dating is the oldest and most well-known of the radiometric dating methods ("Dating Rocks and Fossils," 2013; Gaur, 2020). Carbon-14 is a radioactive carbon isotope which makes up 0.00000000010 % of atmospheric carbon (Gaur, 2020). The half-life of C-14 is approximately 5,730 years: it takes 5,730 years for a current amount of C-14 to decay until half of the amount is remaining (Gaur, 2020). The C-14 concentration in the atmosphere is maintained at a constant level due to the activity of ionizing radiation that produces C-14 from nitrogen molecules in the upper atmospheric levels (Gaur, 2020). Due to this, living organisms uptake C-14 at a relatively constant level from the environment as well, as C-14 is incorporated into carbon dioxide and other carbon-based compounds (Gaur, 2020). However, after the organism's death, the C-14 in its body stops being replenished, and so starts reducing in concentration as it decays (Gaur, 2020). This decay of C-14 in fossils allows for a comparison between C-14 concentrations in fossils and the atmosphere, and fossil ages can be estimated by calculating how many half-lives are needed for the C-14 atmospheric concentration to reach the concentration found in the fossil ("Dating Rocks and Fossils," 2013;Gaur, 2020;Sullivan et al., 2020). The ratio of C-14 to stable carbon isotopes (such as C-12 and C-13) is usually measured in order to more accurately estimate the original amount of C-14 in the organism when it was alive, and thereby estimate the amount of half-lives needed for the present level (Gaur, 2020). C-14 dating can estimate ages of fossils from 50,000 to 70,000 years at most; after 70,000 years, the C-14 levels in the specimen become too low to be accurately detected.

There are other limitations to C-14 dating as well. C-14 dating interacts directly with the organic material, as the carbon isotope ratios need to be measured, which usually partially damages the specimens being studied. This makes it difficult to apply to valuable hominin fossils that are rare or historic finds; additionally, hominin fossils are often categorized into different species, or used

as a basis for discovery of a new species, based on not only age and geographical data, but also morphological features (Appelt, 2017;Bermúdez de Castro, Arsuaga, et al., 2019;"Dating Rocks and Fossils," 2013). Morphological data are instrumental in evaluating the degree of differentiation between different fossils, which are often dental samples or fragments of larger bones such as the pelvis (Appelt, 2017; Bermúdez de Castro, Arsuaga, et al., 2019). As fossil preservation is necessary for many hominin fossil discoveries, the uses of carbon-14 dating can be limited even when the fossil is young enough for the method to be accurate (Gaur, 2020). Although C-14 dating is still useful for dating younger fossils and organic materials that are found alongside them, there are other radiometric techniques that are better suited to older hominin fossils.

Potassium-Argon Dating

Potassium-argon dating is most often used to date rocks, especially rock formations that are not sedimentary (Gaur, 2020). For example, igneous formations that result from volcanic eruptions covering strata in which fossils are found can be dated using this method, which is useful in narrowing down the age ranges of different specimens (Gaur, 2020). The method utilizes the difference in radioactive decay rates between Argon-40 and Potassium-40, comparing the ratio of K-40 to Ar-40 in samples (Gaur, 2020). There are three naturally occurring isotopes of potassium-K-40, K-39, and K-41 (Gaur, 2020). K-40 is the radioactive isotope, and can decay into two elements, calcium-40 and argon-40, in a ratio of 89:11 (Gaur, 2020). When lava flows start cooling and solidifying, the decay of potassium produces argon-40 that accumulates as a gas trapped in the rock layer (Gaur, 2020). The older the rock, the more argon-40 will accumulate in it (Gaur, 2020). The amount of argon-40 trapped in the rock can be compared to the potassium to estimate the age (Gaur, 2020). This is done by melting the rock samples and measuring the quantity of argon-40 with a mass spectrometer (Gaur, 2020). Potassium/argon dating has been particularly useful in dating hominid remains found in between lava flows,

especially in eastern Africa (Gaur, 2020). It was also used to date the fossil of Australopithecus afarensis known as Lucy, found in Ethiopia (Gaur, 2020).

Since the half-life of potassium-40 is 1.3 billion years, potassium/argon dating can be used for very old fossils and samples (Gaur, 2020). Potassium/argon dating has limited usefulness when dating samples younger than 100,000 years old, however, as the amount of argon-40 produced is too small to measure (Gaur, 2020). Another limitation of this method is that it can only be used on stratigraphic formations rather than the fossils themselves and is best suited to rock layers from volcanic origins (Gaur, 2020).

Argon-argon Dating

The argon-argon dating method works on the same principles as the potassium-argon method and is a more widely applicable version of it (Jourdan et al., 2014). Instead of measuring the amount of potassium-40, the amount of argon-39 present is used and compared to the amount of argon-40 ("Argon Geochronology," n.d.). The argon-39 acts as a proxy for potassium-40 as it is produced from potassium-40 by a fast neutron reaction ("Argon Geochronology," n.d.). By utilizing this method, rock samples that don't contain potassium can also be dated with only the ratio of the different argon isotopes ("Argon Geochronology," n.d.). The sample is irradiated in order to produce argon-39 ("Argon Geochronology," n.d.).

Uranium-series Dating

Uranium-series dating, also known as the uranium disequilibrium method, is based on three decay chains in the uranium series ("U-Series Dating," n.d.). The chains start with uranium-238, uranium-235, or thorium-232, and all the starting isotopes eventually decay into stable isotopes of lead ("U-Series Dating," n.d.). Rather than the ratio of isotope amounts, the ratio of the radioactive activity of the different isotopes is measured in order to determine the age of sample ("U-Series Dating," n.d.). This is because the isotopes are part of a decay chain, and so their activity rates relative to each other change and equilibrate with time ("U-Series Dating," n.d.).

Uranium-thorium dating, for example, can be applied to samples containing calcium carbonate, including shells and rock formations ("U-Series Dating," n.d.). This method involves measuring the disequilibrium between the radioactive decay of the isotopes uranium-238 and thorium-234 ("U-Series Dating," n.d.). Uranium-thorium dating is often paired with uranium-234/uranium-238 dating in order to improve the accuracy of the age estimate ("U-Series Dating," n.d.).

Uranium-series dating can be used on materials found encasing the hominin fossils, as well as directly on the fossils themselves (especially dental materials) (McDermott et al., 2012). Limitations of uranium-series methods include the different uranium uptake rates of fossilized dental materials, which lower accuracy when compared to speleothem formations (stalactites, stalagmites, flowstones) and similar materials that surround fossils (McDermott et al., 2012). Direct estimates for bones and shells are therefore less reliable than for speleothems (McDermott et al., 2012). However, the half-lives of the parent uranium and thorium isotopes used for this method range from approximately 700 million years all the way to 14 billion years ("Geologic Time", 2019). Since these isotopes are very stable and have very long half-lives, they can be used to date a large range of materials and samples.

Electron Spin Resonance Spectroscopy

Electron spin resonance (ESR) spectroscopy is a relatively new dating technique that works on a wide range of materials and samples, including tooth enamel, speleothems, shells, corals, and volcanic minerals (Grun & Stringer, 1991). ESR dating relies on the properties of minerals such as hydroxyapatite, which is the major mineral constituent of bones and teeth; these minerals, immediately after burial, can contain electrons in either their ground states or excited states (Grun & Stringer, 1991). As time passes, electrons are transferred to the excited state as a result of radioactive activity from the environment (as well as fossil uptake of radioactive isotopes), after which they will usually return to the ground state as it is more stable (Grun & Stringer, 1991). However, these mineral structures have irregularities and impurities that can

affect this process and trap electrons at intermediate states between the ground and excited state (Grun & Stringer, 1991). ESR spectroscopy measures the number of trapped electrons, as the number of traps and therefore the number of trapped electrons increases as the age of the material increases (Grun & Stringer, 1991).

This method can data materials within a wide age range, from approximately 500 years old to nearly 10 million years old (Blackwell, 2005). The error ranges from 2 to 20 %, and the method has been refined to get more accurate estimates directly from fossils, including non-dental fossil materials (Blackwell, 2005). Other important advantages for ESR spectroscopy include the ability to directly date fossils, improved accuracy with dating mollusk fossils in comparison to uranium-series dating, and a wider range of datable materials relative to other radiometric methods such as potassium-argon or argon-argon dating (Blackwell, 2005). These properties make ESR spectroscopy suited to analysis of hominin fossils, both alone and in combination with other methods; for example, ESR spectroscopy was instrumental in the dating of fossilized teeth from Flores, Indonesia, which are attributed to *Homo floresiensis* (Blackwell, 2005).

Optically Stimulated Luminescence

Optically stimulated luminescence (OSL) dating works by measuring the last exposure of the fossil to sunlight (Aitken, 2001). It works in a similar way to ESR spectroscopy, as it measures the number of trapped electrons in the given material (Aitken, 2001). The trapped electrons are stimulated by optical means, including lasers, xenon lamps, halogen lamps, and light-emitting diodes (Aitken, 2001). This optical energy input allows for trapped electrons to gain energy and diffuse throughout the material (which is usually crystalline) (Aitken, 2001). As they diffuse through the crystal structure they tend to gather at recombination centers, which are locations in the material that have a net positive charge and will therefore stabilize the free electrons by making them part of a bond (Aitken, 2001;Baker & Bradley, 2006). This reaction results in the release of energy as photons, which can then be measured and compared with the energy

released when the sample is dosed with nuclear radiation from a calibrated source (Aitken, 2001). The dose of nuclear radiation needed to produce the same luminescence as exposure to natural light does in the sample is then observed, and the dose is divided by the dose rate in order to find the time of last exposure to sunlight for the sample (Aitken, 2001). This method can be used to date any samples with mineral content, including rock formations, soils, and volcanic rock from around the fossil of interest (Aitken, 2001). OSL dating can reliably estimate ages up to a million years (Aitken, 2001). Since the method cannot date the fossil directly, it is used to date the sediments immediately underlying and overlying hominin fossils, and can date the fossil by providing the timeframe of deposition of the fossil-bearing soil or rock layer (Demuro et al., 2019).

Thermoluminescence

Thermoluminescence (TL) dating is very similar to OSL dating (Aitken, 2001). The trapped electrons in the sample are stimulated through thermal tools such as hot gas, hot air, lasers, and hot planchets (Schauer et al., 2003). The material then releases the excess energy as photons, which can be measured and analyzed in the same way as for OSL (Aitken, 2001; Schauer et al., 2003). TL and OSL dating are often combined when estimating the ages of fossil-bearing sediment and rock layers (Aitken, 2001; Demuro et al., 2019).

The sample can also be irradiated from a light source with known strength, and then heated at a constant rate, which results in the emission of thermal radiation (Abraham et al., 2018). The intensity of the emitted radiation is plotted as a function of the sample temperature (Abraham et al., 2018). The sample's sensitivity to radiation exposure, as well as the rate at which it is irradiated over time in the environment, can both be calculated in order to estimate the age of the sample based on the strength of the radiation it emits with increasing temperature (Abraham et al., 2018).

Amino Acid Racemization

Amino acid dating can also provide age estimates for fossils and rock layers (Ryan et al., 2020). All amino acids, with the exception of glycine, are optically active, and have both D- and L- configurations that are mirror images (Ryan et al., 2020). Since living organisms exclusively use the L-isomer for all amino acids, the ratio of the D- to the L- isomers can indicate how long ago a specimen died (Ryan et al., 2020). After an organism dies and fossilizes, the ratio of the D- to the L- isomer increases from near zero to one as time passes, as the amino acids left racemize (Ryan et al., 2020). Therefore, the closer the D- to L- ratio of amino acids from the fossil and rock is to one, the longer the time elapsed since the death of the organism (Ryan et al., 2020). The shells of molluscs found around the target fossil are particularly useful in yielding age information from amino acid isomer ratios (Kosnik et al., 2017). The use of amino acid racemization is useful as it can date mollusk shells, bones, and teeth directly (Aitken, 2001).

The reliability of this method has improved over time, as specific amino acids (aspartic acid, isoleucine, and alanine) have been identified as better preserved and more accurate as chemical clocks (Aitken, 2001). The measurement of aspartic acid racemization can yield estimates from 50 to 100 thousand years ago, while isoleucine can be used to estimate dates up to 500 thousand years ago (Aitken, 2001). This is due to isoleucine's tendency to epimerize (change from L- to D- configuration at one of two stereocenters) into D-alloisoleucine (Aitken, 2001). The D- and L- forms of amino acids can be differentiated and detected only through optical means, as their chemical and physical properties are very similar (Aitken, 2001). In the case of epimerization, as with isoleucine, the epimer has different physical and chemical properties as well, and so can be detected and measured more accurately (Aitken, 2001).

Characteristic amino acid isomer ratios (D- to L-) have also been established for specific climatic periods, which has improved the accuracy of amino acid dating of different specimens by taking into account the environmental effects on stereoisomer ratios (Aitken, 2001).

Molecular Clocks

Although genetic data are usually not well-preserved in hominin fossils, there have been advances in dating techniques that can extract increasing amounts of information from the genetic material that is found (Ho et al., 2016). The rates of recombination, DNA mutations (especially in non-coding regions), protein structural changes and amino acid substitutions, etc. can all be used to compare different genetic samples and detect how long ago the species originated and diverged from modern species (Ho et al., 2016). These rates of genetic changes are assumed to be constant over time and can therefore provide estimated ages of genetic material found in or with hominin fossils (Ho et al., 2016). For example, the analysis of an amino acid sequence that coded for collagen in bone can be used to date fossils as belonging to Neanderthals living around 40 thousand years ago (Welker et al., 2016). The role of molecular clocks in dating samples from hominin species is generally limited however, due to the dearth of preserved DNA, but where possible they can help refine and confirm age estimates obtained by other methods (Jensen-Seaman & Hooper-Boyd, 2013).

Mitochondrial DNA

Mitochondrial DNA (mtDNA) is another type of evidence that can help add to and refine timelines and age estimates for hominin fossils, as well as reveal more information about interactions between different hominin species (Douka et al., 2019). While mtDNA suffers from the same limitations as genetic material in general does, it can reveal more specific information about hominin species when it is available, due to mtDNA being inherited only from the mother (Douka et al., 2019). DNA sequencing, and the information revealed by DNA analysis, were both integral to the discovery of the existence of Denisovans, a hominin group whose remains were found in Siberia (Douka et al., 2019). The genetic information found was also important in determining the age of the Denisovan remains, with the oldest fossil being dated at 195 thousand years old (Douka et al., 2019). The case of the discovery of the Denisovans also

illustrates the utility of mtDNA analysis in discovering genetic admixture between different hominin groups, as it provided evidence of genetic admixture between Neanderthal and Denisovan populations (Douka et al., 2019).

Accelerator Mass Spectrometry (AMS)

Accelerator mass spectrometry is not a dating method itself, but is a valuable analytical technique that can determine the concentration of radioactive isotopes in a relatively small amount of a sample (Linick et al., 1989). It is most used in conjunction with radiocarbon dating, and involves accelerating ions in the sample to very high velocities, which allows it to separate radioactive isotopes like C14 from other atoms and functional groups that have the same molecular weight and are present in much higher quantities (Linick et al., 1989).

Zooarchaeology by Mass Spectrometry

Zooarchaeology by mass spectrometry, or ZooMS, is a minimally destructive dating and species identification method that can be used on mineralized collagenous materials such as bone (McGrath et al., 2019). Collagen is highly conserved across vertebrates, and is therefore a dominant protein in fossil remains; however its amino acid sequence demonstrates sufficient variation to discriminate between the remains of closely related species, which is highly useful for taxonomic classification of fossil specimens that are often heavily fragmented and yield no morphological information (McGrath et al., 2019). It involves demineralizing bone samples in order to isolate the collagen, which can then be identified and separated from the collagen of other individuals through the detection of the presence or absence of specific peptide markers (McGrath et al., 2019).

Magnetostratigraphy Dating

Magnetostratigraphy is a dating method that depends on sedimentary rocks acquiring magnetic particles as they form, with the magnetic field being oriented in the same direction as the Earth's magnetic field at the time of formation (Garces, 2015). Then, the reversals of Earth's magnetic field over time can be used to zone stratigraphic layers into different time periods, as the

changes in the magnetic field direction are non-periodic, meaning that each reversal has a different length of time associated with it (Garces, 2015).

Part Three: Taxonomic Approaches

Definition of a species

Populations that live today are often classified as different species based on different criteria and definitions of species. Many of these criteria are not suitable for the classification of fossils from the hominin fossil record-the definition used by the biological species concept, for example, has limited scope when trying to place fossils in relation to each other because it requires information reproductive isolation and the viability (or lack thereof) of hybrids between different populations (Lagache et al., 2013). Most species concepts rely on empirical observations of populations, which is also not possible in the case of hominin species (Lagache et al., 2013). DNA evidence is uncommon, and even when present may not be available for analysis due to the importance of hominin fossil preservation (Balakrishnan, 2005). Morphological information plays a significant role in the placement of hominin fossils as belonging to one species or another, so information that can only be analyzed by damaging samples, such as genetic information, has a relatively limited scope(Wood & Lonergan, 2008). Due to limitations of the fossil record, the phylogenetic species concept is the most useful in delineating different species within *Homo*.

Taxonomic Hypotheses

The criteria for the degree and number of differences that are sufficient to delineate different species has to therefore be adapted for the limitations of the fossil record. There are two broad categories that the various taxonomic hypotheses on hominin speciation can be divided into: the ‘lumper’ approach and the ‘splitter’ approach.

Lumping and Splitting Taxonomy

The ‘lumping’ taxonomic hypothesis is the less speciose of the two, and involves grouping many fossils (and the individuals or populations they represent) into a relatively small number of species (Wood & Lonergan, 2008). This approach has a relatively higher threshold for the degree of differences that are needed to classify a fossil as belonging to a new species (Wood & Lonergan, 2008).This splitting taxonomic hypothesis is more speciose, and generates many more species (Wood & Lonergan, 2008). The degree of difference and variation in fossils needed to support the existence of a new species is lower in this approach (Wood & Lonergan, 2008). Many fossils that are classified under H. *habilis* and *H. erectus* in the previous hypothesis are classified as belonging to new and separate species with the splitter approach (Wood & Lonergan, 2008).

Factors in the Interpretation of Morphological Data

Biological Age and Sex

The age of the fossil, as well as the age of the individual at the time of death, can both be significant in the classification process (Wood & Lonergan, 2008).The sex of the individual to whom the fossil belonged can affect inferences about the lifestyle and behavior of the individual, which can then affect whether it is classified as a member of a pre-existing species or as evidence for a new species (Choudhuri, 2014; Wood & Lonergan, 2008). For example, if a fossil of a relatively small individual is found, the question of whether it belongs to a predetermined species can be decided by how the relative size and morphological differences are interpreted; the fossil can be viewed as within the normal estimates for sexual dimorphism in the old species, or it can be seen as evidence for the existence of a separate population that was genetically different enough to produce phenotypic differences beyond what could be accounted for by sexual dimorphism (Alonso-Llamazares & Pablos, 2019). Bones that are sexually dimorphic, such as the pelvic or foot bones, are important in classifying the sex of the individual

specimen as well as better defining the amount of variation within established species (Alonso-Llamazares & Pablos, 2019).

Disease

Evidence of disease and various health conditions present in a fossil can support inferences about diet, lifestyle, and movement patterns of the individual (Wood & Lonergan, 2008). This then provides clues as to which species most closely fits the inferred characteristics, or if the individual is different enough in both morphology and behavior to provide evidence for a new population or species (Wood & Lonergan, 2008). Whether the fossil specimens under consideration are from individuals who were affected by health conditions and developmental abnormalities can affect the inferences made for both phylogenetic and taxonomic placement.

Expected Range of Variation

The estimates of phenotypic variation within an established species, such as *H. erectus*, affect whether the differences found in a new fossil will be classified as belonging to a separate species, or as close enough to the expected characteristics of the established species to be classified as belonging to it (Wood & Lonergan, 2008).

Geography

The geographical location of the fossil provides additional valuable information about the individual-it narrows down the possible species that the fossil could belong to, and also allows for inferences on how the individual interacted with its environment, and whether those interactions are evidence of a new population that hasn't been previously discovered (Wood & Lonergan, 2008). Geographical range overlap is also a factor in determining lineages of different populations (Wood & Lonergan, 2008).

Part Four: Re-evaluation of Taxa in the genus *Homo*

The label of hominin is inclusive of six genera: *Homo*, Australopithecus, Paranthropus, Ardipithecus, Orrorin, and Sahelanthropus. This paper is concerned with the evaluation of the

species classifications and relationships within the genus *Homo*, which encapsulates all of the human species known to have existed (Robson & Wood, 2008). Depending on the taxonomic hypothesis, different phylogenetic trees can be generated that have very few or very many hominin species and relationships (Robson & Wood, 2008). The current evidence for the existence of each species in the genus *Homo* will be reviewed in order to ascertain the classification of different fossil discoveries across the hominin phylogenetic tree that is most consistent with the available data and most recent findings in fossil analyses.

Phylogenetic Tree Size Range

The phylogenetic tree with the smallest number of species classifies all fossils from the genus *Homo* under one of three species: *Homo erectus*, *Homo habilis*, and *Homo sapiens* (Gunbin et al., 2015; Wood & Lonergan, 2008). The fossils that form the basis for additional species classifications in the splitting taxonomy are instead classified under various subspecies of these three species (Wood & Lonergan, 2008). The largest phylogenetic tree includes the three previous species, as well as *H. rudolfensis*, *H. ergaster*, *H. floresiensis*, *H. antecessor*, *H. heidelbergensis*, *H. naledi*, *H. luzonensis*, *H. neanderthalensis*, and *H. denisova* (Gunbin et al., 2015;Wood & Lonergan, 2008).

Classifications under debate

In the lumping taxonomy, *H. rudolfensis* is classified as a subspecies of *H. habilis*, while *H. ergaster*, *H. floresiensis*, *H. antecessor*, and *H. heidelbergensis* are all classified as subspecies of *H. erectus* (Wood & Lonergan, 2008). Neanderthals and Denisovans are classified as *Homo sapiens* neanderthalensis and *Homo sapiens* denisova respectively, as subspecies of *H. sapiens* (Gunbin et al., 2015). Other lumping taxonomies may also classify *H. neanderthalensis* as a subspecies of *H. erectus* and may also classify *H. antecessor* and *H. heidelbergensis* as subspecies of *H. sapiens* (Wood & Lonergan, 2008).

Homo erectus

H. floresiensis, *H. luzonensis*, *H. ergaster*, and *H. antecessor* are classified as subspecies of *Homo erectus* under the least speciose lumping taxonomy. Although *H. neanderthalensis* is more often classified as a subspecies of *H. sapiens*, there are taxonomic hypotheses that place it under *H. erectus* as well (Gunbin et al., 2015; Wood & Lonergan, 2008). *H. erectus* may also include *H. heidelbergensis* under lumping taxonomies (Gunbin et al., 2015; Rightmire, 2004; Wood & Lonergan, 2008). The question of which fossils should be included under *H. erectus* intersects with the question of whether fossil groups from the same population are distinct enough to be classified as their own species. Discussions of the variation present in the *H. erectus* hypodigm when different fossils are excluded or included are therefore relevant to the taxonomic and phylogenetic placement of fossil groups that have been discovered across Europe and Asia, as well as eastern and southern Africa. The eastern African fossils consist of those attributed to African *H. erectus*, or *H. ergaster*. African *H. erectus* also includes fossils from Dmanisi, Georgia, the fossils found in Indonesia and China constitute the Asian *H. erectus* variant, and fossils attributed to *H. antecessor* and *H. heidelbergensis* from across Europe may also be classified as European *H. erectus* (Terhune et al., 2007).

Homo floresiensis

The fossils for *H. floresiensis* were discovered in 2003, close to Flores, Indonesia, in the Liang Bua cave (Wood & Lonergan, 2008). The first fossil specimen, LB1, consists of a partial adult skeleton (Wood & Lonergan, 2008). In LB1 the skull as well as well as the right pelvic bone, tibia, and femur have been preserved (Wood & Lonergan, 2008). The second fossil, LB2, consists of a left P3 tooth (Wood & Lonergan, 2008). A left radius was also found at this site (Wood & Lonergan, 2008). On the basis of these fossils, the existence of the population they belonged to has been dated to between 95 and 12 thousand years ago; multiple dating

methods, including radiocarbon, electron spin resonance, luminescence, and uranium-series techniques, were used to determine this range (Wood & Lonergan, 2008).

There are a range of hypotheses regarding the placement of *H. floresiensis* in the hominin phylogenetic tree (Argue et al., 2017). One is that it is a separate species on its own derived from *H. erectus*, and a further variant of this view places *H. floresiensis* as a subspecies of *H. erectus* (Argue et al., 2017). Another view is that it is descended from an older species with roots in Africa, such as *H. habilis* (Argue et al., 2017). The third hypothesis places *H. floresiensis* as a population of *H. sapiens* that had a pathology, causing it to be reduced in stature (Argue et al., 2017).

Possibility of *H. erectus* or *H. habilis* lineage

H. erectus was well distributed throughout Asia, and Asian *H. erectus* fossils have been found in Indonesia, although they have not been found at Flores or in the Liang Bua cave (Argue et al., 2017; Wood & Lonergan, 2008). Arguments for *H. floresiensis* being descended from Asian *H. erectus* have two variants; the first is that it is a distinct species derived from *H. erectus*, and the second is that it is a distinct population that is descended from *H. erectus* but not a separate species altogether (Argue et al., 2017; Wood & Lonergan, 2008). The grounds for asserting that *H. floresiensis* is descended from *H. erectus* include the similarities in geographical distribution and dental characteristics (Argue et al., 2017; Wood & Lonergan, 2008; van den Bergh et al., 2016). The geographical distribution of *H. erectus* increases the probability of a closer relationship with *H. floresiensis*, as *H. erectus* is the only hominin known to have lived in the islands of Southeast Asia before the arrival of *H. sapiens* (Baab et al., 2013; Kaifu et al., 2015; Wood & Lonergan, 2008).

The dental morphology of *H. floresiensis* is somewhat anomalous compared to any of the older species that it could be related to; a comparison of teeth from the fossils LB1, LB6, LB15, and LB2 with teeth from Indonesian *H. erectus* as well as *H. habilis* revealed that 10 out of 26 dental traits were relatively primitive and similar to the dental traits of the posited ancestral populations (van den Bergh et al., 2016). 4 characteristics were unique to *H. floresiensis*, and a further 2 showed higher similarities to the teeth of *H. sapiens* (van den Bergh et al., 2016). Another 10 traits were also primitive, but shared with *H. sapiens* due to the large variation in dental morphology exhibited by anatomically modern humans (van den Bergh et al., 2016). *H. floresiensis* exhibits primitive traits for canines and premolars, but shows very modern traits for the molars, which is unlike the patterns exhibited by the *H. erectus*, *habilis*, or sapiens (Argue et al., 2017; van den Bergh et al., 2016). The primitive dental traits are most similar to those of *H. erectus*, and many of them are traits that appear in the fossil record after *H. habilis* (van den Bergh et al., 2016). Therefore, when considering dental characteristics, despite the unique differences *H. floresiensis* has, it is most likely to be related the closest to *H. erectus* (van den Bergh et al., 2016).

LB1, which is the most complete fossil specimen for this population, consists of a skull that shows many features that are common to *H. erectus*; these include increased skull thickness, low cranial vault, and a mastoid fissure (Baab et al., 2013; van den Bergh et al., 2016). There are fewer postcranial similarities between *H. floresiensis* and *H. erectus* (Baab et al., 2013; Kaifu et al., 2015). There is also a significant difference in cranial volume; the measurements of endocranial volume (ECV) ranged from 380 to 430 cubic centimeters (cc), with the average around 400 cc (Kubo et al., 2013). The ECV was again measured to produce a more accurate value of 426 cc (Kubo et al., 2013). This has been interpreted both as pointing to a lineage from *H. habilis*, or as pointing to *H. erectus* lineage due to the cranial size being large enough to have been a case of an *H. erectus* subpopulation that underwent island dwarfing (Kubo et al., 2013).

The small cranial capacity has been used to argue that *H. floresiensis* is descended from an older population than the Indonesian *H. erectus* as well. However, the relative lack of evidence for the existence of the more primitive species within *Homo* across Asia (and Southeast Asia especially) suggests that a lineage through *H. erectus* is more likely (Kubo et al., 2013).

Possibility of *H. sapiens* lineage

Although *H. floresiensis* specimens have morphological traits that are primitive and more similar to *H. erectus* or *H. habilis* compared to *H. sapiens*, they also show modern or derived characteristics, as well as numerous differences and unique feature patterns, especially in the postcranial fossils (Kubo et al., 2013). There are a number of modern features that have been used to suggest that *H. floresiensis* was not only not a separate species, but was instead a population of *H. sapiens* that was afflicted by a pathology that stunted its growth and stature (van den Bergh et al., 2016). For example, it was suggested by Thorne et. al that *H. floresiensis* was an *H. sapiens* population affected by Down's Syndrome (Baab et al., 2013). However, more recent analyses of those traits of Down's syndrome that can be detected in hard tissue support the hypothesis that *H. floresiensis* did not have DS (Baab, Brown, et al., 2013). The endocranial volume of LB1, which was used to argue the presence of pathology, was found to be significantly smaller than the endocranial volume of present-day DS patients, who have volumes around 1174 cc (Baab, Brown, et al., 2013). An analysis of cerebellum size yielded similar results, with LB1 demonstrating a reduced cerebellar volume but increased cerebellar width, which is uncharacteristic of DS patients (but is similar to modern humans without pathology) (Baab, Brown, et al., 2013). DS patients have a flat cranial base relative to controls, and the cranial base of LB1 was found to be even further away from the DS average than modern human controls (Baab, Brown, et al., 2013). Additionally, where DS patients have an underdeveloped mandible, the mandible of LB1 is especially large for its size, and is relatively long as well (Baab, Brown, et al., 2013). The short stature of LB1 and LB8 were found to be

outliers compared to DS patients across several populations, and although the femur: foot ratio is increased in both DS patients and LB1 relative to modern human controls, the LB1 femur: foot ratio of 0.68 is extremely distant from both DS patients (0.56) and controls (0.53) (Baab, Brown, et al., 2013).

This hypothesis was also first proposed on the basis of erroneous initial age estimates for the LB group of fossils (Brown et al., 2004). The initial dates were estimated by dating the charcoal samples directly above or in the stone layer from which the fossil was recovered, along with faunal remains that were preserved with them (Brown et al., 2004). LB1, which was designated the type specimen for the taxon, was dated to 18 thousand years old by accelerator mass spectrometry (Brown et al., 2004). The upper and lower brackets were from 35 to 14 thousand years old, found by luminescence dating of charcoal from the stratigraphic layer of LB1 (Brown et al., 2004). LB2, a premolar, was found in a slightly older stratigraphic layer and was given a lower bound of 37.7 thousand years by U-series dating of the stratigraphic layer above it, as well as an upper bound of 74 thousand years by ESR and U-series dating of a *Stegodon* molar that was found in the layer below that of LB1 (Brown et al., 2004). These ages, if accurate, would have increased the likelihood of *H. floresiensis* having descended from or been a variant of *H. sapiens* due to providing evidence of their coexistence in Indonesia, especially as faunal remains from the fossil site were dated to have existed as early as 12 thousand years ago (Sutikna et al., 2016). However, in a revised stratigraphic and direct fossil analysis, Sutikna et al. used U-Th dating on three *H. floresiensis* ulnae that yielded minimum age estimates of 54.6 thousand years for the youngest bone, and 71.5 thousand years for the oldest. This was combined with a reanalysis of the stratigraphic layer that *H. floresiensis* was discovered in, which found that the deposits that contained the fossils were sediment layers that were interstratified with layers of limestone, speleothem, and gravel, and that these deposits were covered by a two-meter-thick set of tephras (layers of rock fragments resulting from volcanic eruption) (Sutikna et al., 2016). The tephras formed a pedestal extending into the center of the

cave, and some of the tephra layers had been reworked into younger rock depositions, while tephra fragments had become intermixed with overlying sediment layers (Sutikna et al., 2016). Due to this, the sediment samples that had been dated using luminescence, which were collected from the sediment layer of *H. floresiensis* as well as layers up to one meter above it, were contaminated with grain mixtures sourced from multiple depositional layers, which when reanalyzed with TL and infrared stimulated luminescence gave ages from 170 to 10 thousand years ago, confirming the lack of reliability of the previously used samples (Sutikna et al., 2016). When the true fossil-bearing pedestal deposits themselves were dated, they gave ages of 100 to 60 thousand years ago, corroborating the direct dates obtained from the ulnae (Sutikna et al., 2016). The newer and more robust date ranges suggest that the survival of *H. floresiensis* after 50 thousand years ago is unknown, and so it cannot be assumed that *H. floresiensis* coexisted with *H. sapiens,* although modern humans had reached Australia by that time period (Sutikna et al., 2016). The revised dates indicate that it is unlikely that *H. floresiensis* descended from *H. sapiens.*

Apart from the temporal range data, the morphological analysis of LB fossils provides additional evidence against the hypothesis of *H. floresiensis* having any *H. sapiens* lineage or pathology (Baab, Brown, et al., 2013). A larger proportion of the features that *H. floresiensis* has that aren't similar to *H. erectus* are primitive rather than modern, or are unique to the population, which suggests strongly that the youngest possible origin population of *H. floresiensis* would be *H. erectus* (Baab, Brown, et al., 2013).

Homo antecessor

Homo antecessor fossils were first discovered in a series of explorations in Spain between 1994 and 1996 (Wood & Lonergan, 2008). They were labeled as ATD6-1 and ATD6-5, and more fossils have been discovered since, as recently as 2007 (Bermúdez de Castro, Carbonell, et al.,

2017). The fossils consist mostly of cranial and dental fragments (Bermúdez de Castro, Carbonell, et al., 2017; Wood & Lonergan, 2008). The oldest remains have been dated to at least 780 thousand years ago, and the temporal range for this population is estimated to be from 1.2 million to around 80 thousand years ago (Bermúdez de Castro, Carbonell, et al., 2017). The main hypotheses on *H. antecessor*'s placement in hominin phylogeny include *H. antecessor* as the ancestral species for Neanderthals (Bermúdez de Castro, Carbonell, et al., 2017).

The majority of *H. antecessor*'s cranial and dental features are primitive, and resemble *H. erectus* and *H. ergaster* (which is also classified as African *H. erectus*) (Bermúdez de Castro, Carbonell, et al., 2017). According to an analysis of the hand and foot bones attributed to *H. antecessor*, most morphological characters are more similar to modern humans than to other European hominids that existed in the Middle to Late Pleistocene (Carretero et al., 1999). The postcranial features have been used to support the analysis that *H. antecessor* was the last common ancestor for *H. sapiens* and *H. neanderthalensis* (Carretero et al., 1999).

The antiquity of *H. antecessor* and its temporal range have been verified using a robust combination of dating techniques. ESR was directly used on the specimen ATD6-92, which is a tooth from Gran Dolina, Spain (Duval et al., 2018). This allowed for a narrowing of the age range to between 624 and 949 thousand years ago, and this range was further narrowed to between 772 and 949 thousand years by the collection of magnetostratigraphic data from TD6, the unit that contained the fossil (Duval et al., 2018). This range places *H. antecessor* as containing the oldest fossils in Western Europe, and indicates that *H. antecessor* predated the divergence of modern and archaic humans (Duval et al., 2018).

While its antiquity makes it a potential candidate for the last common ancestor of modern humans and Neanderthals, as proposed by Bermudez de Castro, Carbonell, et al., it also increases the likelihood of *H. antecessor* having been a distinct European variant of *H. erectus*. A recent analysis of the dental proteomes of ATD6-92 and D4163, a dental specimen from

Dmanisi, Georgia, that is attributed to *H. erectus*, found that the pairwise divergence between the amino acid sequences of *H. antecessor* and the clade consisting of Neanderthals, Denisovans, and modern humans was significantly higher than between the members of the clade (Welker et al., 2020). This strongly suggests that *H. heidelbergensis* rather than *H. antecessor* is the common ancestor for the species of that clade, and that it is instead a taxon closely related to the last common ancestor (Welker et al., 2020).

The amino acid data combined with the ESR dates provide support for two further hypotheses: that *H. antecessor* is a separate species closely related to the ancestor of *H. heidelbergensis*, or that it is a subspecies of that ancestral population. Due to the age of *H. antecessor* specimens, their origin from the ancestral population of *H. heidelbergensis* is probable, and it has been noted by Welker et al. that the protein analyses reflect a relatively archaic lineage. Since there is significant evidence to support *H. erectus* as the ancestor for *H. heidelbergensis*, it can be inferred from the data that *H. antecessor* is descended from *H. erectus* (Manzi, 2016). *H. antecessor* is most often classified as its own species even in phylogenies that place it as a descendent of *H. erectus*, owing to an analysis of ATD6-69 (a partial face) that found many modern facial features, especially at the midface (Bermudez de Castro & Martinon-Torres, 2019). However, an examination of 14 mandibular features from ATD6-96 that were previously used to support the close relation of *H. antecessor* to *H. sapiens* found that all but one are present in *H. erectus*, especially the Asian fossils which are often labeled as the classic variant of *H. erectus* (Trafi et al., 2018). The distinctness of the midfacial morphology may also be less supportive of the status of *H. antecessor* as a separate species, since ATD6-69 is a juvenile specimen; a simulation of the developmental trajectories for *H. sapiens*, Neanderthals, ATD6-69, and specimens from older samples such as *H. erectus* and *H. habilis* found that that some traits considered characteristic of *H. sapiens* were also present in Middle Pleistocene humans, with older fossils such as Sangiran 17 and Dmanisi 2700 (both attributed to *H. erectus*) falling

within the range of variation between Neanderthals and *H. sapiens* for the most significant principal components (Friedline et al., 2013). The principal components in this simulation were the result of principal component analysis performed on the facial morphology of Neanderthals and *H. sapiens*, and are constructed from combinations of morphological traits in order to maximize the amount of variance captured in one component (Friedline et al., 2013). These results suggest that most of the features of ATD6-69 that are similar to those of modern humans are retained from the ancestral population, and were present to different degrees in populations such as Asian *H. erectus* (Friedline et al., 2013). They also suggest that these features may have evolved more than once in human lineages (Friedline et al., 2013).

Considering the craniofacial similarities with *H. erectus* fossils despite the presence of modern facial traits, and the age of the fossils attributed to *H. antecessor*, the evidence best supports the classification of *H. antecessor* as a subspecies of *H. erectus*.

Homo ergaster

Homo ergaster consists of the set of *H. erectus* fossils from East Africa, including its type specimen, which is KNM-ER 992, a mandible with incisors missing (*"Homo ergaster:* KNM ER 992*", n.d.*). The fossils that have been most important for morphological inferences include KNM-WT 15000 (also known as Turkana Boy), KNM-ER 3883, KNM-ER 3733, and OH 9 (*"Homo ergaster"*, n.d.). Turkana Boy is a nearly complete skeleton, while the KNM-ER and OH fossils are partial crania (*"Homo ergaster"*, n.d.). There are three prominent taxonomic hypotheses regarding *H. ergaster*; that *H. ergaster* is the African subspecies of *H. erectus*, that it is a separate species, and that the *H. ergaster* fossils are too widely varied to be a single species and instead belong to multiple separate species (Tattersall, 2013).

Evidence for the splitting of *H. ergaster*

The hypothesis that the set of fossils grouped under *H. ergaster* include more than one separate species is based on the morphological differences between KNM-WT 15000 and the KNM-ER specimens (Tattersall, 2013). The cranial features of WT 15000 differ from ER 3883 and ER 3733 in a number of ways; the remains of the nasal bones suggest that the individual had a flatter face, while the shape of the skull is rounder and relatively short, while the ER specimens have longer crania (Tattersall, 2013). Additionally the face of WT 15000 is longer and narrower, and has been noted to have higher alveolar prognathism, so the part of the jaw that holds the upper teeth protrude more than in ER 3883 and 3733 (Tattersall, 2013). WT 15000 also has a nasal aperture that is narrower and located higher than in the ER fossils, including KNM-ER 3732, which is another partial cranium (Tattersall, 2013). These differences, though significant, may also be due to the juvenile status of WT 15000, as the individual was around eight years old, and in terms of development was equivalent to a modern human child of 12 years (Tattersall, 2013).

While it can be argued that these differences in WT 15000 would have only become further exaggerated as the individual grew into adulthood, this hypothesis is made less likely by the differences in cranial morphology between *H. erectus* and *H. sapiens* fossils, which suggest that *H. erectus* adults retained a lower proportion of juvenile feature than do modern humans (Antón, 2003). Since *H. erectus* adults were less neotenous in cranial morphology, there is an increased likelihood that WT 15000 may be morphologically different due in part to juvenile status, and that these differences may have reduced or disappeared as the individual became older. .

Evidence for *H. ergaster* as a species

H. ergaster is classified as a separate species on the basis of the differences between the African, European, and Asian *H. erectus* fossils, as well as the similarities between the fossils in each group (Tattersall, 2013). African *H. erectus*, or *H. ergaster*, corresponds to the fossils found in Koobi Fora, Kenya, while European *H. erectus*, or *H. antecessor*, corresponds to fossils

found in western Europe, and Asian *H. erectus* includes fossils from Indonesia and China (Groves, 2018). Fossils from Dmanisi, Georgia, have also been grouped under *H. erectus*, although whether they are best classified with the Asian or African fossils (or as a separate species entirely) is unclear due to their location and morphology (Groves, 2018).

The morphological differences between the East African fossils and the rest of the specimens attributed to *H. erectus* are used to support the hypothesis that *H. ergaster* was a separate species (Terhune et al., 2007). The most significant differences are those between the Koobi Fora fossils and the Asian *H. erectus* specimens, including those from Sangiran, Zhoukoudian, Ngandong, and Sambungmacan (Terhune et al., 2007). An analysis of temporal bone morphology across all the different fossil groups, conducted by Terhune et. al, compared the variation found in *H. erectus* to the variation found in extant primates (Terhune et al., 2007). They performed principal component analysis in order to determine the extent of the variation captured by different specimen groups, and found that there was distinct division between the *H. ergaster* and Asian fossils (Terhune et al., 2007). KNM-ER 3883 and 3733, along with WT 15000, were found to form a cluster that was also distant from other *H. ergaster* specimens such as OH 9 and Dmanisi 2280 (also a partial skull) (Terhune et al., 2007). Along the first two principal components, the Kenyan fossils showed higher within-group variation as well, and KNM-ER 3883 was found to less distant from the Asian fossils when compared to KNM-ER 3733 (Terhune et al., 2007). The most significant morphological differences found between the set of KNM-ER and -WT fossils and the Asian group of fossils (including OH 9) were that the Asian set had a smaller glenoid region that was more medially placed, as well as a deeper mandibular fossa and taller articular eminence (Terhune et al., 2007).

Terhune et al. also calculated the Procrustes distances for a number of groups within the fossil set in order to characterize and compare the intraspecific and interspecific variation present. Procrustes analyses compute the distance and variation between multiple different shapes, allowing for the distance between physical traits that occupy more than one dimension to be

calculated (Terhune et al., 2007). They found that the average variation within the fossils was greater than that of the extant hominids, and that the African fossils were more variable than the Asian set (Terhune et al., 2007). Similarly, when the fossils were analyzed by age, the 'early' fossils were more variable than the late group, and the 'early' set also varied more than the samples of common chimpanzees and bonobos, while the 'late' set only showed a statistically significant difference when compared to the entire group of great apes (excluding modern humans) (Terhune et al., 2007).

The results of this analysis support the hypothesis that *H. ergaster* is a separate species due to the finding that the variation within *H. erectus* is larger than for any extant hominid. The cluster analyses also support the grouping of KNM-ER and -WT fossils as morphologically separate from the rest of the fossils, providing further support for the distinctness of the African and Asian fossil sets, and the distinctness of *H. ergaster* (Terhune et al., 2007). The authors found that the results most support a two-species model with *H. ergaster* referring to the Koobi Fora fossils and *H. erectus* including the Dmanisi fossils along with the Indonesian and Chinese sets. However, as noted by the authors themselves, as well as an earlier analysis of *H. erectus* fossils, pairwise comparisons of fossils clustered in the same groups also yield larger distances than present for extant groups, indicating a high degree of overlap between intra- and inter-specific variation (Lockwood et al., 2005). This high intra-group variation remains across different partitions of the fossils, which suggests that it is a contributing factor to the relatively high intraspecific variation observed when all fossils are grouped under *H. erectus*.

Evidence for *H. ergaster* as a subspecies

Although there is evidence for the distinctness of the Koobi Fora fossils within *H. erectus*, as well as distinctness of the Asian specimens, and this evidence can be interpreted as supporting the existence of *H. ergaster* as a separate species, this morphological differences must also be viewed in light of analyses of other morphological traits. A recent analysis of the middle cranial

fossa, which is a depression of the skull base and an index of temporal lobe development, found that the observed variation between the Koobi Fora fossils and the Javanese *H. erectus* fossils was within the variation observed among a modern human sample (Pearson et al., 2020). The comparison was between CT scans of 41 modern human skulls, three Koobi Fora fossils (KNM-ER 3883 and 3733, KNM-WT 15000) and four Indonesian specimens (Sangiran 2,4, 17, and Sambungmacan 3) (Pearson et al., 2020). Although the small sample size limits the robustness of the result, the analysis considers the most significant of the Koobi Fora fossils, and includes the subset of Asian *H. erectus* which is furthest in temporal bone morphology from the African set in the study by Terhune et al.. That the variation in the middle cranial fossa across the *H. erectus* hypodigm is lower than for *H. sapiens* suggests that the high intraspecific variation *H. ergaster* and other subpopulations show may be dependent on the traits measured. This best supports the hypothesis that *H. ergaster* was morphologically distinct enough to be a subspecies but not so differentiated, relative to other populations, to be classified as a separate species.

Homo heidelbergensis

In the lumping taxonomy *H. heidelbergensis* is most classified under *H. sapiens*, and less commonly under *H. erectus* (Stringer, 2012; Wood & Lonergan, 2008). In more liberal classifications it is considered its own species (Wood & Lonergan, 2008).

The first fossil discovery for this taxon was a nearly complete mandible, named as the Mauer mandible, found near Heidelberg, Germany, in 1908 (Bermúdez de Castro et al., 2017). The remains have been dated to at or before 700 thousand years old, and *H. heidelbergensis* is estimated to have lived from around 800 to 200 thousand years ago (Bermúdez de Castro et al., 2017; Wood & Lonergan, 2008). The remains were dated using uranium-series and ESR techniques, which are used in combination to improve the accuracy and reduce error (Wood & Lonergan, 2008). Since the initial discovery, fossils thought to belong to this taxon have been

found in sites in Africa, the near east, and in parts of Asia, notably China (Wood & Lonergan, 2008). The first mandible, as well as many of other fossils, are distinguishable from both *H. sapiens* and *H. neanderthalensis* fossils by their relatively higher thickness and density (Wood & Lonergan, 2008). The average brain size calculated with 10 individuals is 1200 cc, which is close to the range for modern humans (Rightmire, 2004). Compared to the average brain size for other *H. erectus* fossils (calculated to be on average 973 cc over 30 individuals), the brain size for *H. heidelbergensis* is an outlier and provides support for the view that it is more closely related to modern humans than to *H. erectus* (Rightmire, 2004).

This also suggests that *H. heidelbergensis* may be the last common ancestor for Neanderthals, Denisovans, and anatomically modern humans (Manzi, 2016). Various fossils have been discovered in Africa and Eurasia that are morphologically different from both the more archaic humans and *H. sapiens*, and may reflect the fossil record of *H. heidelbergensis* (Manzi, 2016). At present, the fossil evidence suggests that *H. heidelbergensis* originated from Africa, and became geographically widespread over time (Manzi, 2016). This supports the placement of *H. heidelbergensis* as a descendent of African *H. erectus*, or *H. ergaster*, and it also suggests that *H. heidelbergensis* represented the first of the more encephalized human species, as reflected by its significantly larger brain when compared to older species such as *H. erectus* (Manzi, 2016). The morphological data from two fossil specimens generally attributed to *H. erectus*, a cranium from Daka, Ethiopia and KNM-ER 42700, have been shown to have a unique cranial morphology compared to other *H. erectus* specimens, providing additional support for a population within *H. erectus* that eventually became a separate species in *H. heidelbergensis*, as well as support for the reclassification of the two specimens as belonging to an early variant of *H. heidelbergensis* (Baab, 2016).

Molecular dating using mitochondrial DNA has placed the divergence of *H. sapiens* and Neanderthals to 500 thousand years ago (Endicott et al., 2010). This is within the range of existence of *H. heidelbergensis* and provides additional support for its status as their common

ancestor. The mtDNA analysis also supports the existence of a widely dispersed ancestral species that became divided into two more genetically diverged populations, which strengthens the case for *H. heidelbergensis* as the ancestral species (Endicott et al., 2010). The relatively high internal variability of *H. heidelbergensis* also increases the plausibility of its subpopulations diverging from one another. The relationship between *H. heidelbergensis* and the Denisova hominins is more ambiguous, due in part to the limited data available for Denisovans. However, given the earlier intra-clade variation observed when comparing the dental proteomes of *H. antecessor* to the clade containing Neanderthals, Denisovans, and modern humans, it may be possible for Denisovans to have also originated from *H. heidelbergensis* (Welker et al., 2020). Further Denisovan genome analysis suggests that Denisovans diverged from modern humans between 200 and 800 thousand years ago, depending on the mutation rates used, and mtDNA analysis has suggested a divergence point up to one million years ago (Meyer et al., 2012; Krause et al., 2010). These results suggest that *H. heidelbergensis* could have been the common ancestor for all three species, although the lack of data limits the scope of any inferences made. The placement of *H. heidelbergensis* is also made more difficult due to how close this taxon was in time to the point of divergence between modern humans and Neanderthals (Stringer, 2012). Therefore although current evidence supports *H. heidelbergensis* as the most recent common ancestor for modern humans and Neanderthals, and possibly Denisovans as well, more evidence in the future may support its reclassification.

Homo luzonensis

The first fossil representing this population was discovered in Callao Cave, Northern Luzon, The Philippines (Détroit et al., 2019). It was found in 2007, and is a third metatarsal that was dated to around 67 thousand years old (Détroit et al., 2019). This bone was accurately categorized as from the genus *Homo*, but there was a lack of information for further classification until the discovery of 12 additional hominin bones from the same rock layer in Callao Cave in 2019

(Détroit et al., 2019). These 12 bones were from three individuals, and consisted of two manual and pedal phalanges each, one femoral shaft, and seven postcanine maxillary teeth (Détroit et al., 2019). One maxillary tooth was directly dated using uranium-series analysis, and determined to have a minimum age of 50 thousand years (Détroit et al., 2019). The individuals were assigned to a new taxon, on account of the combination of primitive and modern traits they exhibited (Détroit et al., 2019).

The more primitive features of *H. luzonensis* include many of the dental morphological characteristics analyzed (Détroit et al., 2019). The premolars were found to be especially large compared to the molars, and had multiple roots, which were both primitive traits, with the first being found only in Paranthropus, and the second being found in Australopithecus, Asian *H. erectus*, and other archaic species in *Homo* as well (Détroit et al., 2019). An analysis of the dental diameters found that *H. luzonensis* clustered closely with measurement for *H. erectus* (Détroit et al., 2019). The molars were found to exhibit more modern (or derived) features, with a reduced number of cusps and a relatively simple surface morphology; these features are found in *H. floresiensis*, *H. sapiens*, and *H. neanderthalensis* (Détroit et al., 2019). The molars were also found to be relatively small, unlike any other species in *Homo*, and differ from the molars of Denisovans as well (Détroit et al., 2019). Additionally, the enamel-dentine junction is similar only to that of *H. floresiensis* (Détroit et al., 2019). However, a limiting factor when classifying this set of fossils is the relative lack of specimens and of genetic data (Détroit et al., 2019). The small size and combination of unique traits with traits found in archaic humans as well as modern humans suggests a similar origin for *H. luzonensis* and *H. floresiensis*, and *H. luzonensis* is most likely a separate species descended from an ancestral population of *H. erectus* that then underwent island dwarfism. The presence of primitive features found in paranthropus and *H. habilis* potentially supports an older origin for *H. luzonensis* than *H. floresiensis*.

Homo habilis

Homo habilis is considered to be the oldest species in the genus *Homo*, and is considered an archaic hominin (Johanson et al., 1987). The first of the fossils in this taxon to be recognized was called OH-7, found in Olduvai Gorge, Tanzania, in 1959 (Wood & Lonergan, 2008). It was dated to about 1.8 million years ago, and consists of a partial skull and hand [8(Johanson et al., 1987). The cranial portion also includes a partially preserved mandible (Johanson et al., 1987). *H. habilis* is estimated to have lived from around 2.3 to 1.4 million years ago (Spoor et al., 2015). Because it is the oldest species in the genus *Homo*, it is considered the common ancestor for all other later species of *Homo* (Dunsworth, 2010). There are a range of opinions on its place in the phylogeny of the genus *Homo*; the fossil record for early *Homo* that is found in East Africa has been interpreted as evidence for the existence of one species (*H. habilis*), or two, with *H. habilis* as well as another early species of the genus *Homo* coexisting (Johanson et al., 1987). There is no clear consensus on which fossils should be grouped under which of the two posited species (Johanson et al., 1987). There is also debate on whether *H. rudolfensis* is a subspecies of *H. habilis*, if it is a separate species with *H. habilis* lineage, or if it is a species originating from another ancestral population (Johanson et al., 1987;Wood & Lonergan, 2008). The partial preservation of fossils such as OH 7 has increased the difficulty of comparing fossils across different populations in *Homo* (Johanson et al., 1987).

OH 62, a fossil recovered from Olduvai Gorge in 1986 that included large parts of the postcranial skeleton, was attributed to *H. habilis* and dated to at least 1.8 million years ago (Johanson et al., 1987). This fossil had dental and cranial features that indicated membership in the genus *Homo*, as it closely resembled the features of other fossils attributed to *H. habilis*, including OH 24 and KNM-ER 1470 and 1813 (Spoor et al., 2015). It had a molar wear pattern and anterior: posterior dental proportions that were markedly different from those of Australopithecus and characteristic of other *H. habilis* fossils (Spoor et al., 2015). It also had a relatively wide palate, again characteristic of *Homo* rather than Australopithecus (Spoor et al.,

2015). However, its postcranial characteristics were similar to those of australopithecine-in particular, the proportions of the humerus, radius, and segments of the ulna were very similar to those of AL 288-1 (or Lucy as the individual is more commonly known) (Spoor et al., 2015). This suggests the existence of a considerable amount of variation within *H. habilis*, as many of the fossils attributed to it show certain features, such as the cranial traits mentioned above, that mark them as members of early *Homo*, but also show considerable similarity to australopiths in other ways.

Other analyses suggest that there are *H. habilis* fossils that are outside the expected variation for the species. A recent reconstruction of the OH 7 mandible demonstrates many primitive traits (Spoor et al., 2015). The dental arcade, which refers to the shape made by the teeth attached to the upper jaw, is long and narrow, which is similar to Australopithecus afarensis, while the dental arcades later species of *Homo*, including *H. erectus* and *H. sapiens*, have a characteristically parabolic shape (Spoor et al., 2015). The shape of the dental arcade was further tested in order to determine whether it was within the bounds of within-group variability for extant apes and humans (Johanson et al., 1987). It was found that the dental arcade shape was similar to that of KNM-ER 1802 and OH 13, which are mandibles from the fossil record for early *Homo* (Johanson et al., 1987). It was also found that the dental arcade shape was closer to that of the great apes and australopiths than to that of *H. sapiens* (Johanson et al., 1987). It was further found to be significantly different from *H. erectus* and the early *Homo* fossils KNM-ER 1482 and KNM-ER 60000, with the difference as large as the difference between Gorilla gorilla (gorillas) and Pan troglodytes (chimpanzees) (Spoor et al., 2015).

Spoor et al. also analyzed the within group variation for groups of fossils attributed to *H. habilis* (OH 7, OH 13, KNM-ER 1802), *H. rudolfensis* (KNM-ER 60000, KNM-ER 1482), and *H. erectus* (Dmanisi fossils). All of these fossil clusters had within-group dental arcade shape variations that were similar to those for extant hominids (Spoor et al., 2015). However when these fossil clusters were grouped together in any combination, the within-group variations significantly

exceeded those for extant hominids (Spoor et al., 2015). Moreover, the distributions of the traits in each of the pooled groups were bimodal, indicating that there were two different values for the trait that was being selected for, rather than the groups simply demonstrating more deviance from the mean (Spoor et al., 2015). The results of this analysis support the hypothesis that *H. rudolfensis* could have been a separate species of its own, or was at least a very distinct population within *H. habilis*. This is further reinforced by the finding that the pooled variation in arcade shape for the set of early *Homo* fossils significantly exceeds the variation found in extant hominid species (Spoor et al., 2015). It also suggests that there may be traits for which fossils grouped under *H. habilis* diverge to different values for, indicating that populations within *H. habilis* may have been growing further apart genetically due to different selection pressures, either to the point of becoming separate subspecies or different species altogether.

Homo rudolfensis

The earliest discovered fossil to be attributed to *Homo rudolfensis* was KNM-ER 819, and was discovered in 1971 in the Koobi Fora Formation in Kenya (Wood & Lonergan, 2008). The most complete fossil that is considered the best representative for this population is KNM-ER 1470, which was also discovered in Koobi Fora, in 1972 ("*Homo rudolfensis*," 2010; Wood & Lonergan, 2008). KNM-ER 1470 is a cranium, and was the first fossil to be attributed to *H. rudolfensis*, while KNM-ER 819 is a mandible fragment (Antón, 2012). There are two main hypotheses regarding the placement of *H. rudolfensis* in the hominin phylogenetic tree; the first is in line with the lumping taxonomy, and regards *H. rudolfensis* as a subspecies of *H. habilis*, while the second regards *H. rudolfensis* as a separate species of its own (Wood & Lonergan, 2008).

KNM-ER 1470 was initially dated to around 2.9 million years ago, and the other fossils recovered from the area were dated from 2.6 to 2.9 million years ago, based on potassium-

argon dating of the volcanic ash layers surrounding the specimens (Leakey, 1973). However these dates were revised in 2012, when McDougall et al. used argon-argon dating to redate the volcanic rock samples and found that the age range of the fossils were from 1.9 to 2.1 million years ago instead (McDougall et al., 2012). This range overlaps with that of *H. habilis*, which supports the coexistence of these two taxa.

The geographical ranges for these two populations also overlap, as fossils for both of them have been found in the Koobi Fora Formation (Leakey, 1973).

KNM-ER 1470 was initially assigned to *H. habilis*, and although there was some debate on whether it could belong to Australopithecus, both Richard Leakey (the scientist who discovered the cranium) and Alan Walker (who proposed the hypothesis on australopith origin) accepted that it was most likely a member of *H. habilis* (Walker & Leakey, 1978). The view that KNM-ER and the fossils that were discovered along with it (KNM-ER 1472, 1475, and 1481) actually belonged to a separate species was first put forth by scientist Valery Alekseev, who gave it its current name (Wood, 1999).

The primary evidence used to separate KNM-ER 1470 and other associated early *Homo* fossils into *H. rudolfensis* as a distinct species consists of differing patterns of primitive and derived traits. The face of *H. rudolfensis* specimens is widest in the middle, while the face of *H. habilis* specimens (those that are attributed only to *H. habilis* and not *H. rudolfensis*) is widest at the top (Wood & Lonergan, 2008). Additionally, KNM-ER 1470 shows a wide and flat palate, as well as a supraorbital region that is similar to Australopithecus rather than *H. habilis* (Leakey, 1973). The size and shape of the skull are characteristic of *Homo* and similar to other *H. habilis* specimens, and the postcranial fossils, two femora, are similar to those of *H. sapiens* (Leakey, 1973). This pattern has made the true placement of *H. rudolfensis* among the other species of *Homo* more ambiguous (Leakey, 1973). As discussed previously, the multivariate regression analysis of different fossil groups in early *Homo* by Spoor et al. indicates that the question of whether early *Homo* is comprised of multiple species or just H. *habilis* depends significantly on

the level of morphological variation that is considered plausible for a single species to show, and how bimodal the population distribution for specific traits can get before the taxa are distinct species rather than subspecies.

KNM-ER 1470's classification as *H. rudolfensis* also depends on the estimated sexual dimorphism for *H. habilis*. If the sexual dimorphism was relatively high compared to extant hominids, as well as later *Homo* like *H. erectus*, then KNM-ER 1470 could likely represent a male individual from *H. habilis* (Lieberman et al., 1988). This is a plausible outcome because sexual dimorphism is a significant source of variation between individuals of the same species in (Wood, 1976). The sexual dimorphism explanation was proposed as KNM-ER 1470 is especially large compared to other cranial remains for *H. habilis* from the same site, such as KNM-ER 1813 (Lieberman et al., 1988). Lieberman et al. conducted a quantitative analysis on the probability of sampling an individual as large as KNM-ER 1470 and as small as KNM-ER 1813 from the same population, assuming that this population had the same level of sexual dimorphism as extant gorillas show (Lieberman et al., 1988). It was calculated that the probability of a randomly selected male and female gorilla showing the difference found between the two fossils was 5 percent or less on 10 out of 27 craniofacial measures (Lieberman et al., 1988). 18 of the measures showed a probability of 15 percent or less (Lieberman et al., 1988). These results suggested that, for craniofacial measurements, *H. habilis* would have to be more sexually dimorphic than extant gorillas (which are the most sexually dimorphic of the extant hominids), to include both KNM-ER 1470 and KNM-ER 1813 (Lieberman et al., 1988). This interpretation is supported by the work of Spoor et al. on the mandible OH 7 as discussed previously.

However, a later review of multiple analyses of the sexual dimorphism in *H. habilis* concluded that, based on the problems and limitations of the probabilistic analysis detailed above, there was insufficient evidence to reject the null hypothesis (that KNM-ER 1470 and KNM-ER 1813

were different due to intraspecific variation in *H. habilis*) (Miller, 2000). The male-to-female ratio of the endocranial volume for *H. habilis* (assuming KNM-ER 1813 and other similarly-sized fossils were female) is 1.12, which was lower than 40 percent of the ratios for extant primate species, and also lower than the ratio for modern gorillas (1.15) (Miller, 2000). Additionally, the analysis of 24 of the 27 different craniofacial traits was repeated, this time with modern gorilla crania, and it was found that for four pairings of male and female gorilla crania, 38 to 67 percent of the male:female trait ratios fell outside of the 95 percent limits of the gorilla distributions, similar to the result for *H. habilis* in the previous analysis (41 percent) (Miller, 2000). These and other limitations of Lieberman et al.'s analysis indicate that there is insufficient evidence to consider KNM-ER 1470 as outside of the intraspecific variation of H. *habilis*.

Limitations that must be taken into account when considering these analyses include the lack of well-preserved postcranial fossils across *H. rudolfensis* and *H. habilis*, as robust comparisons of postcranial morphology may reveal different patterns than cranial morphology.

Homo naledi

The fossils classified as *Homo naledi* were found in the Dinaledi chamber of the Rising Star cave system, South Africa, from 2013 to 2015 (Berger et al., 2015). In total, the expedition recovered 1550 fossils specimens, representing at least 15 individuals, all attributed to the same hominin population (Berger et al., 2015). The numerous hominin fossil specimens found, and the relatively large number of individuals they represent, enable more robust inferences to be made about the species classification of these individuals.

H. naledi remains were first dated using morphometric and dated Bayesian analyses, due to the difficulty in dating the fossils directly without destroying them, and the lack of volcanic rock layers (Dembo et al., 2016;Dirks et al., 2017;Thackeray, 2015). Biochronological methods could not be used, as the specimens found in the cave were all hominin fossils, with the exception of a few faunal fossils that provided negligible information (Berger et al., 2015; Dirks et al., 2017).

The use of stratigraphic methods also encountered problems, as the layers of rock in caves are reworked over time and cannot be reliably dated (Dirks et al., 2017). A morphometric analysis of the *H. naledi* fossils yielded an age estimate of 2 million years ago, due to the high prevalence of primitive features and relatively increased similarity to early *Homo* species such as *H. erectus* (Thackeray, 2015). A subsequent dated Bayesian analysis of the *H. naledi* fossils returned a revised age estimate of 900 thousand years (Dembo et al., 2016). The rock layers and the fossils were directly dated by Berger et al. (the team responsible for the fossil discovery) in 2017; the sediments from the fossil site were dated with optically stimulated luminescence, and these estimates were combined with a paleomagnetic analysis of flowstones in order to isolate the stratigraphic layer from which the sediments containing *H. naledi* specimens originated (Dirks et al., 2017). Three *H. naledi* teeth were directly dated with uranium-series and electron-spin resonance methods, and the age estimates for the teeth and the rock layer were combined in order to produce a significantly more robust range of 236 to 335 thousand years ago (Dirks et al., 2017). This revised age is significantly lower than the age that was expected based on *H. naledi*'s primitive morphological characteristics, and provides more support for the existence of *H. naledi* as a separate species, rather than a variant of *H. erectus* (Dirks et al., 2017). Additional comparisons between the Dinaledi fossils and the features of different species in *Homo*, as well as comparisons to specimens found in the Lesedi Chamber of the cave system, show that there some consistent similarities to the specimens SK 96 (attributed to paranthropus) and Stw 80 (classified as *Homo sapiens*) (Davies et al., 2020). A quantitative analysis of 78 dental root and crown traits among the *H. naledi* specimens found that all pairwise comparisons between *H. naledi* and other samples from species within *Homo* were statistically significant, and *H. naledi* showed the most divergence from the rest of *Homo* apart from *H. sapiens* (Irish et al., 2018). However, it was also most similar to other species within *Homo*, and was more distant from Australopithecus, indicating that its placement within the genus *Homo* as a separate species is in line with the evidence (Irish et al., 2018).

Homo sapiens

Homo sapiens refers to anatomically modern humans, and is the only extant species in the genus *Homo* (Hublin et al., 2017; Wood & Lonergan, 2008). The oldest fossil attributed to *H. sapiens* has been dated to 315 thousand years old with the use of thermoluminescence dating (Hublin et al., 2017). Under the lumping taxonomy, *H. sapiens* includes both Neanderthals and Denisovans as subspecies (Wood & Lonergan, 2008).

Homo neanderthalensis

The first Neanderthal fossil to be discovered was a child's cranium found in Belgium in 1829 (Wood & Lonergan, 2008). The first adult fossil to be found is known as Neanderthal 1 and was discovered in Feldhofer Cave, Germany in 1856 (Wood & Lonergan, 2008). Neanderthals are estimated to have lived from 400 to 28 thousand years ago, and coexisted with *H. sapiens* in Europe (Harvati, 2011). The arrival of *H. sapiens* in Europe is estimated to have preceded the disappearance of Neanderthals by a few thousand years (Harvati, 2011). The two main taxonomic hypotheses regarding *H. neanderthalensis* are that it is a species separate from *H. sapiens*, and it is a subspecies of *H. sapiens* (Wood & Lonergan, 2008).

One phenomenon that has provided support for the claim that *H. neanderthalensis* is a subspecies within *H. sapiens* is the evidence of interbreeding between the two species. In non-African humans, approximately 1 to 3 percent of the genome is from Neanderthals (Vernot & Akey, 2014). By some definitions of species, such as that of the Biological Species Concept, the evidence of genetic exchange would qualify *H. sp. sapiens* and *H. sp. neanderthalensis* to be part of the same species (Balakrishnan, 2005; Lagache et al., 2013). The genetic similarity indicated by the evidence of interbreeding supports the hypothesis that, although Neanderthals were morphologically and genetically different from modern humans, the two groups were still similar enough evolutionarily to be considered distinct populations within *H. sapiens*.

Furthermore, the presence of Neanderthal DNA in current modern human populations provides evidence of interbreeding that produced fertile and viable hybrids (Juric et al., 2016). However, although specific genes from Neanderthals have been preserved and positively selected for due to beneficial traits they confer (especially with regard to survival in colder temperatures), there is growing evidence that the general trend over time is of weak purifying selection acting against Neanderthal alleles, the majority of which tend to be mildly or moderately deleterious (Juric et al., 2016). Although selection against individual Neanderthal alleles is relatively weak, the deleterious effects may have been stronger in the earliest hybrid generations, leading to a relatively fast decrease in the frequency of Neanderthal-derived alleles in the early hybrid generations (Juric et al., 2016). A simulation of the fluctuations of deleterious allele frequencies in human populations immediately following the period of admixture (estimated to have been between 47 and 64 thousand years ago) shows results supporting a relatively rapid decrease in the frequency of Neanderthal-derived alleles in initial hybrid generations (Harris & Nielsen, 2016). The stronger selection against early hybrids suggests that the degree of admixture between the two populations may have been significantly higher than the percentage of genes that persist today in the human genome (Harris & Nielsen, 2016). A pattern of stronger selection against Neanderthal genes in more highly conserved genomic regions has also been observed, which can be interpreted as evidence of partial reproductive incompatibility, or as a ceiling on the level of admixture that can persist (Sankararaman et al., 2014).

Although morphological data are more limited in validity when inferring levels of speciation and divergence between two populations, current morphological analyses also provide support for Neanderthals being genetically distinct from humans. An analysis of craniofacial traits comparing present-day *H. sapiens* populations, present-day chimpanzee populations, and fossil specimens for both *H. sapiens* and *H. neanderthalensis* finds that the distances between Neanderthals and humans from the Late Pleistocene, as well as between Neanderthals and present-day humans, significantly exceed both the distance between different human

populations and the distance between the two extant species of chimpanzees (Harvati, 2011). These data are generally interpreted as supporting the classification of *H. neanderthalensis* as a separate species under the phylogenetic species concept, and along with the genetic trends, make the case for Neanderthals as a subspecies of *H. sapiens* less certain, and instead provide some evidence of trends in the other direction (Balakrishnan, 2005).

Homo denisova

Denisovans, also referred to as the Denisova hominins, *Homo* altaiensis, and *Homo* denisova, are an archaic hominin group that were first discovered when, in 2008, a finger bone was found in Denisova Cave, which is located in the Altai Mountains in Siberia (Reich et al., 2010). The finger bone was first identified as belonging to an undiscovered hominin population in 2010, when its DNA was sequenced (Reich et al., 2010). Since then, three molars from Denisova Cave, and one mandible from the Tibetan plateau, have been identified as Denisovan (Chen et al., 2019; Slon, Viola, et al., 2017). Due to the small number of specimens, the bulk of the data on Denisova hominins is from gene sequencing (Reich et al., 2010).

Analysis of the Denisovan genome has revealed that it contributed to the genomes of multiple present-day human populations (Reich et al., 2010; Slon, Mafessoni, et al., 2018). Denisovans are estimated to have contributed 4 to 6 percent of their genome to Melanesian populations, and both high-altitude Tibetan populations as well as low-altitude Chinese populations have Denisovan DNA in their genomes (Chen et al., 2019;Reich et al., 2010). They also interbred with Neanderthals, as evidenced by the identification of the fossil Denisovan 11 as a Neanderthal-Denisovan hybrid with a Denisovan father and Neanderthal mother (Slon, Mafessoni, et al., 2018). Genes from an unknown lineage have also been found in the Denisovan genome, implying the existence of an ancient hominin species that has until now not shown up in the fossil record (Reich et al., 2010). The youngest fossil has been dated to 50

thousand years old, and the oldest is dated from around 190 to 220 thousand years old (Douka et al., 2019; Slon, Viola, et al., 2017).

Although the relative abundance of genetic data can shed light on the degree of genetic divergence, the Biological Species Concept is not suitable for determining the taxonomic status of *H. denisova*. The dearth of experimental data, which are necessary for determining the existence and degree of reproductive isolation between populations, also impedes the classification of Denisova hominin fossils. Unlike Neanderthal fossils, which are numerous and well-preserved, Denisova hominin fossils are scarce and yield relatively little morphological information, which limits the utility of the phylogenetic species concept as well (Balakrishnan, 2005).

The most robust morphological data available come from the mandible from Tibet, which has traits most similar to the fossil Penghu 1, which was discovered in Taiwan and is of unclear origin-it has been placed as from a new species in *Homo*, or as an archaic *H. sapiens* sample (Chen et al., 2019). This similarity currently suggests that *H. denisova* may have been a separate species, with the Penghu 1 mandible also of Denisovan origin. The similarity to the Penghu 1 mandible also provides support for the classification of Denisova hominins as an archaic variant or subspecies of *H. sapiens.* As current data are not robust, future fossil discoveries, especially of the postcranial skeleton, may provide evidence for different classifications.

Part Five: The new proposed phylogenetic tree for the genus *Homo*

Based on the evidence outlined above, the phylogenetic tree that I propose (Fig 1) is most in line with the current evidence is one in which the genus *Homo* contains eight main species: *H. habilis*, *H. erectus*, *H. naledi*, *H. sapiens*, *H. heidelbergensis*, H. neanderthalensis, *H. denisova*, *H. floresiensis*, and *H. luzonensis*. *H. habilis* in this tree includes includes *H. rudolfensis* as a subspecies, with the recognition that although *H. rudolfensis* is morphologically distinct from

other *H. habilis* fossil groups, current analyses and available fossil data on variation in *H. habilis* support its ability to include morphologically distinct populations. *H. erectus* includes as subspecies *H. antecessor* and *H. ergaster*, as it is also highly variable in terms of morphology and developmental plasticity-that coupled with the large geographical range the species had suggest that H. *antecessor* and *H. ergaster* may have begun to diverge genetically and morphologically but not to the point that they became separate species (Antón et al., 2016).The rest of the species do not have any subspecies.

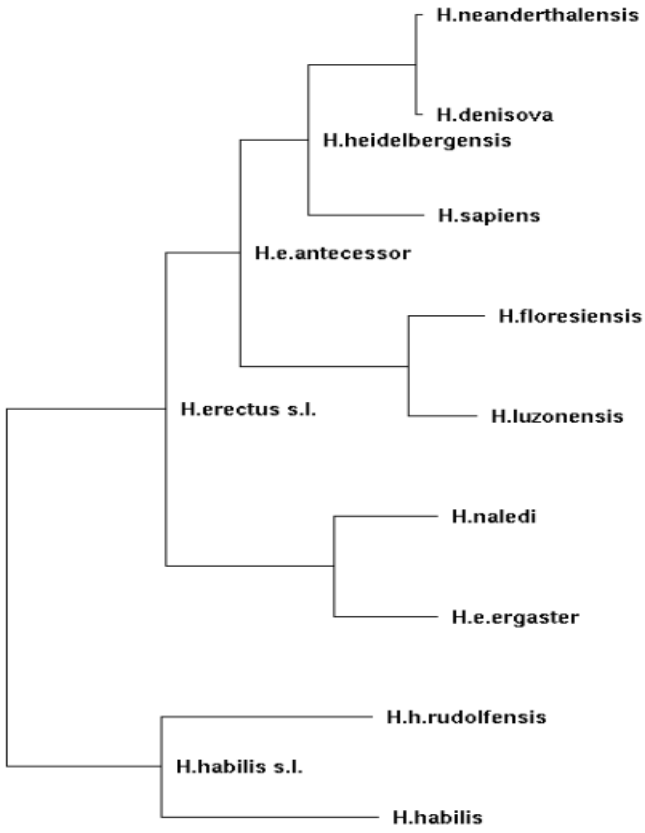

Figure 1. Phylogenetic tree for the genus *Homo*

Uncertainties present in this set of classifications

Currently *H. denisova* as a species does not include many fossil samples, and therefore there is a relatively large amount of uncertainty regarding its origins and its relation to the rest of the species in *Homo* (Chen et al., 2019;Slon, Viola, et al., 2017). Similarly, *H. luzonensis* is also limited by the lack of more robust morphological data, especially from the postcranial skeleton (Détroit et al., 2019). The phylogenetic classification and placement of *H. heidelbergensis* is uncertain due to its status as the last common ancestor of *H. sapiens* and *H. neanderthalensis*, and its existence overlapping with the divergence of

these two taxa (Bermúdez de Castro et al.,2017; McNulty, 2016). There is additional uncertainty regarding the dates of divergence for Denisova hominins and *H. sapiens*, due to variability in estimates based on molecular clocks (Manzi, 2016).

Part Six: Concluding Remarks

Gaps in the data

Some of the limitations of the existing literature on the hominin fossil record are due to difficulties in extracting data from a small quantity of specimens. For example, fossil records are relatively limited for H. *luzonensis* and *H. denisova* (Chen et al., 2019; Détroit et al., 2019). The probability of morphological differences between these limited fossil samples due to random variation is increased due to this. Probabilistic analyses of interspecific distance on different morphological traits across species in the genus *Homo* would also be very useful, as the analyses even for pairs of species reveals patterns in sample variation (Lieberman et al., 1988; Miller, 2000). Repetitions of different analytical methods and comparison across different populations, both extant and extinct, may also help reduce the impact of a limited fossil record on taxonomic and phylogenetic inferences.

Conclusion

According to current morphological and genetic evidence, the best supported taxonomic classifications are that *H. habilis* contains *H. rudolfensis* as a subspecies, *H. erectus* contains *H. antecessor* and *H. ergaster* as subspecies, and *H. naledi*, *H. luzonensis*, *H. floresiensis*, and *H. denisova* remain classified as separate species due to robustness of evidence (in the case of *H. naledi*), unique morphological trait patterns (*H. luzonensis* and *H. floresiensis*), and lack of clear morphological data to support inclusion in any other taxon (*H. denisova*). Additionally, in the case of *H. denisova*, the availability of genetic information supports genome-level differences between the Denisova hominins and both Neanderthals and modern humans, suggesting that it

may have been morphologically separate as well. *H. heidelbergensis* also remains classified as a separate species and the last common ancestor for the Neanderthal-Denisovan-Human clade due to ambiguity in the fossil record caused by the split between humans and Neanderthals.

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Biography

Amrutha Srinivasan was born in Houston, Texas, on December 9, 1997, and she enrolled in the Biomedical Engineering and Plan II Honors programs at the University of Texas at Austin in 2015. She first studied human evolution in her junior year of college. She will graduate in the fall of 2020 and plans to attend graduate school in 2022. Ms. Srinivasan will complete her computational engineering certificate in Spring 2021.