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# Phylogenetic Affinities of *Homo floresiensis* incorporating postcranial characters

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**Phylogenetic Affinities of *Homo floresiensis*  
incorporating postcranial characters**

by

**Kristina Feeney**

**Submitted in partial fulfillment  
of the requirements for the degree of  
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**Phylogenetic Affinities of *Homo floresiensis*  
incorporating postcranial characters**

**Abstract**

The objective of this analysis is to generate hypotheses regarding the evolution and ancestry of *Homo floresiensis*: is *H. floresiensis* more likely descended from early *Homo*, as the cranium suggests, or does the inclusion of postcranial characters alter the likelihood of this scenario? This analysis builds upon the previous study by Argue et al. (2009) by including a much larger sample of postcranial data for a more integrated picture of primitive and derived features across the skeleton. The original paper focused on fifty cranial features and ten mandibular and postcranial features to create a phylogenetic hypothesis regarding the affinities of *Homo floresiensis*; in this study, 77 postcranial characters were added to the matrix. The results of this analysis suggest that *H. floresiensis* has its closest affinities to the australopithecines and early *Homo*, corroborating, in part, previous analyses but also making its inclusion in the genus *Homo* less certain. Possible ancestral populations of *H. floresiensis* are discussed, including *H. habilis* and the australopithecines, along with different scenarios that could have brought them to Flores.

## Introduction

In 2004, *Homo floresiensis* was discovered at Liang Bua Cave on the island of Flores with a blend of derived and primitive features unlike any other known hominin species (Morwood 2004, Brown 2005). Its best known and controversial features include its combination of small stature, unique body proportions, primitive anatomy, and tiny endocranial volume (Falk 2011; Jungers et al., 2009a; Brown et al., 2004; Tocheri et al., 2007; Jungers et al., 2009b; Larson et al., 2009; Orr et al., 2013; Larson., 2007; Zipfel et al., 2009). The original description of *H. floresiensis* suggested it derived from deposits ranging between 94-74 kya to 18 kya (Morwood et al., 2005), overlapping with the time range of *Homo sapiens* on Flores as well (Morwood et al., 2004). New research suggests that the deposits containing *H. floresiensis* actually date to between 100 and 60 kya, a narrower range, but still within in the range of *Homo sapiens* on the island (Sutikna et al., 2016). Its disappearance has been linked to climate change, competition with *Homo sapiens*, or a combination of both (Aiello, 2010). Dates in Sutikna et al., (2016) coincide with the arrival of *H. sapiens* in the area, which points to competition with *H. sapiens* as a reasonable cause for extinction. There is also evidence of a volcanic eruption around 12 kya that may have contributed to the extinction of *H. floresiensis*, if the original date range for the species is accurate (Vaughan and Blaszczyk, 2008).

The announcement of *Homo floresiensis* caused quite a stir among paleoanthropologists because, although many of its features are documented in other hominins, they have not been seen together in combination and their persistence at such young dates initially led to great skepticism regarding the validity of the population as a new species (Falk, 2011; Argue et al., 2006; Martin et al., 2006; Eckhardt 2007; Henneberg et al., 2014; Jacob et al., 2006.). Most of

the postcrania associated with *H. floresiensis* are similar to that of apes and australopithecines in many features (Aiello 2005, Morwood 2005; Jungers et al., 2009a; Brown et al., 2004; Tocheri et al., 2007; Jungers et al 2009b; Larson et al., 2009; Orr et al., 2013; Larson., 2007; Zipfel et al., 2009), while Brown et al. (2004) and Argue *et al.* (2009) suggested the cranium resembles early *Homo*. Falk (2011) studied endocasts of *H. floresiensis* and determined that they had cranial volume of 417 cm<sup>3</sup>; within the range of chimpanzees and australopithecines. However, the configuration of the brain of *H. floresiensis* indicates much more advanced behavior, perhaps even having the ability to “read components of the natural world” such as animal tracks (Falk, 2011). There are stone tools and butchered animals found at Liang Bua but there is no hominin associated with them found in deeper deposits than *H. floresiensis* (Morwood, 2004). It is possible that they were manufactured by *H. floresiensis*, but currently it is unclear.

Since its discovery, researchers have been trying to incorporate *H. floresiensis* into an evolutionary scenario that “makes sense” with what we currently know about hominin evolution. Is it more parsimonious to assume that *H. floresiensis* represents a strange offshoot of a late occurring *Homo* species, or is it more likely that *H. floresiensis* represents an early hominin migration out of Africa for which there is a significant ghost lineage until ~100 kya? *H. floresiensis* displays many distinct traits in the postcrania: it has iliac blades that flare laterally, a short clavicle and low humeral torsion. The tibia is oval and it has a high bicondylar angle (Brown *et al.* 2004, Morwood *et al.* 2005, Aiello 2005; Tocheri et al., 2007; Jungers et al 2009a; Jungers et al 2009b;). *H. floresiensis* also has relatively short legs, long feet, and ape-like wrist bones (Aiello 2005, Morwood 2005; Jungers et al., 2009a; Brown et al., 2004; Tocheri et al., 2007; Jungers et al 2009b; Larson et al., 2009; Orr et al., 2013; Larson., 2007; Zipfel et al.,

2009). Falk (2011) describes the *H. floresiensis* brain as expanded in similar ways to *Au. africanus* (Dart, 1949). Most of the literature describes many of the *H. floresiensis* traits as “ape-like” or “australopithecine-like” but still attempts to justify its placement in *Homo*. The face of *H. floresiensis* was also believed to be “modern-looking” but this was found to be a result of allometric scaling (Aiello, 2010). *H. floresiensis* has proportions similar to A.L.-288-1, and its stature is within the range of australopithecines as well (Morwood et al., 2005; Morwood and Jungers, 2009). For example, *H. floresiensis* has a humerofemoral index of 85.4, which is within the range of australopithecines and not *Homo* (Larson, 2009). In the wrist the neck of the capitate is “highly excavate or waisted along its radial aspect” in *H. floresiensis*, this is the same condition found in African apes and *Australopithecus* (Larson et al., 2009). Many primitive features are also found in the lower limb of *H. floresiensis*. The flare of the iliac blades, the bicondylar angle, and the talar neck angle are all similar to those seen in the australopithecines (Jungers et al., 2009a). The talar torsion is less than that of australopithecines and *H. sapiens*, and is similar to that of the African apes (Jungers et al., 2009b). The distinctive hourglass shape of the pedal phalanges in *H. sapiens* is not present in *H. floresiensis* or the australopithecines, and the foot lacks a longitudinal arch, which is considered a hallmark of the human foot (Jungers et al., 2009b; Morwood and Jungers, 2009). The *H. floresiensis* navicular also retains the primitive condition of lateral pinching that is present in African apes and australopithecines, and present but reduced in *H. habilis* (Jungers et al., 2009b). Voisin (2006) also indicates that *H. floresiensis* displays the primitive double curvature of the clavicle in posterior view. This is present in the African apes as well as all known hominins with the exception of *H. sapiens*. These features together form a hominin unlike any seen before and create an abundance of

questions.

As alluded to above, this unique mosaic of features and possible temporal overlap with *H. sapiens* has led to several hypotheses to explain the origination of the species. The first theory is that *H. floresiensis* is an isolated *H. sapiens* with a pathology that creates this combination of primitive and derived features (Jacob et al., 2006; Obendorf et al., 2008; Martin et al., 2006; Hershkovitz et al., 2007; Argue et al., 2006; Aiello, 2010). Other researchers have proposed a second theory: *H. floresiensis* results from dwarfed *H. erectus* living on the island. This theory relies on the fact that *H. erectus* is the first known hominin to leave Africa and is also found throughout Southeast Asia from ~1.8 Ma – 800-880 kya (e.g., Aiello and Dean, 1990; Aiello, 2010). In support of this hypothesis, Van Bergh et al (2016) have found a 700 kya hominin mandible and isolated teeth on Flores in the So'a Basin that resemble *H. floresiensis* and suggest the features present also indicate clear phylogenetic affinities to *H. erectus*. Yet a third theory posits that *H. floresiensis* is descended from a small bodied, small brained hominin, possibly an Early *Homo* population, an australopithecine, or a previously unknown hominin, that dispersed Out of Africa with a heretofore undiscovered fossil record between Africa and Flores.

Those who believe in the pathological theory contend that *H. floresiensis* is *H. sapiens* afflicted with some pathology that created its distinct features, especially its short stature and small brain. These pathologies include cretinism, microcephaly, Laron's Syndrome, and Down's Syndrome (Obendorf et al., 2008; Jacob et al., 2006; Martin et al., 2006; Hershkovitz et al., 2007; Henneberg et al., 2014). The researchers who favor this theory believe that these pathologies can explain all of the features of *H. floresiensis*. However, their explanations never account for all the unique features of *H. floresiensis*; for example, there are no known

pathologies that account for ape-like wrist bones and unique non-human body proportions (see Tocheri et al., 2007; Jungers et al., 2009a; Aiello, 2005; Baab et al., 2016). The shape of the cranium and the brain size have been determined to be non-pathological, as well (Baab et al., 2016; Falk et al. 2005; Falk et al., 2007). In addition, from a purely probabilistic standpoint, the idea of a colony of hominins with an extremely high percentage of uncommon pathologies does not make sense, as there are multiple individuals found from multiple points in time. Aiello (2005) has stated that it is not impossible that *H. floresiensis* was affected by disease, just that an appropriate one has not been found, which is what these researchers have clung to. Some of these depend on how little we know about how diseases affect other hominin species and there are possibly diseases that affected ancient hominins that are unknown to us. We do not know how diseases may have affected other hominin species nor what currently unknown diseases may have existed in the past. However, as the pathology hypothesis has largely been disproven at this point, it is beyond the scope of this paper and other theories will be examined in this thesis.

In the announcement of the species, Brown et al (2004) originally suggested *H. floresiensis* was likely the result of insular dwarfing in *H. erectus*. In many ways, this was the most logical conclusion based on the evidence available at the time; *H. erectus* is the first known hominin to leave Africa, and it is found throughout East and Southeast Asia during the Pleistocene (Rightmire, 1990). In this scenario, the decreased body size characteristic of *H. floresiensis* may have resulted from food and predator scarcity (Brown, 2004). However, the *H. erectus* dwarfing hypothesis does not account for some of the differences seen between the two species (Brown, 2012; Aiello, 2005), such as the broad *Australopithecus*-like pelvis, the primitive wrist, and the long neck of the femur (Vaughan and Blaszczyk, 2008, Jungers et al.,

2009; Tocheri et al., 2007; Orr et al., 2013) exhibited by *H. floresiensis*, but not found in *H. erectus*. These features would have had to re-evolve along with decreasing stature if *H. floresiensis* were descended from *H. erectus*.

A second reasonable hypothesis is that *H. floresiensis* is descended from an early *Homo* species (more primitive than *H. erectus*) or an australopithecine. According to Wong (2005), the discoverers of *H. floresiensis* originally proposed that it was a member of the *Australopithecus* family based on the primitive features, but decided that the most logical explanation was a dwarfed *Homo erectus*. If none of the previously discovered species are good candidates for an *H. floresiensis* ancestor, then it is possible that we are looking at the descendant of a previously unknown hominin species similar to Early *Homo* and the australopithecines. This explanation requires more speculation and much more data since there is currently no evidence of either of these species outside of Africa.

Regardless of which theory one subscribes to, the issue of convergent evolution must be addressed. Many traits found in *H. floresiensis* are similar to those in other hominin species. Did a more primitive species evolve traits similar to that of *H. erectus* and *H. sapiens*? Did *H. sapiens* and *H. erectus* shrink and re-evolve traits seen in australopithecines and Early *Homo*? The answer to these questions lies in an accurate reconstruction of the phylogenetic position of *H. floresiensis*.

In order to determine the taxonomic and phylogenetic affinities of *H. floresiensis*, researchers have studied various independent sections of *Homo floresiensis*, focusing widely on craniodental features. While looking at each piece of the puzzle gives insight into the species, it does little to determine the position of *H. floresiensis* in the hominin family tree. One study

attempting to address this issue was conducted by Argue et al (2009), who looked at 50 cranial features and ten mandibular and postcranial features, totaling 60 traits. Using parsimony analysis in PAUP\* (Swofford, 2002), they found that based on those 60 features, *H. floresiensis* is most likely descended from a member of Early *Homo*, finding two most parsimonious trees where *H. floresiensis* branches before *H. habilis* but after *H. rudolfensis* and another where it branches off after both of these species. The analysis by Argue *et al.* suggested that *H. floresiensis* was most likely pre-*erectus* and most closely related to early *Homo*, either *H. habilis* or *H. rudolfensis*.

While the analysis by Argue et al. (2009) was an important first step, their analysis includes a disproportionate amount of data on the cranium and only a small sample of mandibular and postcranial features. This is not due to a lack of information: many postcrania have been discovered, including a nearly complete skeleton and various other fossils from at least 9 individuals (Brown, 2012). Studies of the postcrania have shown that *H. floresiensis* retains many primitive features in the wrist, shoulder, foot, and pelvis not found in *H. erectus*, but which are common in early *Homo* as well as australopithecines (Aiello, 2005, Morwood, 2005; Jungers et al., 2009a; Brown et al., 2004; Tocheri et al., 2007; Jungers et al 2009b; Larson et al., 2009; Orr et al., 2013; Larson, 2007; Zipfel et al., 2009). Evidence of obligate bipedalism alone is often enough to place a species in the hominin lineage when it is available: “it is now generally considered that the development of obligate bipedal locomotion was one of the most significant adaptations to occur within the hominin lineage” (Harcourt and Aiello, 2004). Nearly all of the adaptations of bipedalism are represented in the postcrania, so excluding the postcrania overlooks data crucial to understanding the full picture of hominin evolution. Excluding postcranial data makes the evolutionary context and phylogenetic relationships of *H. floresiensis*

unclear.

The evolutionary relationships among hominins have become more important and relevant as we learn more about human evolution and discover more species. There are approximately 20 species attributed to the hominin lineage (Fleagle, 2013), with multiple additions since 2004 when *H. floresiensis* was discovered (e.g., *H. naledi* and *Au. sediba*; [Berger et al., 2015; Berger et al., 2010]). Every time a new species is discovered it should remind us that we do not know nearly as much as we believe about hominin evolution and many hypotheses still need to be explored.

The objective of this analysis is to generate hypotheses regarding the ancestry of *Homo floresiensis*: is *H. floresiensis* more likely descended from early *Homo*, as the cranium suggests, or does the inclusion of postcranial characters alter the likelihood of this scenario? This analysis builds upon the previous study by Argue et al. (2009) by including more postcranial data for a more integrated picture of primitive and derived features across the skeleton. Parsimony analyses using a matrix of cranial and postcranial characters will be conducted, and competing phylogenetic hypotheses will then be evaluated by comparing the resulting phylogenetic trees. Ultimately, this project hopes to provide a more comprehensive analysis of the likely phylogenetic position of *H. floresiensis*.

## **Methods**

Postcranial data were compiled from published data collected by previous investigators (Table 1) in order to better understand the phylogenetic affinities of *H. floresiensis*. A majority of the measurements were published in relation to a particular fossil, including LB1 for *H.*

*floresiensis* and A.L. 288-1 for *Au. afarensis*. These studies considered various species for a particular area, such as many humeral measurements, carpal measurements, femoral measurements, and pedal measurements for comparison. In general, the exact measurements were published as part of the analyses or within the accompanying supplementary data (see Table 1). For example, Susan Larson's (2007) investigations of the hominin shoulder contained relevant information and relied on morphometric measurements contained within various graphical displays. Where appropriate, this data was utilized by estimating the values displayed in the graphs (Table 1).

Data was collected for 10 species of hominin, nine extinct as well as one extant, and two extant great apes (Table 1). The 12 species used by Argue et al (2009) in their analyses allowed their data to be used in conjunction with the data collected here and for comparisons. These species are *Homo sapiens*, *H. erectus*, *H. ergaster*, *H. georgicus*, *H. rhodesiensis*, *H. rudolfensis*, *H. habilis*, *Au. africanus*, *Au. afarensis*, and *H. floresiensis*; the great apes included are *Pan troglodytes* and *Gorilla gorilla* which were used as outgroups. The character traits used in this analysis were highly dependent on what had been previously published for each species. Sharing this kind of data has become more common, making morphological measurements accessible for all species. For many of the historically "older" species (i.e., species described almost 100 years ago or more) such as *H. erectus*, *Au. africanus* and *H. rhodesiensis*, it was very difficult to find this kind of data. This is partly due to the changing nomenclature, which is discussed later in more detail, and partly because this kind of published data on these species is not readily available. The nature of the fossil record also contributed to the available data since the same parts of the body are not equally distributed among species. For example, there are no wrist

bones definitively attributed to *H. erectus*.

The data presented in the analysis of Argue et al. (2009) was refined in order to better represent polymorphisms that were present. Instead of treating the polymorphisms as an either/or, they were instead assigned their own intermediate character states in many cases since, in most instances, they most likely represent an intermediate condition for a population between two fixed endpoints. For example, take the hypothetical mandibular character “development of the median mental foramen”, with two fixed character states “present” and “absent”. Our general understanding of population genetics would predict that in order for a population to move from a fixed condition of “present” to a fixed condition of “absent”, there must have been a period in time when the population was variable with some individuals exhibiting the “present” state and others exhibiting the “absent” state. Thus, coding an intermediate polymorphic condition between two fixed endpoints (0=absent, 1=polymorphic, 2=present) is a much more accurate way to model the evolution of this character than using the variable 0/1 or ? coding solutions and results in more accurate phylogenetic trees (e.g., see Wiens, 2000; Poe and Wiens, 2000). For two-state characters showing no polymorphisms between the fixed states, additional states were assigned to maintain the same number of steps between all of the states, in recognition of the likely polymorphic state that simply was not sampled by the existing data. In total, 42 of the 60 original traits in Argue et al. (2009) were altered in some way. Of those 60 traits, 50 were ordered, eight were left unordered, and two characters were removed from the matrix: bar-glenoid angle and humeral torsion. These two characters are duplicated and better-represented as quantitative characters in the postcranial matrix created here. Only 10 traits were ordered in the original analysis in Argue et al., mostly from the limited postcrania.

In addition to re-coding polymorphisms, additional cranial data were added in places it was missing. This includes data on the P<sub>4</sub> root morphology, occipitomastoid crest, and various tympanic data. For a complete list of characters included in this study including their definitions, character states, and reference in the literature, see Table 2.

Before quantitative data/characters could be used in this study, a series of adjustments had to be made. First any quantitative traits were size-corrected. This was accomplished by dividing the average raw data values for of each taxon by the cube root of the average estimated body mass for that taxon, in order to maintain standard units. The body masses for *H. sapiens* and *P. troglodytes* were compiled from Grabowski et al (2015). *Gorilla gorilla* was found in Robson and Wood (2008). *H. floresiensis* is from Holliday & Franciscus (2009); *H. rudolfensis*' body mass was taken from McHenry & Coffing (2000) and *H. rhodesiensis*' body mass was taken from Pycraft (1928). For the remaining hominins, *H. georgicus*, *H. habilis*, *Au. africanus*, *Au. afarensis*, and *H. ergaster*, body mass values were collected from Pontzer (2012). Because many species do not have representative values from both sexes, raw values were collected for male specimens, where available, and specimens of unknown sex were assumed to be males. Male body mass estimates were then used for all size corrections.

The size-corrected postcranial traits were then tested for allometric influence. This was done by correlating the size-corrected value for each character (see above) to the body mass estimates used in the size corrections as per Gilbert et al. (2009). Of the quantitative features studied, only the bar-glenoid angle was found to be allometrically influenced. Body mass was then also added to the matrix as a character. The bar-glenoid angle was then coded using the general allometric method. For each species, “0” or “1” was assigned based on the residual from

the line of best fit for this character (Gilbert et al., 2009; 2013). The remaining characters were then divided into three categories using gap weighted coding (Thiele 1993) in order to separate them more objectively.

In total, the added postcranial data includes 77 traits representing areas of the clavicle, scapula, carpal bones, humerus, pelvis, femur, tibia, and talus. These traits were combined with the data from Argue et al. (2009) to bring the total traits included to 132 traits (see Table 2). Of these 132, 124 were ordered and 8 were unordered (Table 2). Once all of the data had been collected and coded, a NEXUS file was prepared and uploaded to PAUP\* v. 4.0b10 for Windows (Swofford, 2002). The analyses performed were done using a 10,000 replication parsimony heuristic search with *G. gorilla* and *P. troglodytes* assigned and constrained as successive outgroups. This was done to ensure the trees found resembled what is known of the extant apes relationship to the hominins included and to each other, and was critical to setting polarities for the analysis.

Four main analyses were performed. In order to determine the effect and phylogenetic signal of only the postcranial data set, the first two analyses used all 132 characters, first on all 12 taxa then repeated to the exclusion of *H. rhodesiensis* and *H. rudolfensis*. These two taxa were removed because they have the least amount of data associated with them, having only minimal fossils definitively assigned to each species, particularly in the postcrania. Both of these species have only a single femur and *H. rhodesiensis* has some pelvic remains attributed to them in addition to the skulls. The next two analyses used only the 77 postcranial characters, first on all 12 taxa and then as in the previous analysis with *H. rhodesiensis* and *H. rudolfensis* removed. In addition, a bootstrap analysis was performed with 10,000 reps; the same formula from the

previous two tests was used. This was done first with all 132 characters and then repeated with the exclusion of the cranial characters.

## Results

In the first analysis, with all 132 characters and all 12 taxa, one most parsimonious tree (MPTs) was produced (Figure 1). In this tree, *Au. afarensis* branches off first. The tree then diverges with a clade of *H. floresiensis* and *Au. africanus* reconstructed as sister taxa with *H. rudolfensis* at the base of the clade. On the other side of this divergence, *H. habilis* branches off leading to a clade with *H. sapiens* being the sister taxon to a clade consisting of *H. erectus*, *H. rhodesiensis*, Dmanisi, and *H. ergaster*, with successive branching of *H. erectus*, *H. rhodesiensis*, and Dmanisi+*H. ergaster*.

Once *H. rudolfensis* and *H. rhodesiensis* were removed, four MPTs were recovered (Figures 2a-2d). In the first of these four trees (Fig. 2a), *H. erectus* and *H. ergaster* are reconstructed as sister taxa with the Dmanisi hominins, *H. sapiens*, *Au. afarensis*, *H. habilis*, *H. floresiensis* and *Au. africanus* successively branching out towards the base of the tree. In the next tree (Fig. 2b), *Au. africanus* and *H. floresiensis* diverge successively at the base, followed by a split of the remaining taxa into two clades: (*H. habilis*, (*H. sapiens*, *A. afarensis*)) and (*H. erectus*, (Dmanisi, *H. ergaster*)). In the third tree (Fig. 2c), *H. erectus* branches off first, followed by *H. habilis*. *H. floresiensis* and *Au. africanus* are reconstructed the sister clade to the remaining taxa forming a clade consisting of (*A. afarensis*, (*H. sapiens*, (*H. ergaster*, Dmanisi))). In the fourth MPT (Fig. 2d), *H. erectus* branches off immediately followed successively by *H. floresiensis*, *A. africanus*, *H. habilis*, *A. afarensis*, *H. sapiens*, and *H. ergaster*+Dmanisi. The

strict consensus tree does not provide support for any specific clade (Fig. 3), and the majority rule consensus of these four trees showed support only for a Dmanisi/*H. ergaster* clade (Fig. 4).

Once the cranial characters are removed, eight MPTs were recovered with all 12 taxa, (Figs. 5a-5h). In all eight trees, *H. floresiensis* is reconstructed as the sister taxon of *Au. afarensis* (see Figs. 6-7 for consensus trees). This differs from the trees that contain craniodental data where *H. floresiensis* was most often reconstructed as the sister taxon to *Au. africanus*. This is also dissimilar to Argue et al.'s (2009) trees, where *H. floresiensis* shows an affinity towards early *Homo* rather than the australopithecines. When *H. rhodesiensis* and *H. rudolfensis* are removed, the trees stabilize and only two MPTs are produced (Figs. 8a-8b). These trees differ only in the placement of *Au. africanus*. In both trees, *H. habilis* diverges immediately at the base of the group. In the first MPT, *A. africanus* is the next taxon to diverge, followed by (*A. afarensis*, *H. floresiensis*), (*H. sapiens*, (*Dmanisi*, (*H. erectus*, *H. ergaster*))). The relationships in the second tree are the same, except *Au. africanus* branches off immediately after the *A. afarensis*/*H. floresiensis* clade rather than immediately before. In both trees, *H. floresiensis* is reconstructed as sister taxa with *Au. afarensis*.

The results of the bootstrapping analysis of all 12 taxa was not conclusive; there was no support for any of the clades (Fig. 9). This was similar to results obtained by Argue et al., (2009) in their analysis as well, where there was also little bootstrap support. The bootstrap values for only the postcranial characters show low support (52%) for an early divergence of *H. habilis*, but otherwise no support for any other clade (Fig. 10).

## Discussion

Does this analysis bring us any closer to discovering the true ancestry of *H. floresiensis*? Not entirely, but we can be fairly certain that *H. erectus* should be eliminated from candidacy. Not one of recovered MPTs in this study reconstructed *H. floresiensis* and *H. erectus* as sister taxa. Furthermore, the results of the study done by Argue et al. (2009) also show no recent common ancestor between *H. floresiensis* and *H. erectus*. This is further supported by a more recent study done by Argue et al. (2017) which included more hominin species and more characters. In all but one of the MPTs recovered by Argue et al. (2017), *H. floresiensis* was reconstructed as sister taxa of *H. habilis*. In that one, *H. floresiensis* is reconstructed as branching off immediately before *H. habilis*.

The results obtained in the current study are quite similar to the conclusions reached by Argue *et al* (2009) in their analysis. As mentioned above, their analysis indicated that *H. floresiensis* is more closely related to early *Homo* and the australopithecines. However, the MPTs in their study differed in the precise placement of *H. floresiensis* relative to the results obtained here. The first MPT from the Argue et al. (2009) analysis suggests that *H. floresiensis* evolved after *H. habilis* and *H. rudolfensis*, but before the Dmanisi hominins and *Homo erectus/ergaster*. In the second MPT, *H. floresiensis* is hypothesized to have branched off between *H. habilis* and *H. rudolfensis*. The MPTs found by Argue et al. (2009) also display the same issue with the placement of *H. rhodesiensis*, *H. ergaster*, *H. erectus*, and *H. sapiens* that was found in this study, but to a lesser degree. However, between their two MPTs there is huge difference. In the first MPT, *H. rhodesiensis* is the sister taxon of *H. ergaster*, and *H. erectus* and *H. sapiens* branch off from that clade. In the other tree, *H. rhodesiensis* and *H. sapiens* are sister

taxa, and so are the Dmanisi hominins and *H. ergaster* with *H. erectus* a lone branch between these two clades.

In summary, Argue et al. (2009) present two possibilities regarding the phylogenetic affinities of *H. floresiensis*. In the first, *H. floresiensis* is reconstructed as diverging after early *Homo* but before the rest of hominins, and in the second, *H. floresiensis* is reconstructed within early *Homo* but after the australopithecines. In general, in this study, *H. floresiensis* fell either within an early *Homo* group or within a group with early *Homo* and Australopithecine taxa combined. In nearly every MPT in this study, *H. floresiensis* and either *Au. africanus* or *Au. afarensis* are reconstructed as sister taxa. In the few MPTs where this is not the case, *H. floresiensis* branches off between *H. habilis* and *Au. africanus* or branches off successively following *H. habilis* and *Au. africanus*. This only occurs when *H. rhodesiensis* and *H. rudolfensis* are excluded from the analyses with all 132 characters. This is a stark contrast to the most recent study done by Argue et al. (2017) where *H. floresiensis* is most often reconstructed as the sister taxon to *H. habilis*. The analyses which recovered more than one MPT most often did so due to lack of resolution between *H. sapiens*, *H. erectus*, *H. ergaster*, *H. rudolfensis* and the Dmanisi hominins.

A character transformation analysis highlighted synapomorphies for a *H. floresiensis*/*Au. africanus* clade include a relatively long fifth metatarsal, a relatively long medial epicondyle, and a scapular spine orientation between 41° and 60° (Table 3). The clade containing *H. rudolfensis* and *Au. afarensis* as well as *H. floresiensis* and *Au. africanus* had synapomorphies including relatively long fleshy foot size. It is interesting that this character was reconstructed as a synapomorphy for this clade since it is a distinctive character of *H. floresiensis*. In fact, it

appears to be shared to some degree with both australopithecines and *H. rudolfensis* but none of the other hominins, and may be an interesting indicator of descent. Other characters that are shared between these four taxa include low bar-glenoid angle and lack of palmar expansion. The clade containing *H. rhodesiensis*, *H. ergaster*, *H. erectus*, and *H. sapiens* contained synapomorphies in the lower limb such as lower talar torsion and a medium sized femoral head diameter.

Despite the intriguing results of this study, there were many underlying issues that made creation of the matrix difficult. The two biggest issues are changing nomenclature and scarcity of materials. Nomenclature was a limitation because for many species there is not a consensus about which fossils belong to which species nor the degree of variation within each species. This includes *H. habilis* being used as a repository for early *Homo* with no clear affinities. It has been pointed out that there is a great deal of variation within the species *Homo habilis* (Falk 2011). If many specimens that do not fit elsewhere are being assigned to *H. habilis*, it is possible that the *H. floresiensis* ancestor is among them and has already been found. Future endeavors may include an analysis of cranial traits of different specimens of what is now *H. habilis* to see if any fit the evolutionary trajectory toward *H. floresiensis*. Milford Wolpoff argues that many fossils found in Indonesia in the 1940s are poorly studied and have been misclassified as *Homo erectus* (Wong, 2005), citing variation too great for one species. The counter argument has been that most adaptations of *H. floresiensis* that resemble that of australopithecines are due to small size (Holliday and Franciscus, 2009). Small stature and stature in general have been linked to both phylogenetic and adaptive significance (Brown et al., 2004). This does not mean small statured individuals have to be descended from other small statured individuals, but it is strong evidence

in favor of it. Insular dwarfism does not account for the primitive wrist, foot, or pelvis, however. *H. floresiensis* would have had to re-evolve a series of the primitive traits as a result of shrinking in stature (Jungers, 2009a). One example is clearly demonstrated in the foot of *H. floresiensis*. The endurance running adaptations of the foot evolved around 1.5 million years ago, but this adaptation is not present in *H. floresiensis* (Lieberman, 2009). This means that *H. floresiensis* would have had to re-evolve the primitive foot of hominin clade in addition to acquiring small stature. The same is true of the wrist adaptations; they would have had to re-evolve many of the primitive features because they had not been present since 800 kya in hominins (Morwood and Jungers, 2009) and are not present in *H. sapiens*, *H. neanderthalensis*, or *H. antecessor*.

*H. habilis* is not the only hominin species to suffer from a nomenclature problem among the ones represented here. Particularly troublesome are *H. erectus* and *H. ergaster*. There is some debate as to whether or not these two species are geographic variations of the same species, or two separate species (Wood, 1992). This makes it difficult to gather data on either of the species. Previously, both species were referred to as to as *H. erectus*, the African variety is now *H. ergaster* and the Asian fossils are referred to as *H. erectus*. However, this distinction is not universal. Much of the literature uses *H. erectus* to encompass both the Asian and African specimens (Rightmire, 1986; Rightmire, 1990; Wood, 1992; Baab, 2008). Doing a basic search on *H. erectus* will bring up mostly African fossils such as KNM-WT 15000. Because of this, there is very little postcrania attributed to these species. Many primitive features found in *H. floresiensis* are in the wrist joints and pedal bones but there are few fossils of these areas for *H. erectus* and *H. ergaster*. Based on a capitate from *Homo antecessor* it appears that the modern wrist configuration is present by 800 kya (Tocheri et al., 2007). We know that the modern wrist

was present in both Neanderthals and in *Homo sapiens*, but it is unclear whether it was present in *H. erectus* or not (Orr et al., 2013). So, *H. floresiensis* must be descended from a species before this unless these primitive features re-evolved. There has also been some debate regarding *H. rhodesiensis*' status as its own species. It has been put forth that *H. rhodesiensis* is actually *H. heidelbergensis* (Relethford, 2010) and *H. rhodesiensis* refers specifically to the Broken Hill fossils. If *H. rhodesiensis* is actually *H. heidelbergensis*, this would increase the amount of available data on this species. Only the Broken Hill fossils were used in this analysis to stay consistent with Argue *et al*'s data. An alternative theory posits that *H. rhodesiensis* and *H. heidelbergensis* are analogous to *H. ergaster* and *H. erectus*, where *H. rhodesiensis* is an Africa-specific variant and *H. heidelbergensis* is a European variant (Relethford, 2010).

The most obvious limitation about these analyses is the nature of the fossil record and the process of taphonomy. We can only study what does fossilize. There is a lack of postcrania attributed to many species, especially *H. rhodesiensis* and *H. rudolfensis*. Two of these analyses thus exclude this data/these species. Because we know so little about Indonesian hominin evolution and relationships, it is important to include as many species as possible. While much of the postcrania of *H. floresiensis* is described as primitive particularly in the wrist and the pedal bones, not every species has fossils representing these sections of the body. Many of the measurements for *H. rhodesiensis* come from a monograph from 1928 from a few specimens found at Broken Hill, Kabwe. *H. rudolfensis* has a single cranium, as well as some additional facial and mandibular material and a femur (Wood, 1992; Leakey et al., 2014). The nature of the fossil record makes it difficult to gather a large number of attributes across many species particularly without any access to the fossils or casts. Some species are represented by only a

skull or a single finger bone, while others have femora, humeri, and pelves; this lack of similarity in the postcrania that have been found makes it difficult to do analyses of this nature. This also creates small sample sizes, for some species there are few measurements for particular characters because we lack the specimens. It is impossible to know if something is representative of a species when there is not adequate representation. So we could be using anomalies to reconstruct hominin evolution.

In addition to the issues creating the postcranial matrix, changes to the matrix of Argue *et al.* (2009) were required. The changes made to rectify these issues were discussed in the Methods section to a lesser extent, but not the rationale for these changes. For some characters, data for *H. sapiens*, *Pan troglodytes*, and *Gorilla gorilla* were missing. For these particular species there are many specimens and additional data studies available. These changes were necessary because many of the assumptions made in Argue *et al.*'s analysis are demonstrably poor ways to model evolution; e.g., using the 1/2 designation for polymorphic characters, unordering many characters with little justification, and the lack of quantification in many characters. Thus, the assumptions made in this study are much more reasonable evolutionary assumptions. Perhaps with a more comprehensive set of craniodental data, such as that of Strait and Grine (2004) (their matrix contained 198 craniodental characters and 19 taxa, based on Collard and Wood [2000] with additional data added by the researchers.), the MPTs recovered would resemble a more consensus view of the hominin lineage. Using a data set such as the one collected by Strait and Grine (2004) supplemented with data for *H. floresiensis* may reconstruct trees that are more accurate.

With *H. erectus* no longer a likely candidate as the ancestral population of *H. floresiensis*,

there are many questions that need to be investigated, most importantly, how did this ancestral population arrive on Flores? Without any other hominins on Flores for comparison, this becomes difficult to answer. Sea level changes and other natural occurrences play a role in dispersing primate species (e.g., Fleagle and Gilbert, 2006). *H. floresiensis* was present on Flores at least 74 thousand years ago. Morwood and Jungers (2009) estimate that the ancestors of *H. floresiensis* exited Africa between 1.8 - 2.6 million years ago based on the appearance of particular primitive features found in *H. floresiensis*. This includes features of the wrist: the trapezoid, scaphoid, and capitate. These show none of the derived features of *H. sapiens* or *H. neanderthalensis*. According to Tocheri et al., (2007) “wrist morphology can be a powerful indicator of phylogenetic relationships in Mammalia,” making the lack of carpal bones from *H. ergaster* and *H. erectus* particularly important. Features of the primitive wrist of *H. floresiensis* includes a wedge shaped trapezoid which is more similar to the condition in the African apes than to *Homo sapiens* which has a boot shaped trapezoid. *H. floresiensis* also has a j-hook on the distal aspect of the scaphoid which resembles *Au. afarensis*, *Pan troglodytes*, and *Pan paniscus* but not *H. sapiens* or *Au. africanus*. The capitate lacks the enlarged palmarly placed articular surface for the trapezoid as seen in *Homo sapiens*. The *H. floresiensis* wrist resembles a wrist that was present before the modern wrist configuration found in *H. sapiens* (Tocheri et al., 2007; Orr et al., 2013). This means a primitive wrist was evolved again on Flores or the ancestor of *H. floresiensis* dispersed before the modern configuration evolved. The wrist is not the only region displaying primitive morphology: *H. floresiensis* also shares features of the tarsus, navicular, ilium, and clavicle with early *Homo* and *Australopithecus*. The flare of the iliac blades, the bicondylar angle, and the talar neck angle are all similar to those seen in the australopithecines (Jungers et

al., 2009a). The talar torsion is less than that of australopithecines and *H. sapiens*, and is similar to that of the African apes (Jungers et al., 2009b). The *H. floresiensis* navicular retains the lateral pinching that is present in African apes and australopithecines, and present but reduced in *H. habilis* (Jungers et al., 2009b). *H. floresiensis* displays the primitive double curvature of the clavicle in posterior view (Voisin, 2006).

Based on limited information on what the ancestor of *H. floresiensis* should look like, we should be able to figure out where they come from. The ancestral population could have travelled one of two ways: they could have traveled out of Africa through Asia toward Indonesia, they could have traveled over-water through a chance event, or a combination of both. In terms of chance events, rafting is the most likely candidate. Although such an event is quite unlikely as a single episode, given a large enough sample size (and/or time), rare events do happen. In either case, there is no evidence of a journey over land or water, and travel by sea would leave little trace of the voyage anyway. Typical materials for watercrafts would not fossilize so there would be no evidence it, if it were built.

Flores has never been connected to the continental shelf and has always been at least 19 km from the nearest island, ruling out the possibility of a land bridge, so the only possibility is that the population arrived via watercraft whether intentional or unintentional (Dennell et al., 2014). There seems to be some debate about whether *H. erectus* had the cognitive capabilities to create a watercraft and sail anywhere deliberately (Morwood et al., 1998). If *H. erectus*' capabilities are the subject of contention it is safe to say that the abilities of earlier hominins and australopithecines are as well. It would require a brain more complicated than that of at least *H. erectus* to build a watercraft. Bednarik (2003) demonstrated that a watercraft could be made with

the tools found in the Middle Pleistocene that could sail ~1 km. But would a pre-*erectus* hominin have the cognitive capabilities to use these tools to create a watercraft? If a pre-*erectus* hominin could intentionally build a watercraft, why don't we find any hominins on other islands in between African and Flores? If the *H. floresiensis* ancestor travelled through Europe and Asia and departed from there, why don't we find any fossil evidence in Asia before *H. erectus*? Just because they have not been found, does not mean they are not there. There are many uncertainties in this situation and very little evidence, but without evidence to the contrary, water travel makes the most sense. So, it must have been unintentional.

If *H. floresiensis* is descended from australopithecines or early hominins, there must be another way they crossed the water. Accidental vegetation rafting has been documented in primate species in the past, such as the origination of New World monkeys in South America which is discussed below (Houle, 1999). This is an implausible explanation but it is not impossible. Natural disasters such as storms, tsunamis, or cyclones could have created one of these rafts occupied by viable hominins (Dennell et al., 2014; Houle, 1999; Fleagle and Gilbert, 2006). The likely options for the source of the ancestral population are Java and Sulawesi (Dennell et al., 2014). However, there is no documented evidence of early *Homo*, like *H. habilis*, or australopithecines in Indonesia. The most favored option is Sulawesi. Morwood and Jungers (2009) have estimated that changing sea levels may have left that distance as little as 80 km between Sulawesi and Flores and wind currents would have been favorable for a journey between the two islands (Dennell et al., 2014). Stone tools have been discovered at Sulawesi dating back to 194 kya which indicate that there were hominins occupying the island but no fossil hominins have been discovered (Bower, 2016). If hominins are discovered on Sulawesi, it

could help elucidate the phylogenetic affinities of *H. floresiensis* and the hominin activity in the area. Van der Bergh *et al.*, (2016) have recently published findings at Meta Mange of a similar but not identical hominin living on Flores. The evidence is sparse, only a mandible and isolated teeth that demonstrates that *H. floresiensis* is not an anomaly on the island. If Indonesia is not the source of the ancestral population, then Africa is the next logical place. Could a group of hominins survive a journey from Africa to Indonesia? New World Primates are hypothesized to have travelled from Africa to South America via raft (Fleagle 2013). Orlosky and Swindler (1975) estimated that at the time of the dispersion there would have 1300 miles (or just short of 2100 km) separating Africa and South America. Flores is significantly further from even the closest point in Africa. Is this trip possible? Houle (1999) looked at the various hypotheses for platyrrhine origins including rafting and estimates that a 1 kg primate could survive the trip under certain circumstances and with great fortune. Paleocurrents and paleo-winds would have made the trip last between 8 and 15 days, so as long as the primates could last this long with limited water, then it is possible. It makes sense for hominins to have left Africa and travelled through Europe and Asia to eventually reach Indonesia. The fact that there is no evidence for early *Homo* or australopithecines outside of Africa does not mean they were not present. Absence of evidence is not evidence of absence. The discovery of *H. floresiensis* has created many more questions than have been answered about human evolution. This serves as a reminder that we are working with an incomplete picture. If Early *Homo* or australopithecines left Africa by foot and travelled through Asia and continued on a similar trajectory to that of *H. erectus* and made it to Java, then the journey by sea would have been much shorter. How hominins were able to reach Flores and flourish is definitively worth investigating.

There is still a significant amount of research needed on the phylogenetic affinities of *H. floresiensis*; adding more postcranial and cranial characteristics to a similar analysis will elucidate more information about the phylogenetic affinities of *H. floresiensis*. John Wiens (2001) suggests adding more characters will help fill in the gaps of missing data so rampant in the fossil record. Of course, this will not work for species where there are only a few fossils attributed to the species. There are only a limited number of measurements and features that can be described on a bone. It is also possible that the issue may be the parsimony model and hominin evolution. It may also be that parsimony is not particularly conducive to reconstructing hominin evolution and there be better methods to model hominin evolution. In future studies this may include using Bayesian methods would better elucidate the complex relationships that hominins seem to have by using prior information in the analysis to reconstruct probable trees from what we do know about hominin evolution. Other areas to investigate could involve bringing in other species, including newly discovered species such as *Homo naledi* and *Au. sediba* to help resolve this contentious issue. Additionally, increasing character numbers, converting many craniodental characters to quantitative ones where possible, and having a single observer or few observers collect all of the data in a single study to reduce interobserver error would also improve upon the results of this study.

Sutikna et al (2016) have suggested that the Denisovans should be investigated in relation to *H. floresiensis*. Very little physical evidence exists for the Denisovan hominins: a distal phalanx of the fifth manual digit was discovered and used to extract mtDNA (Krause et al., 2010). From this mtDNA, it was discovered that the Denisovan sequence differed from *H. sapiens* by 385 positions while Neanderthals differed by only 202. This demonstrates that the

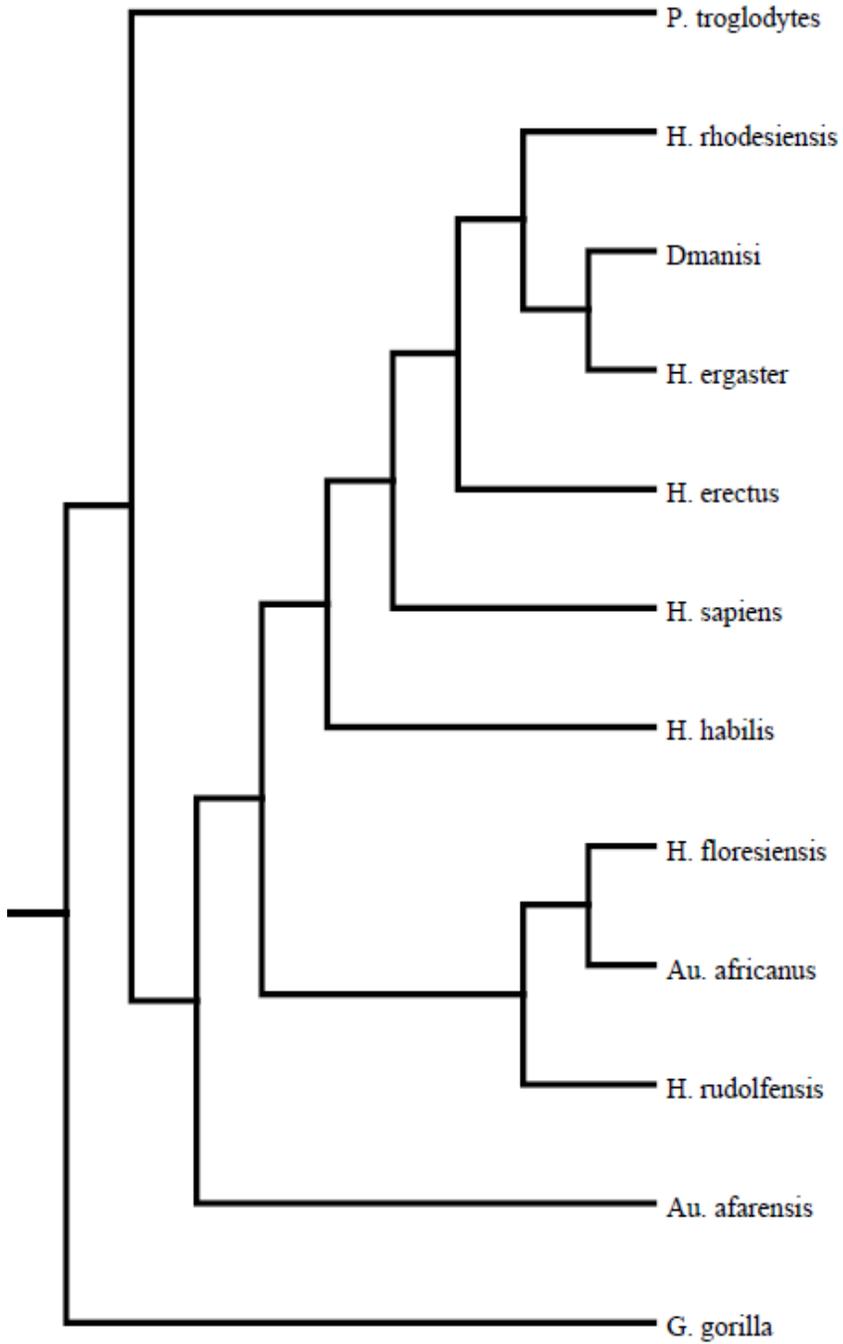
mtDNA branches off before both *H. sapiens* and Neanderthals. This is a totally distinct lineage from *H. sapiens* and could be a candidate for shared ancestry with *H. floresiensis*. However, this cannot be pursued unless more fossils are attributed to the Denisovans or mtDNA from *H. floresiensis* becomes available.

For now, the analyses conducted here suggest that *H. floresiensis* shares the clearest affinities with the more primitive African populations generally attributed to *Australopithecus* and early *Homo*. As more fossils are found and more data becomes available, the phylogenetic position of *H. floresiensis* should become clearer. The paucity of the fossil record is most certainly a barrier that can only be rectified by continuing to do research and discover new fossilized material, perhaps an even larger issue is the lack of secure taxonomy for the hominin lineage. The distinctive features of *H. floresiensis* have made it a topic of great controversy, which should continue to drive interest and research until its origins and phylogenetic position is more secure. As long as the fossil record remains incomplete and disputed, it will be difficult to ascertain the phylogenetic affinities of *H. floresiensis*. This includes data from all species of hominins; as more of each species is discovered and studied, we will have a greater understanding of the hominin lineage. Each species is important not only on its own, but also as part of a complicated evolutionary bush that elucidates our complicated history as *H. sapiens*.

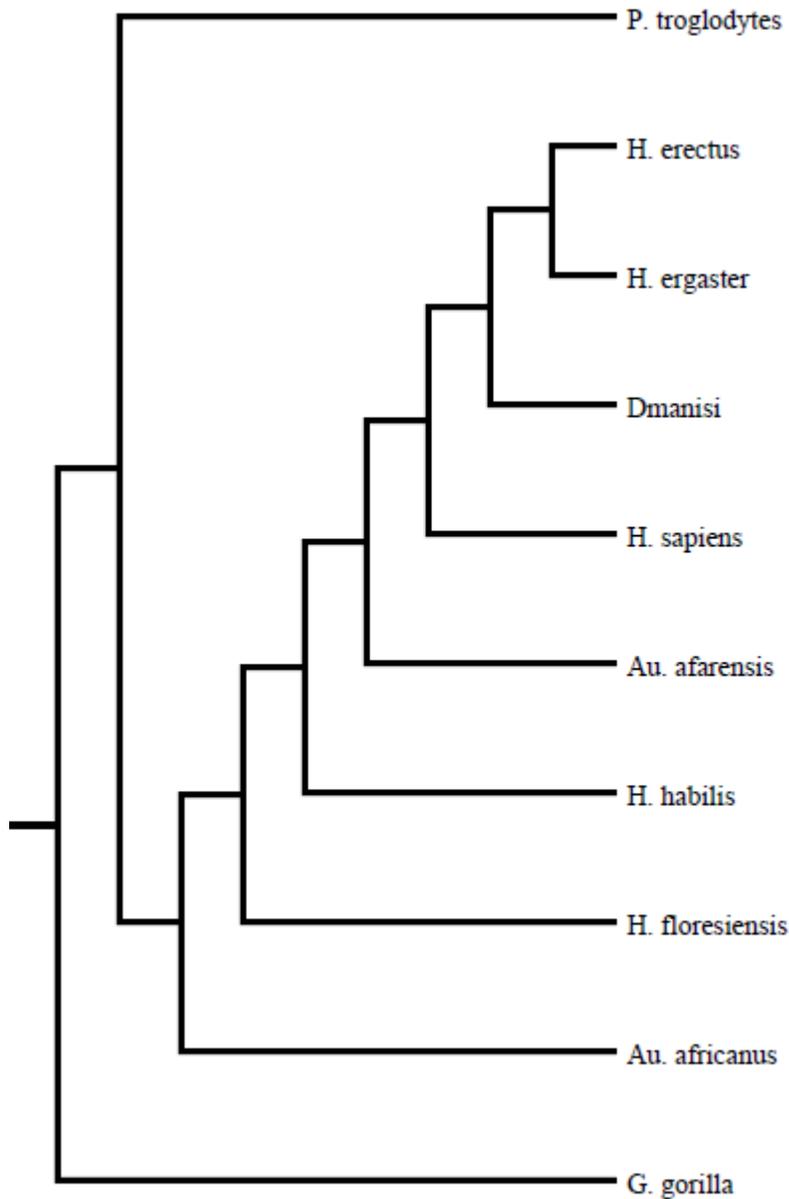
Aiello (2005) summarizes the importance of these finds: “we may be on the threshold of a major transformation in our understanding of human evolution that will have profound and far-reaching implications”. The more we discover about hominin evolution, the more we are reminded that we have barely breached the surface. Every possibility should be explored. A few centuries ago, we had no understanding of the human fossil record, and now we know of at least

22 members on our family tree. There is much more to learn about *H. floresiensis*, and I look forward to future studies improving upon the work begun here.

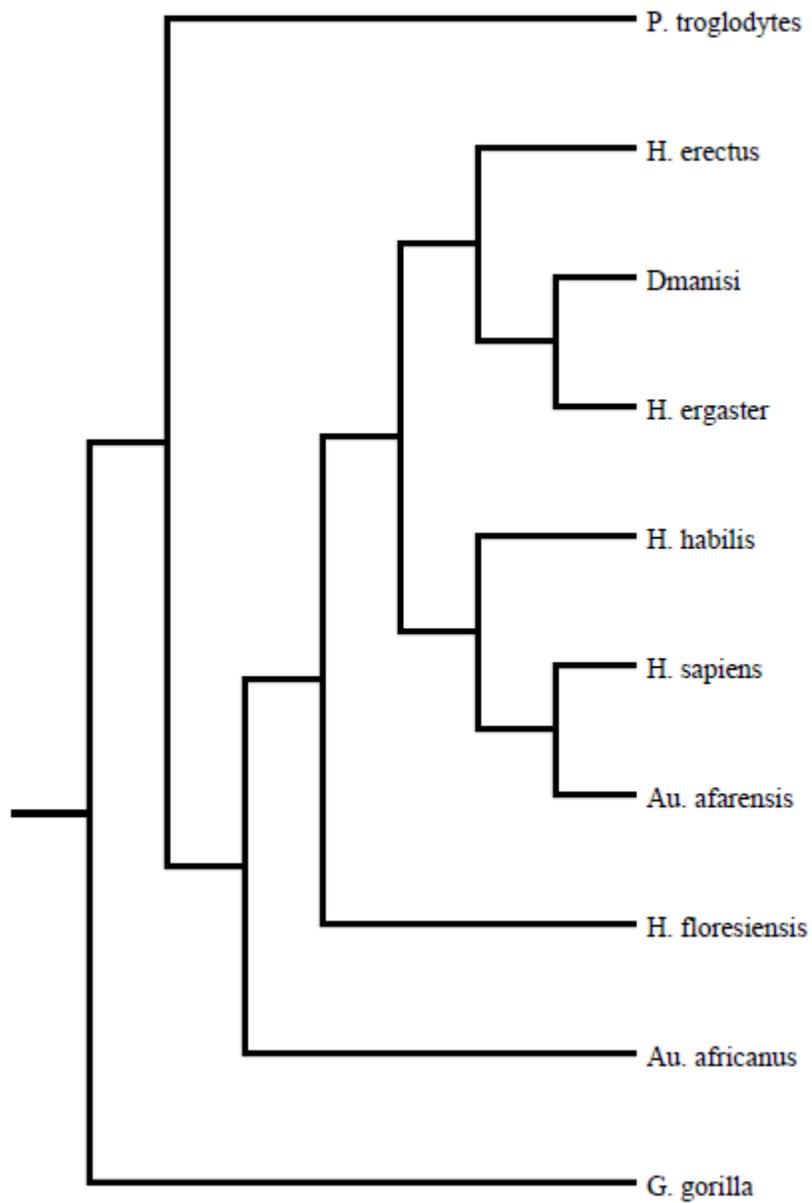
## Figures



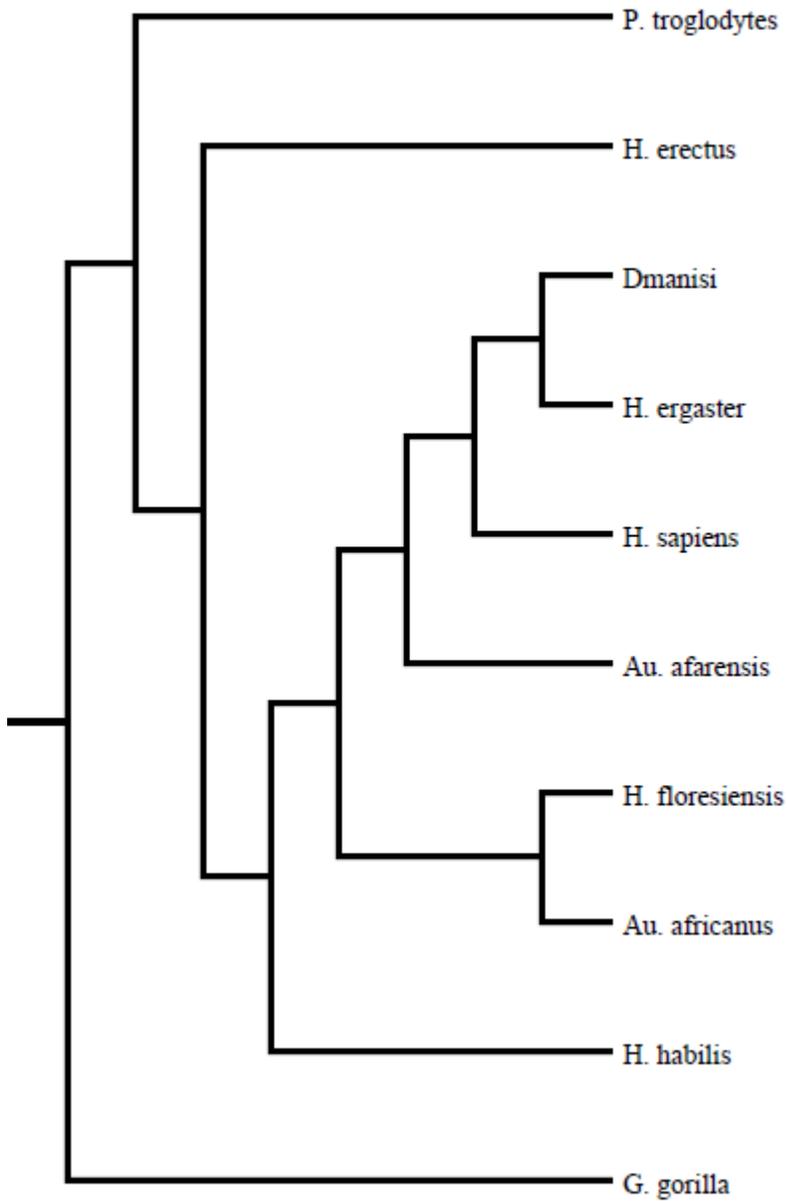
**Figure 1.** MPT from the analysis containing all 12 taxa and all 132 characters. In this analysis, *H. floresiensis* is reconstructed as sister taxa with *Au. africanus*. Length 550 CI: .540 RI: .346 RC: .187 HI: .460



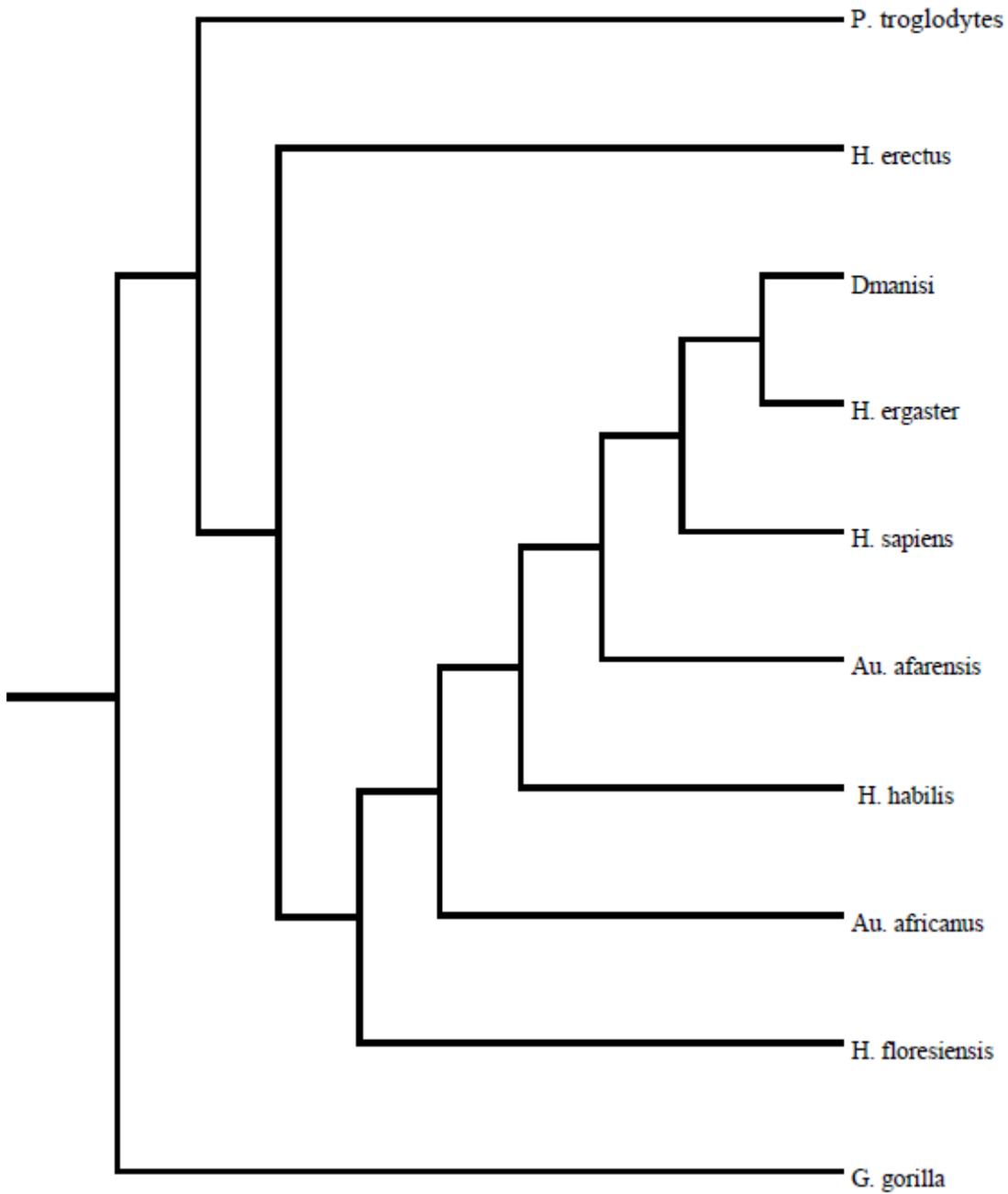
**Figure 2a.** First of three MPTs from the analysis containing all 132 characters that excludes *H. rhodesiensis* and *H. rudolfensis*. *H. erectus* and *H. ergaster* are reconstructed as sister taxa with successive branching of the remaining taxa with *Au. africanus* at the base. Length: 498 CI: .564 RI: .326 RC: .184 HI: .436



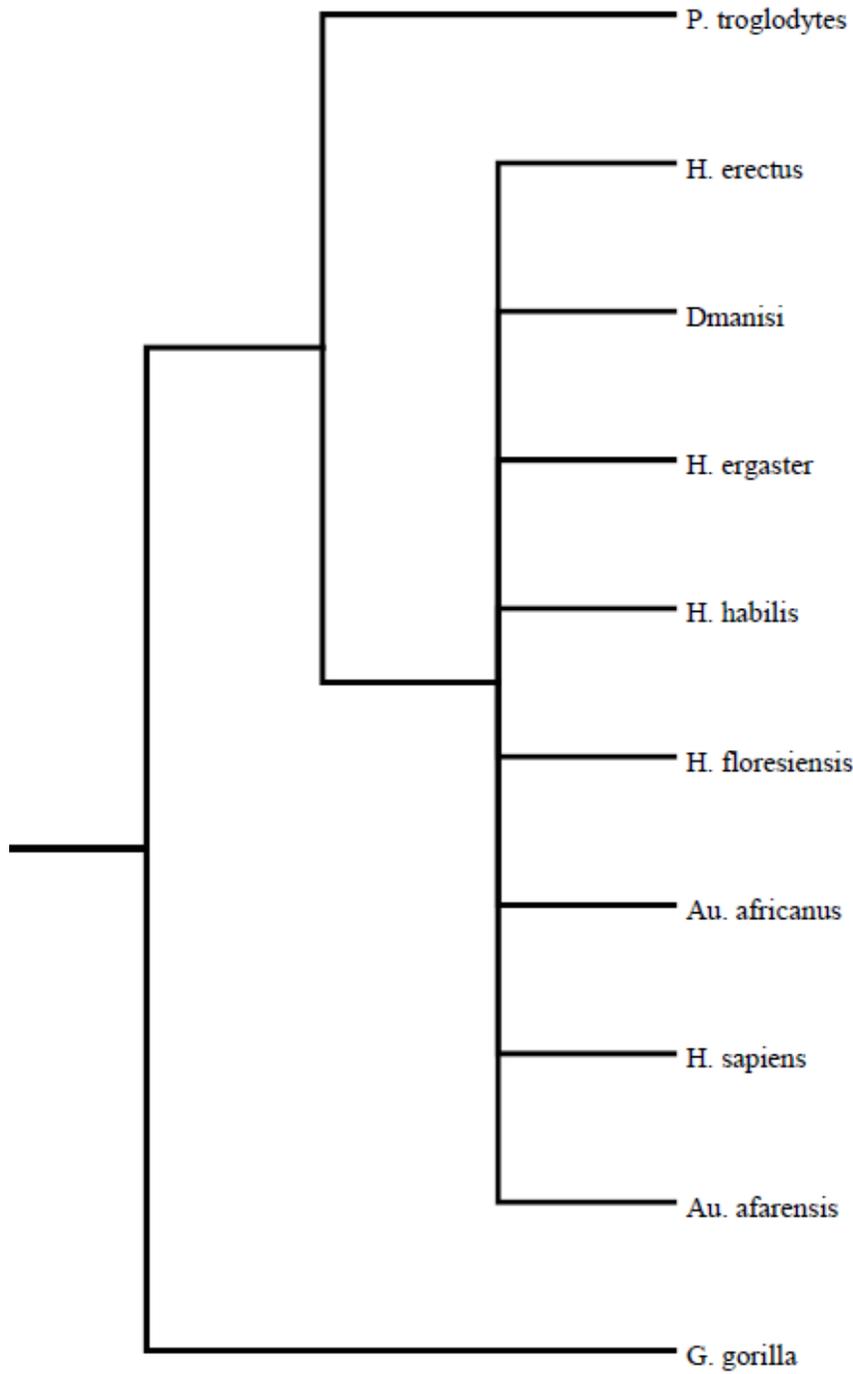
**Figure 2b.** Second of three MPTs from the analysis containing all 132 characters that excludes *H. rhodesiensis* and *H. rudolfensis*. In this MPT, *Au. africanus* and *H. floresiensis* diverge successively at the base, followed by a split of the remaining taxa into two clades: (*H. habilis*, (*H. sapiens*, *A. afarensis*)) and (*H. erectus*, (*Dmanisi*, *H. ergaster*)). Length: 498 CI: .564 RI: .326 RC: .184 HI: .436



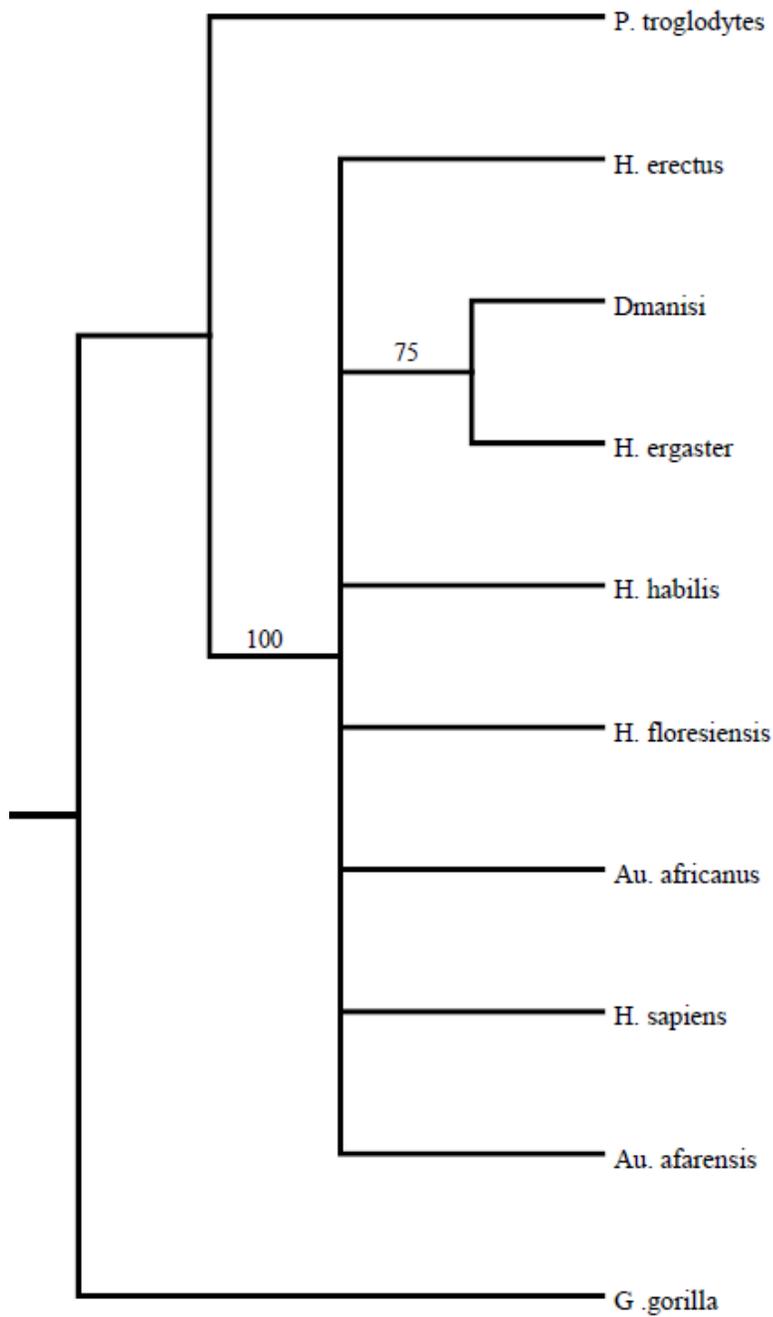
**Figure 2c.** Third of four MPTs from the analysis containing all 132 characters that excludes *H. rhodesiensis* and *H. rudolfensis*. Here, *H. erectus* branches off first, followed by *H. habilis*. *H. floresiensis* and *Au. africanus* are reconstructed the sister clade to the remaining taxa forming a clade consisting of (*A. afarensis*, (*H. sapiens*, (*H. ergaster*, Dmanisi))). Length: 498 CI: .564 RI: .326 RC: .184 HI: .436



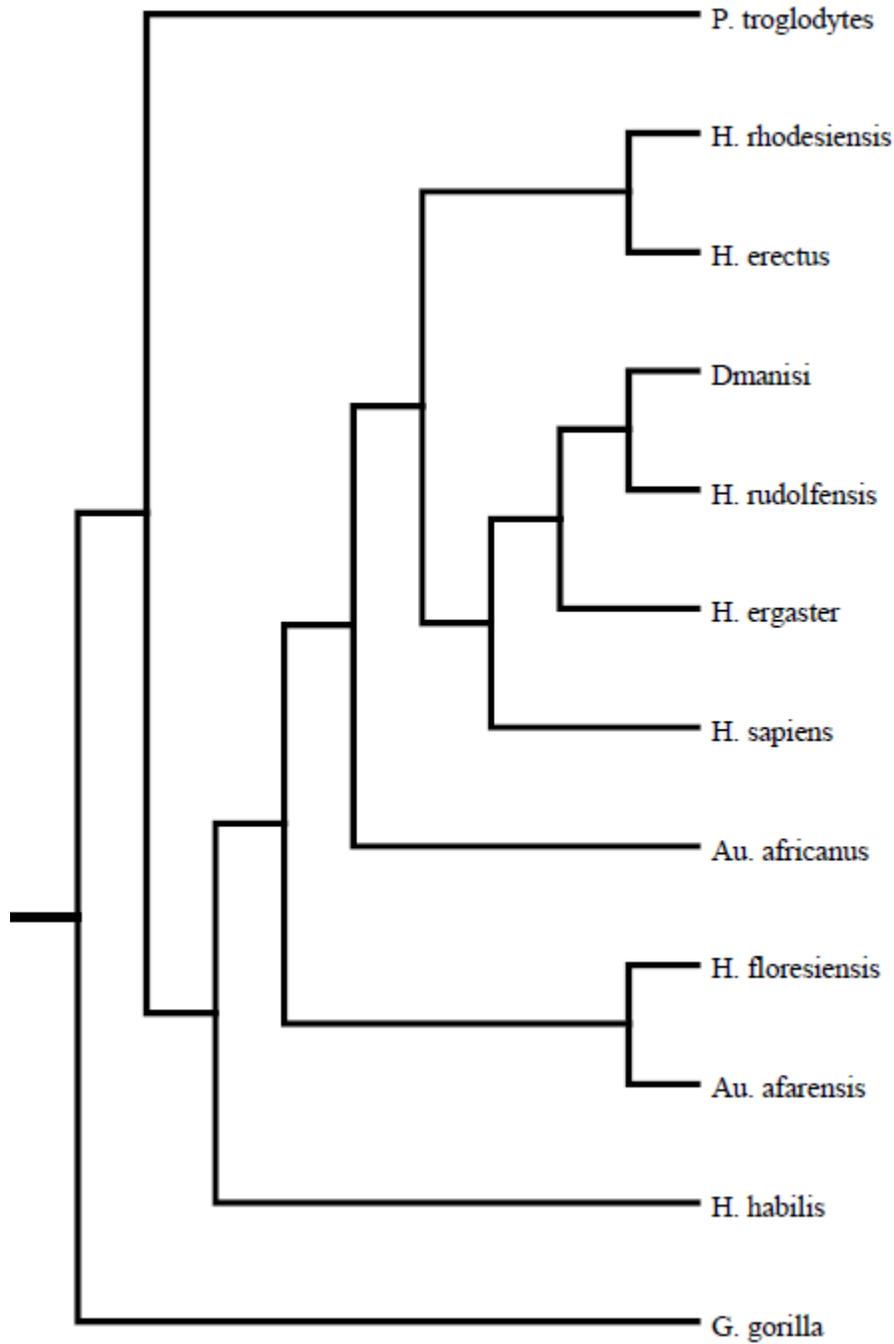
**Figure 2d.** Final of four MPTs from the analysis containing all 132 characters that excludes *H. rhodesiensis* and *H. rudolfensis*. In the fourth MPT, *H. erectus* branches off immediately followed successively by *H. floresiensis*, *A. africanus*, *H. habilis*, *A. afarensis*, *H. sapiens*, and *H. ergaster*+*Dmanisi*. Length: 498 CI: .564 RI: .326 RC: .184 HI: .436.



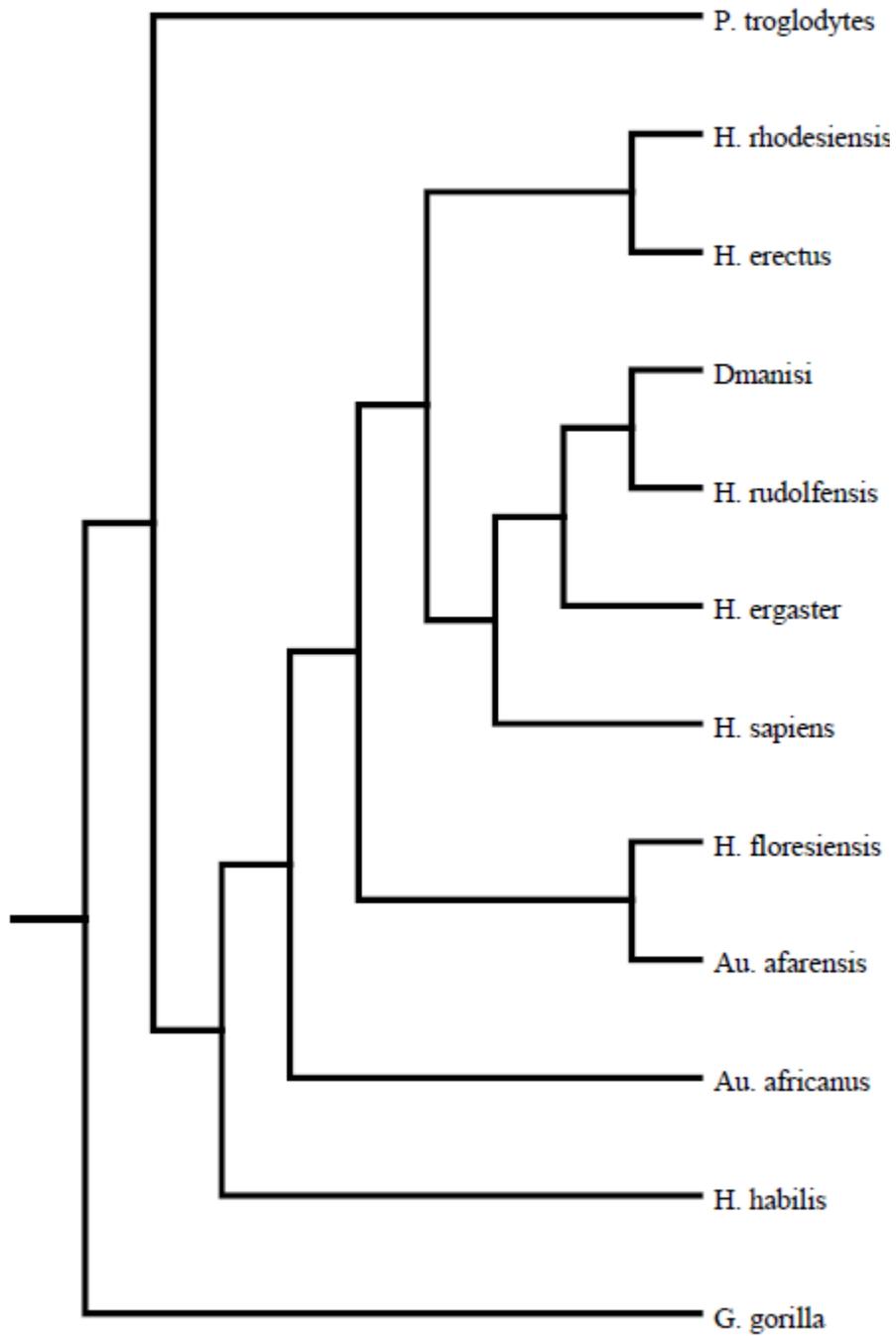
**Figure 3.** Strict Consensus tree of all 132 characters with *H. rhodesiensis* and *H. rudolfensis* excluded from the analysis. There is no bootstrap support for any clades.



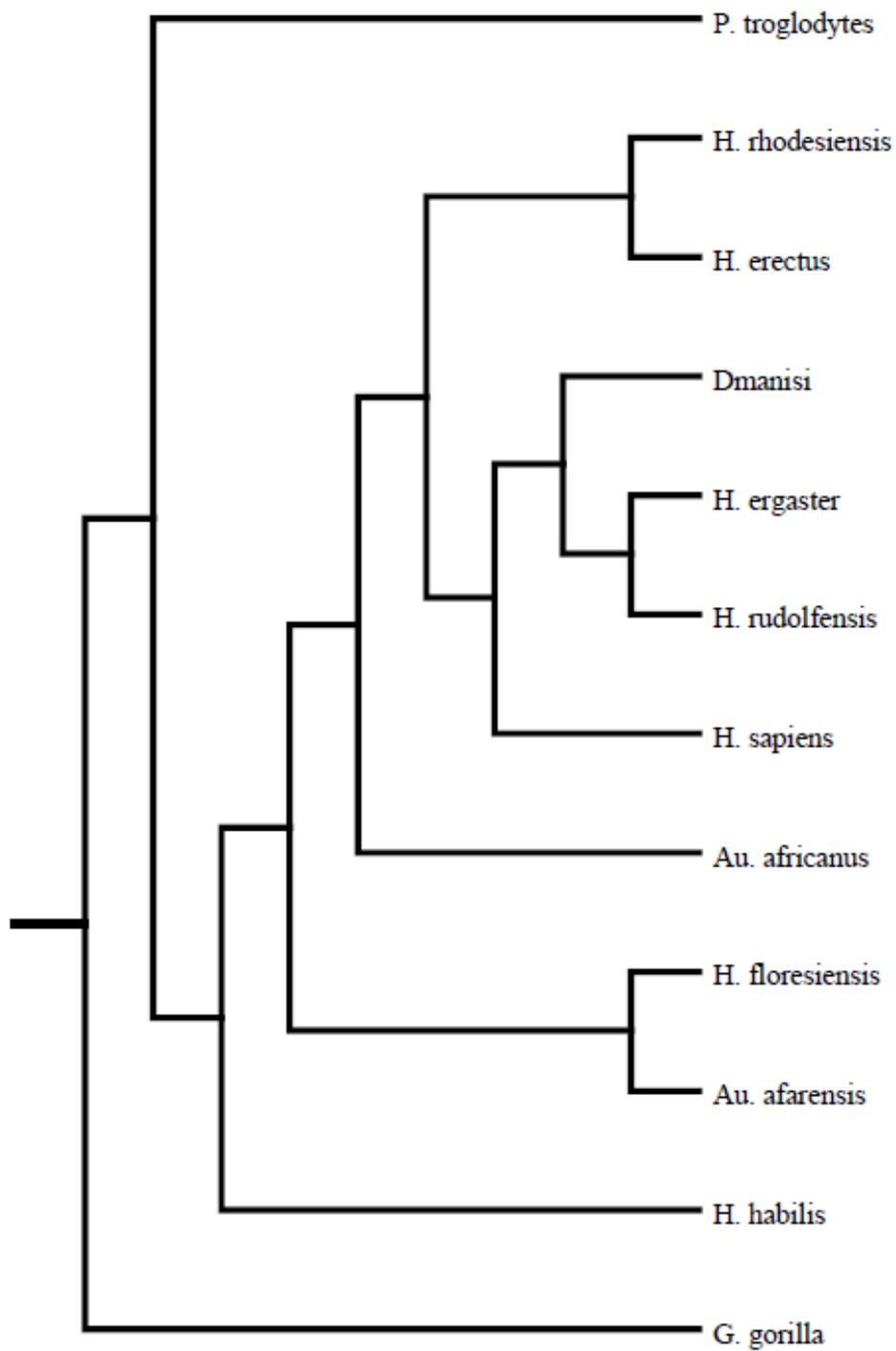
**Figure 4.** Majority Rule Consensus tree of all 132 characters with *H. rhodesiensis* and *H. rudolfensis* excluded from the analysis. In 75% of the trees found, *H. ergaster* and Dmanisi are reconstructed as sister taxa but there is no support for any other clades.



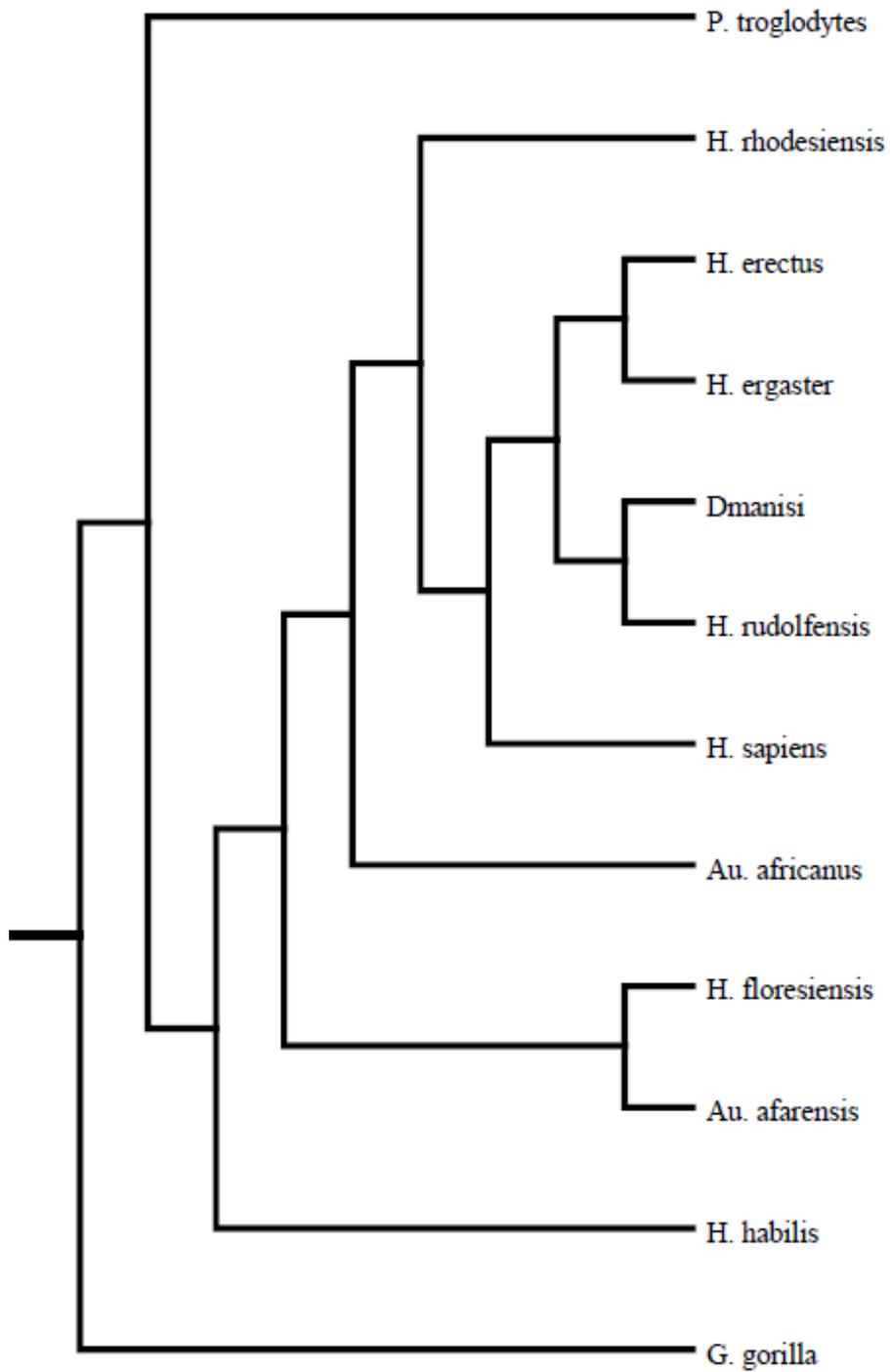
**Figure 5a.** First of eight MPTs from analysis containing only the postcranial characters and all 12 taxa. In all eight MPTs, *H. floresiensis* and *Au. africanus* are reconstructed as sister taxa. The differences in Figures 5a-5h comes from the instability in the remaining taxa. Length: 181 CI: .773 RI: .487 RC: .377 HI: .227



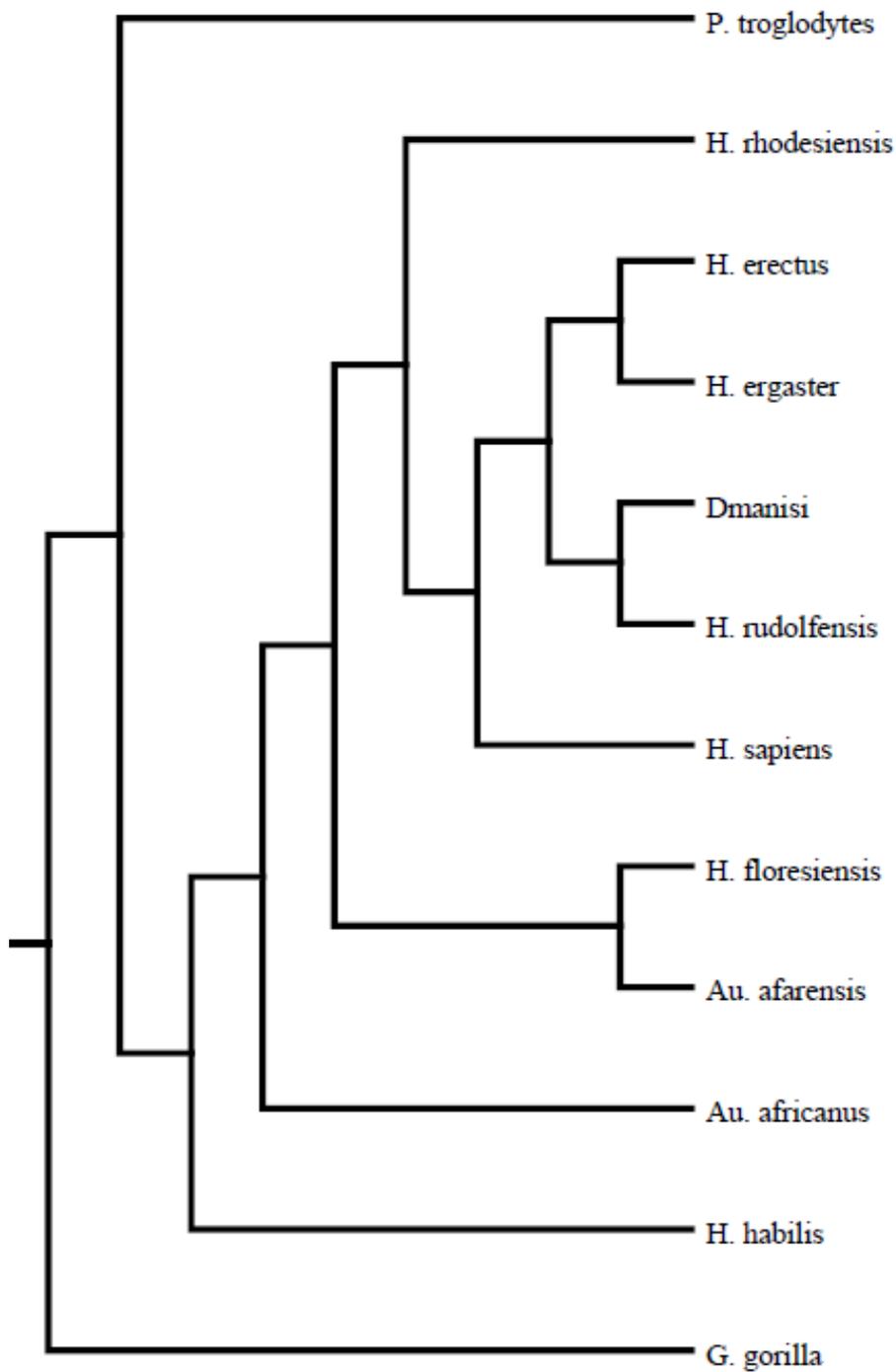
**Figure 5b.** Second of eight MPTs from analysis containing only the postcranial characters and all 12 taxa.  
 Length: 181 CI: .773 RI: .487 RC: .377 HI: .227



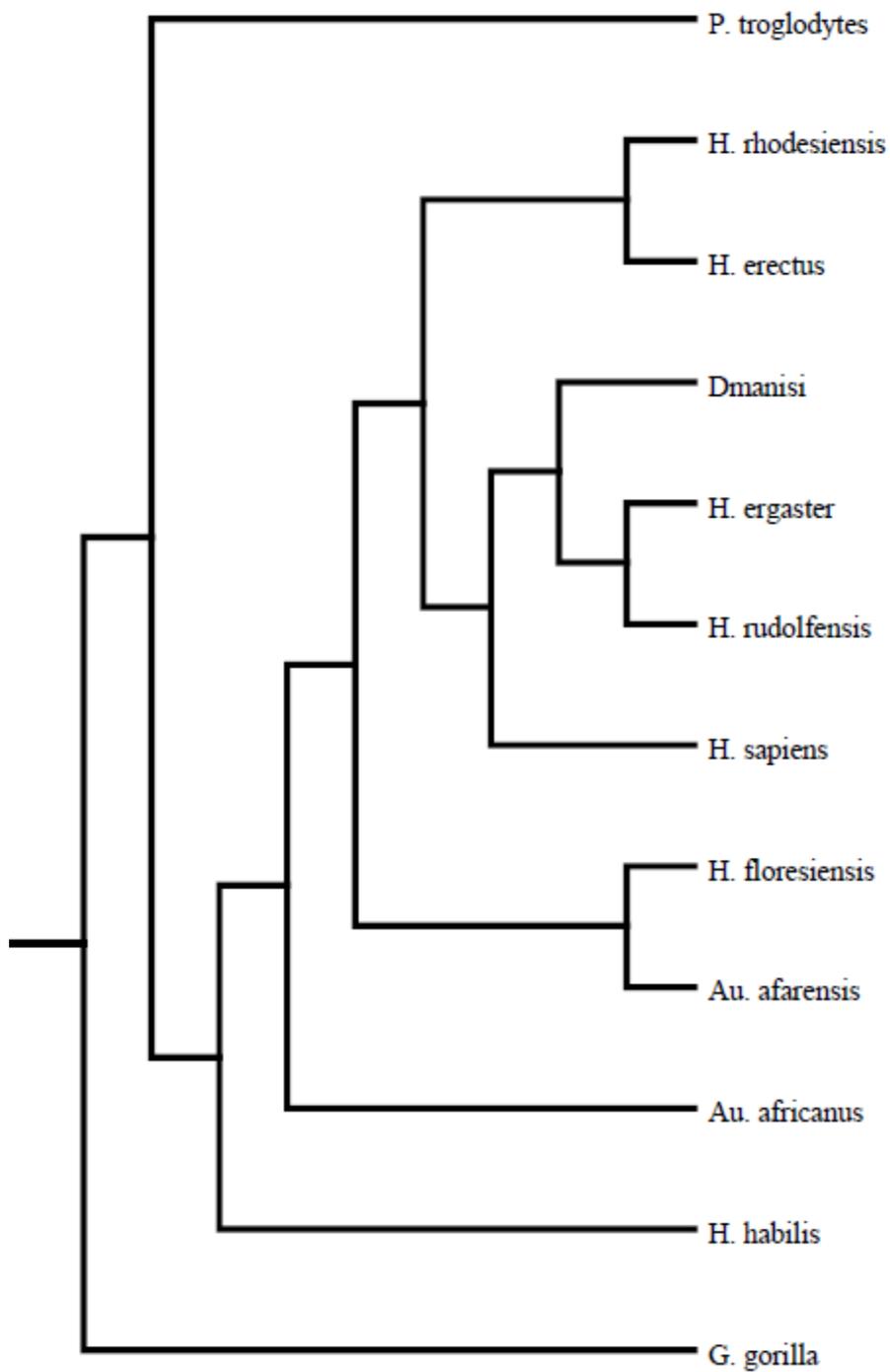
**Figure 5c.** Third of eight MPTs from analysis containing only the postcranial characters and all 12 taxa. Length: 181 CI: .773 RI: .487 RC: .377 HI: .227



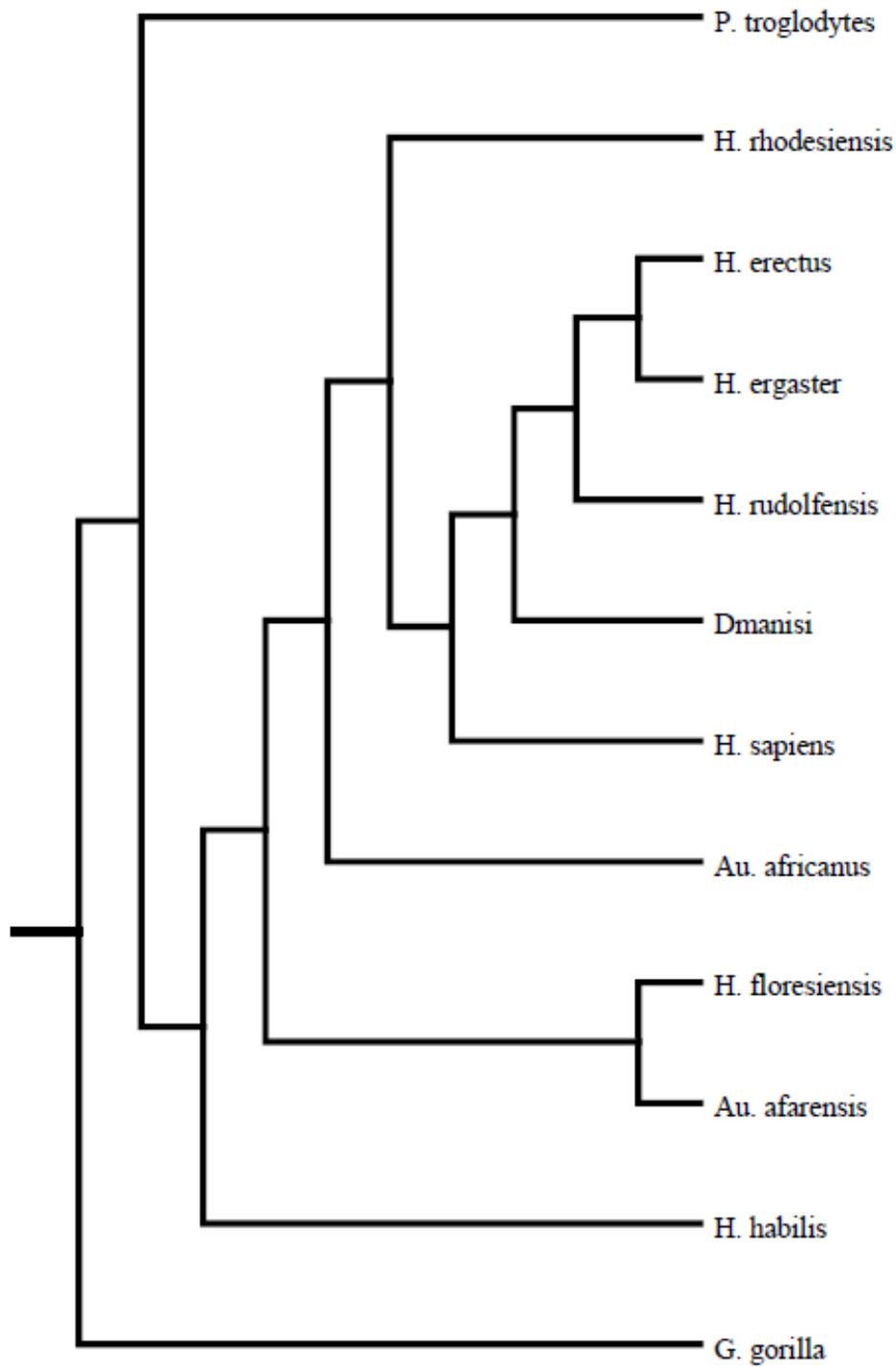
**Figure 5d.** Fourth of eight MPTs from analysis containing only the postcranial characters and all 12 taxa. Length: 181 CI: .773 RI: .487 RC: .377 HI: .227



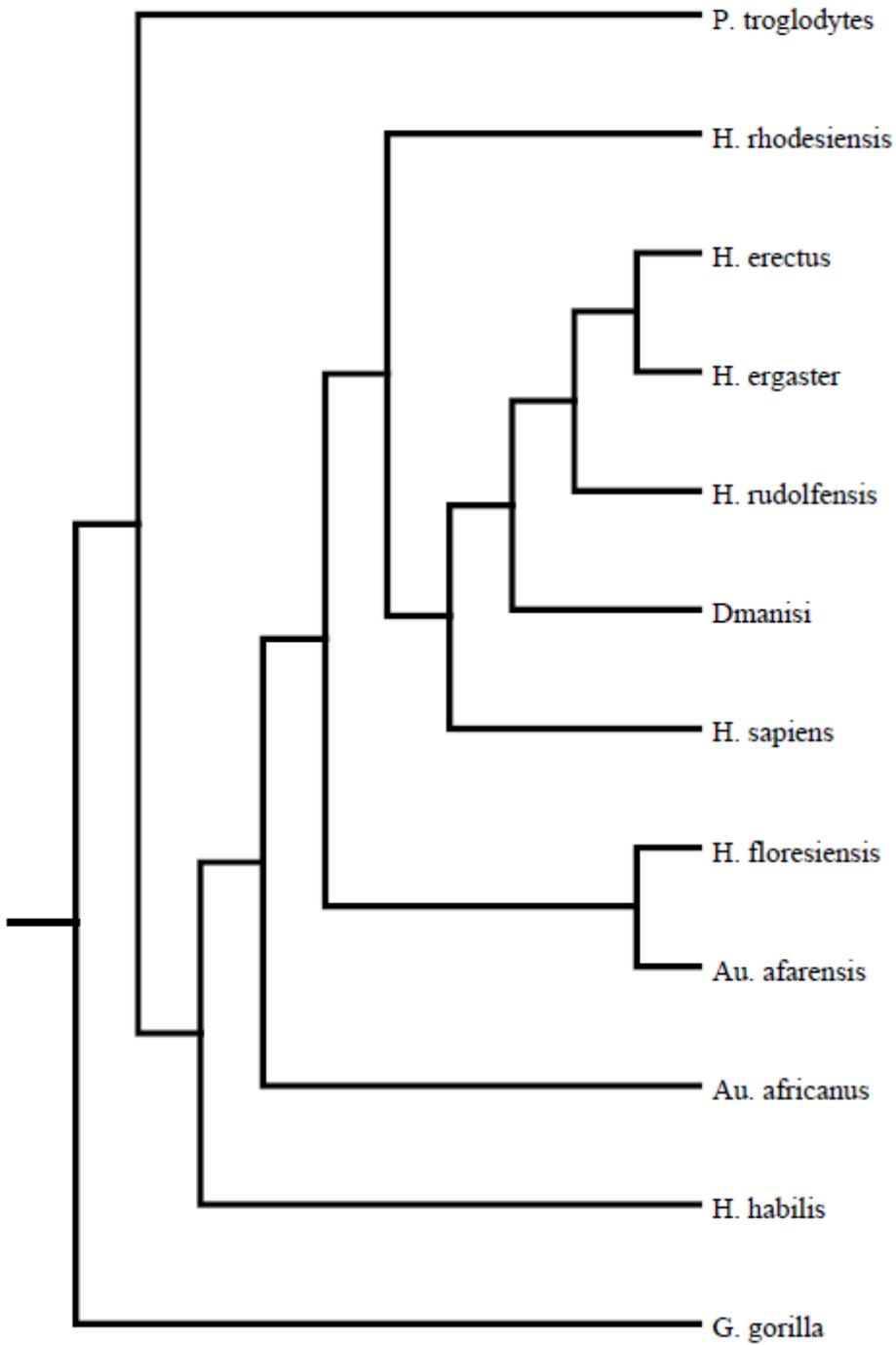
**Figure 5e.** Fifth of eight MPTs from analysis containing only the postcranial characters and all 12 taxa. Length: 181 CI: 773 RI: 487 RC: 377 HI: 227



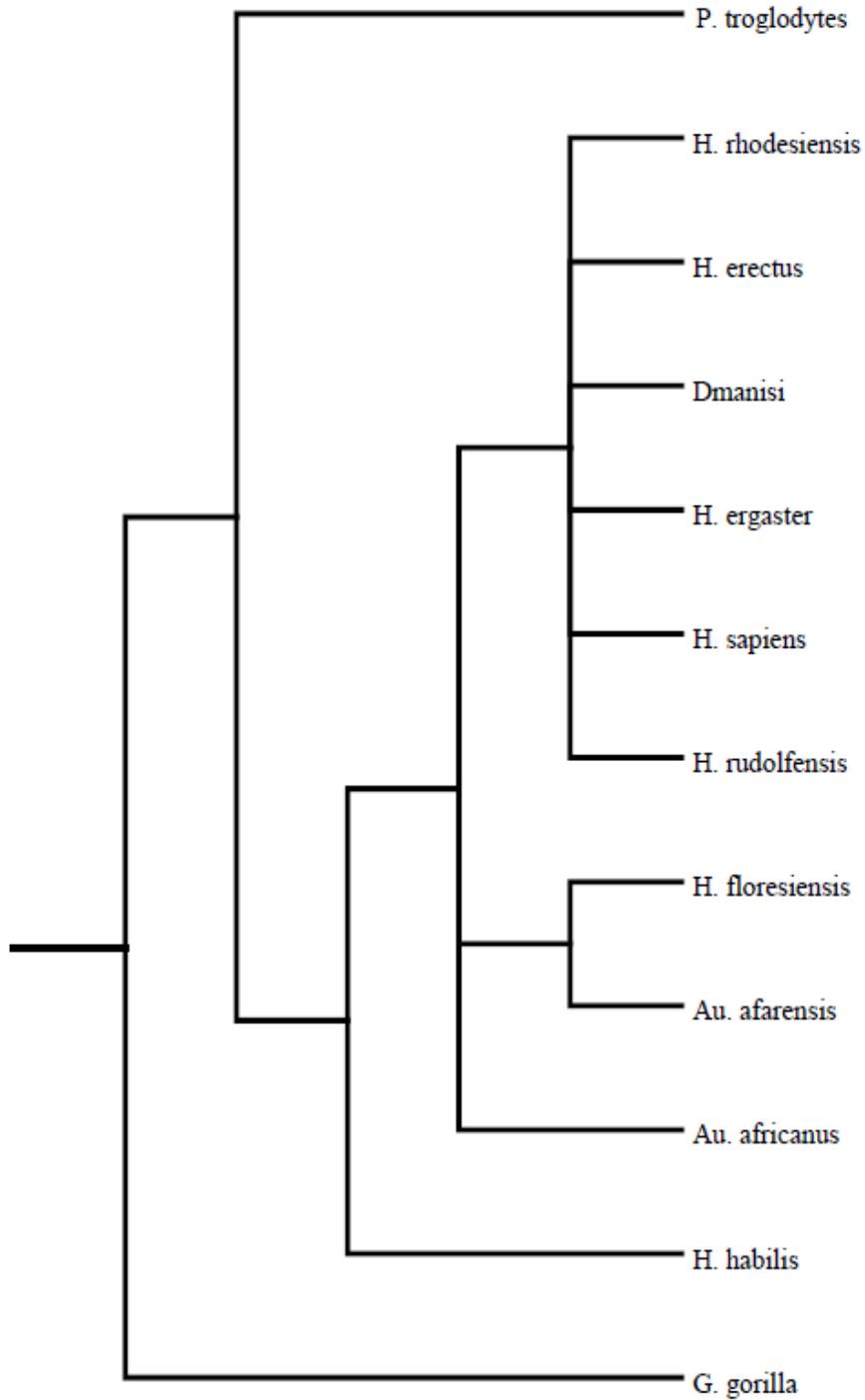
**Figure 5f.** Sixth of eight MPTs from analysis containing only the postcranial characters and all 12 taxa. Length: 181 CI: 773 RI: 487 RC: 377 HI: 227



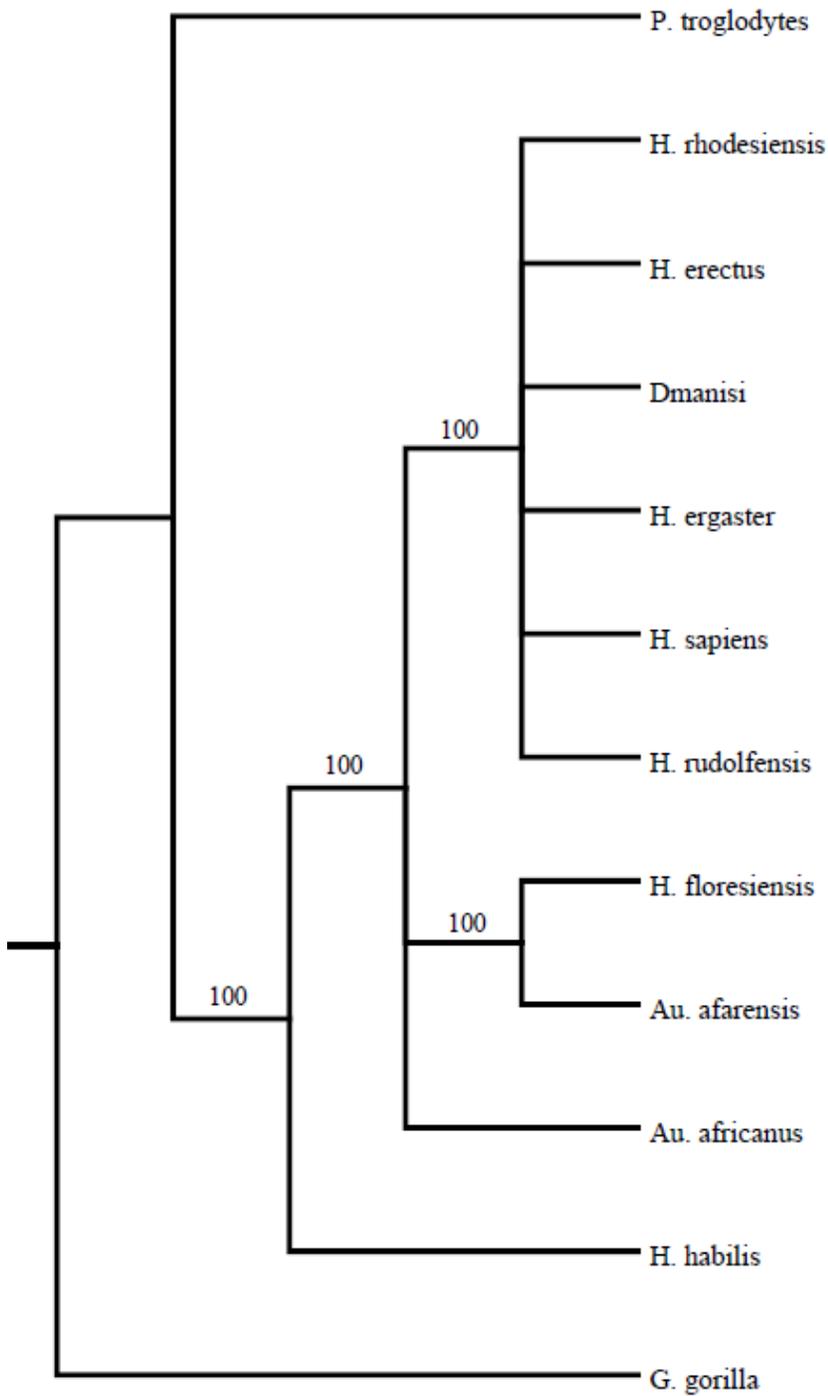
**Figure 5g.** Seventh of eight MPTs from analysis containing only the postcranial characters and all 12 taxa.  
 Length: 181 CI: .773 RI: .487 RC: .377 HI: .227



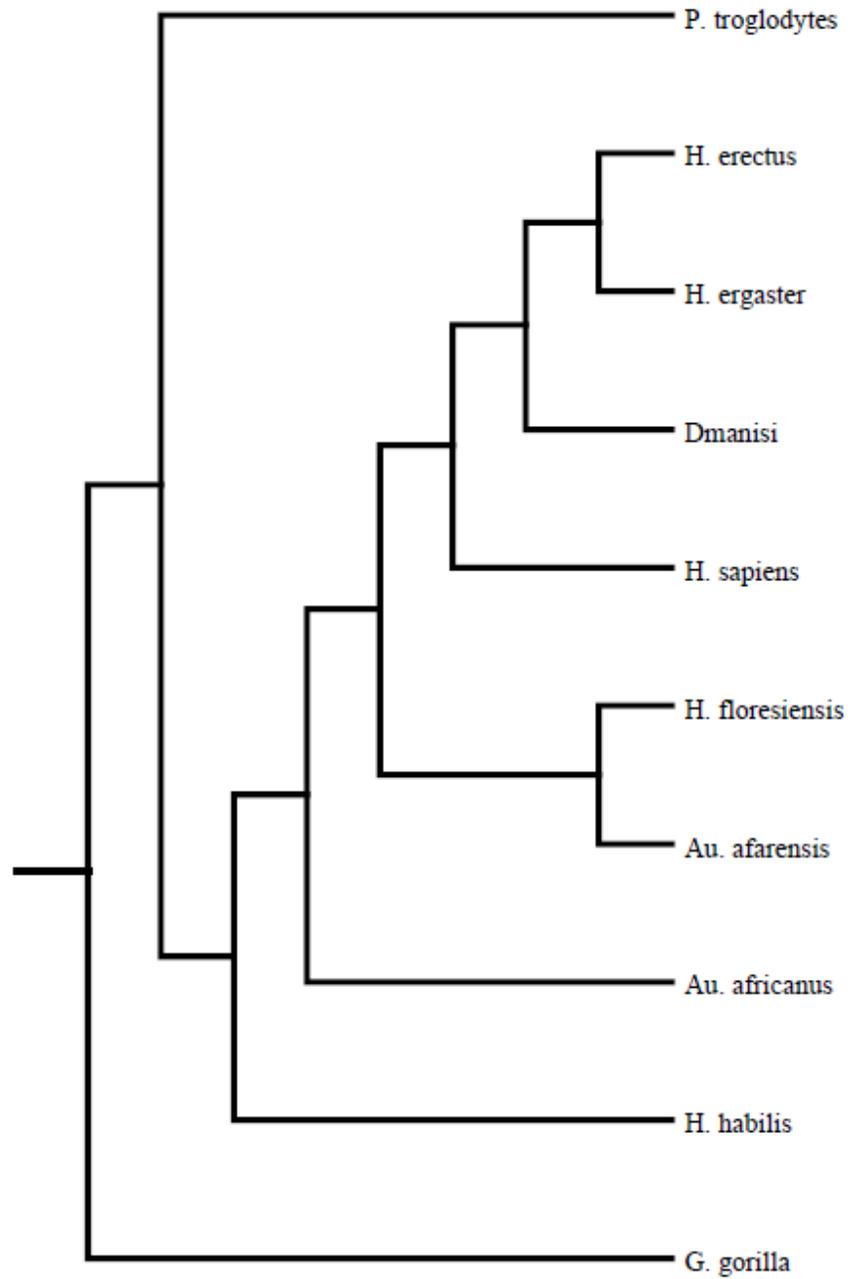
**Figure 5h.** Final of eight MPTs from analysis containing only the postcranial characters and all 12 taxa. Length: 181 CI: .773 RI: .487 RC: .377 HI: .227



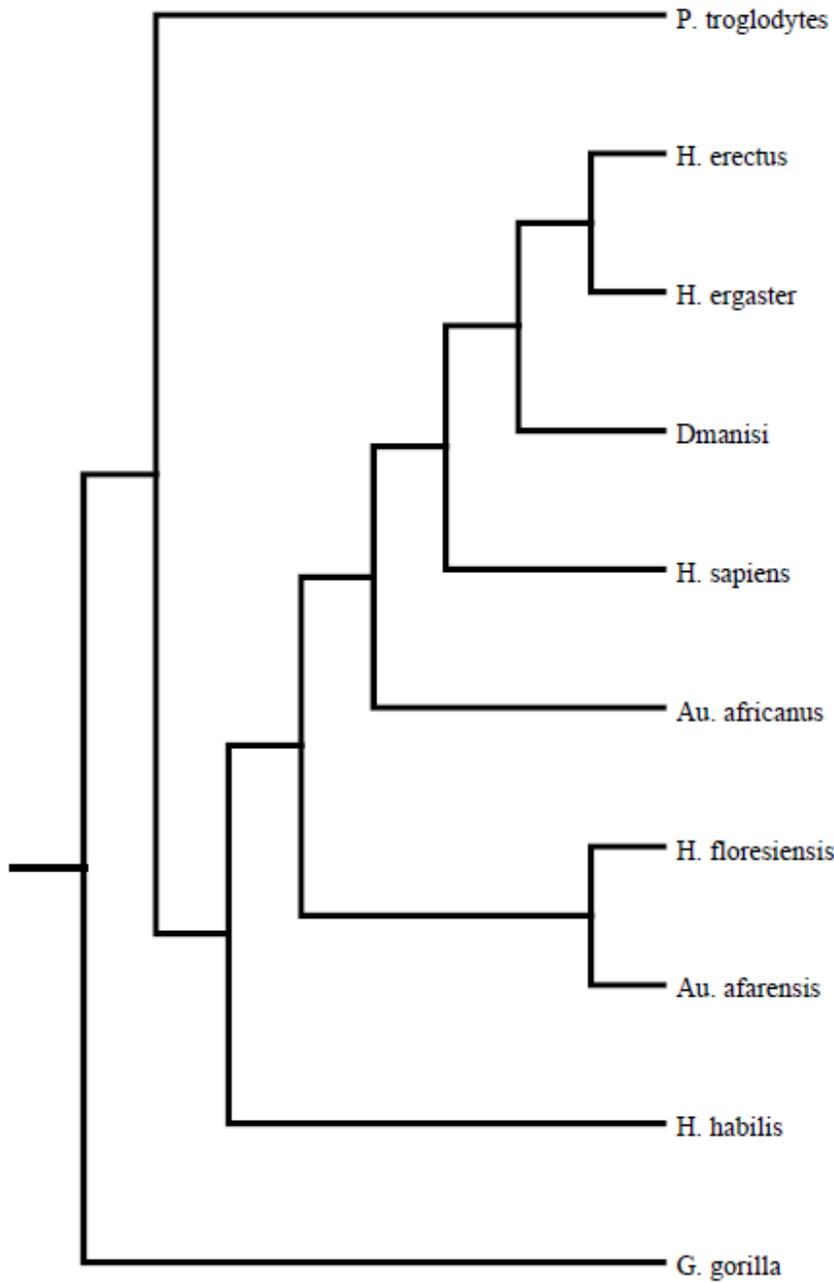
**Figure 6.** Strict Consensus Tree for 77 postcranial characters with all 12 taxa included in the analysis. There is support for a *H. floresiensis* and *Au. afarensis* clade in all MPTs



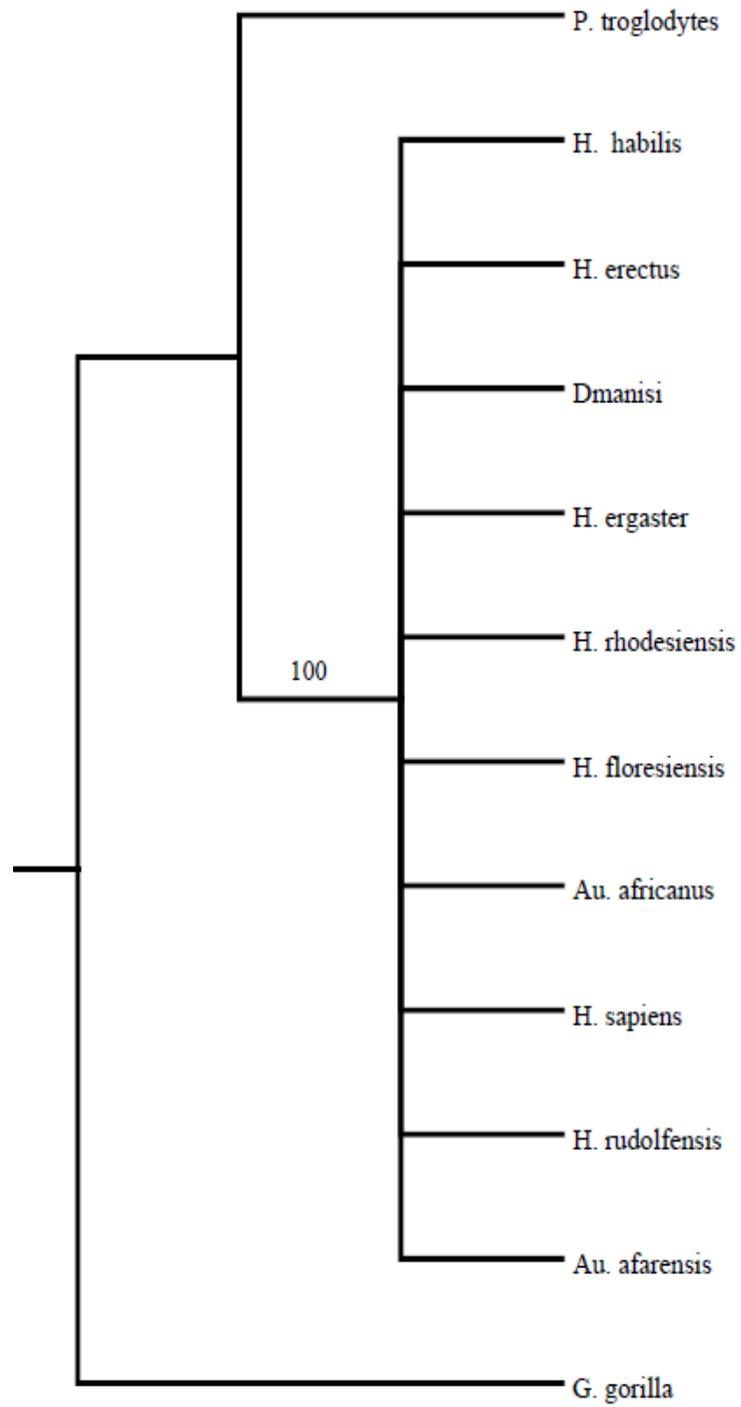
**Figure 7.** Majority Rule Consensus Tree for 77 postcranial characters with all 12 taxa included in the analysis. In 100 percent of the trees found *Au. afarensis* and *H. floresiensis* are reconstructed as sister taxa



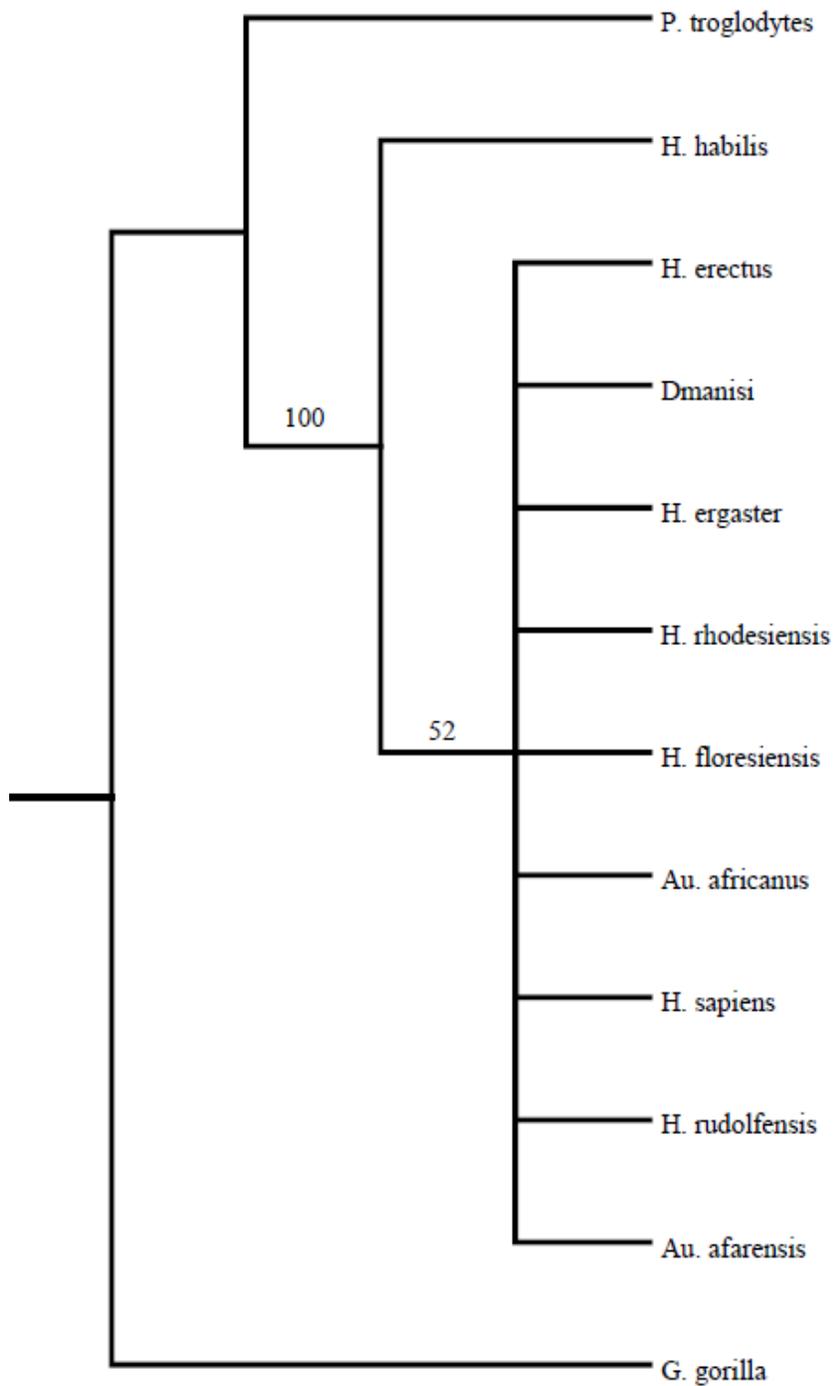
**Figure 8a.** First MPT from analysis containing only the postcranial characters and excluding *H. rhodesiensis* and *H. rudolfensis*. In this MPT, *H. floresiensis* and *Au. afarensis* are reconstructed as sister taxa. Length: 163 CI: .767 RI: .486 RC: .373 HI: .233



**Figure 8b.** Second MPT from analysis containing only the postcranial characters and excluding *H. rhodesiensis* and *H. rudolfensis*. This MPT differs from the previous in the placement of *Au. africanus* immediately before *H. sapiens*. Length: 163 CI: .767 RI: .486 RC: .373 HI: .233



**Figure 9.** Bootstran Analysis of all 132 characters. For this analysis, there is no support for any particular clade.



**Figure 10.** Bootstrap Analysis of postcranial characters. In this analysis, there is low support for *H. habilis* branching off before the other taxa. There is no support for any other clade in this analysis.

## Tables

**Table 1. Hominins used in this study**

<b>Hominin</b>	<b>Sample Size Range</b>	<b>Key Specimens</b>	<b>Reference</b>
<i>Pan troglodytes</i>	17-58		DeSilva et al (2013); Dart (1949); Lordkipanidze et al (2007); McHenry and Brown (2008); Orr et al (2013); Pontzer et al (2010); Walker and Leakey (1993); Larson (2007); Gebo (1992); Zipfel et al (2009); Niskanen and Junno (2009); Hager (1996); Morbeck and Zihlman (1989); Zihlman et al (2008); Lewton (2015); Hager (1996)
<i>Gorilla gorilla</i>	18-46		DeSilva et al (2013); Lordkipanidze et al (2007); McHenry and Brown (2008); Orr et al (2013); Pontzer et al (2010); Walker and Leakey (1993); Larson (2007); Gebo (1992); Zipfel et al (2009); Niskanen and Junno (2009); Hager (1996); Lewton (2015); Hager (1996)
<i>Homo sapiens</i>	26-100		DeSilva et al (2013); Lordkipanidze et al (2007); McHenry and Brown (2008); Orr et al (2013); Zipfel et al (2009); Lewton (2015); Hager (1996); Kennedy (1984)
<i>Australopithecus afarensis</i>		A.L.-288; A.L.-333; A.L.-129; A.L.-137; A.L.-223; A.L.-827;	Johanson et al (1982); McHenry and Brown (2008); Orr et al (2013); Tardieu and Trinkaus (1994); Larson (2007); Ward et al (2012); Ward et al (2015); Dobson (2005); Zipfel et al (2009); Hartwig-Scherer and Martin (1991); Richmond et al (2002); Di Vincenzo et al (2015)
<i>Australopithecus africanus</i>		Sts 34; Sts 14; Stw 114; TM 1513; Stw 573; Stw 181; Stw 347; Stw 358; Stw 363	Dart (1949); McHenry HM (1975); McHenry and Brown (2008); Orr et al (2013); Larson (2007); McHenry (1975); Dobson (2005); Zipfel et al

		(2009); Lovejoy (1978); Lovejoy et al (1976); DeSilva (2009); Di Vincenzo et al (2015); Lovejoy et al (1973);
<i>Homo habilis</i>	OH48; OH8; KMN-ER 3735; OH49; OH53; OH62; OH35;	DeSilva et al (2013); Lordkipanidze et al (2007); McHenry and Brown (2008); Tardieu and Trinkaus (1994); Ward et at (2015); Haeusler and McHenry (2004); Will and Stock (2015); Grine et al(1995); Tardieu and Trinkaus (1994); Richmond et al (2002); Hartwig-Scherer and Martin (1991)
<i>Homo rhodesiensis</i>	Kabwe 1; Broken Hill E 898	Pycraft (1930); Trinkaus (2012); Sankhyan et al (2012); Di Vincenzo et al (2015)
<i>Homo erectus</i>	Trinil I, Trinil II; Trinil III; Trinil IV; Trinil V; Peking I; Peking II; Peking IV; Peking V; Peking VI	Kennedy (1984); Rose (1984); Weidenreich (1941); Sankhyan et al (2012); Day (1971)
<i>Homo ergaster</i>	KNM-WT 15000; KNM-ER 736; KNM-ER 737; KNM-ER 803; KNM-ER 808; KNM-ER 1481; Stw 571; KNM-ER 164; KNM-ER 1812; KNM-ER 741; OH34	DeSilva et al (2013); McHenry and Brown (2008); Rightmire (1990); Larson (2007); Will and Stock (2015); Day and Molleson (1976); Di Vincenzo et al (2015); Walker and Leakey (1993)
<i>Homo georgicus</i>	D2724; D2175; D2680; D4167; D3901; D4507; D2600; D4111; D3442; D3160	Lordkipanidze et al (2007); Larson (2007); Ward et at (2015); Will and Stock (2015); Richmond et al (2002); Di Vincenzo et al (2015)
<i>Homo floresiensis</i>	LB1; LB2; LB3; LB4; LB; LB6; LB8; LB9, LB10, LB11; LB13; LB14	Jungers et al (2009a); Jungers et al (2009b); Larson et al (2009); Orr et al (2013); Larson (2007); Zipfel et al (2009)
<i>Homo rudolfensis</i>	KNM-ER 1472;	DeSilva et al (2013); Mchenry and Corruccini (1978); Larson (2007); McHenry and Corruccini (1978); Will and Stock (2015);

**Table 2. Character States and Definitions**

<b>Character</b>	<b>States</b>	<b>Quantitative (N)/ Qualitative (L)?</b>	<b>Ordered (O)/ Unordered (U)?</b>	<b>References</b>
Shape of frontal edge in norma verticalis	0=linear 1=convex anteriorly 2=variable	L	U	Argue et al., 2009
Position of glabella in norma verticalis	0= glabella is depressed 1=dimorphic (depressed or neither depressed/protruding) 2=neither depressed nor protruding 3=dimorphic (depressed and projects beyond front) 4= projects beyond frontal	L	O	Argue et al., 2009
Continuity of the supraorbital torus	0= no supraorbital torus 1=incomplete, interrupted in the medial zone--there are 2 distinct tori "mono-orbitares" 2=variable 3=continuous torus	L	O	Argue et al., 2009

Superior Surface of orbit margins	0= flow smoothly into front squama 1= horizontal postoral plane from which squama rises posteriorly 2=there is a sulcus between posterior aspect of elevated supraorbital rim and frontal squama	L	U	Argue et al., 2009
Type of orbital arcade-supraorbitals Where "a" is medial, "b" is central and "c" is lateral	0= a>b, b<c, and a<c 1= a>b, b<c, and a>c 2= a<b, b>c, and a>c 3=a>b, b>c, and a>c 4= little or no variation in thickness	L	U	Argue et al., 2009
Prominence of temporal band of the frontal	0= weak 1= variable 2= very prominent	L	O	Argue et al., 2009
Obelionic region	0=keeling present 1=variable 2=no keeling 3=presence of obelionic depression	L	O	
Parietal Bosse	0=absent 1=variable 2=present	L	O	Argue et al., 2009; Berger et al., 2015
Occipitomastoid Crest	0= absent 1= present	L	U	Argue et al., 2009; Berger et al., 2015

Shape of the temporal squama	0=polygon to round 1=triangular	L	U	Argue et al., 2009
Strength of the supramastoid crest in the region of the porion	0=weak 1=variable 2= strong	L	O	Argue et al., 2009; Berger et al., 2015
Continuity of the supramastoid crest with the inferior temporal line	0=no direct link 1=continuity 2= variable	L	U	Argue et al., 2009
Tuberculum supramastoid anterius	0=absent 1=present	L	U	Argue et al., 2009
Strength of mastoid crest	0=weak 1=variable 2=strong	L	O	Argue et al., 2009; Berger et al., 2015
Convergence of mastoid crest and supramastoid crest	0= divergent anteriorly 1=parallel 2=variable	L	U	Argue et al., 2009; Berger et al., 2015
Thickness of tympanal in norma lateralis, anterior edge of tympanal	0= weak 1=variable 2=strong	L	O	Argue et al., 2009
Contribution of the tympanal to mandibular fossa	0= postgleniod process makes up much of the wall 1= the tympanal makes up most of the wall 2=rudimentary or no postgleniod process	L	U	Argue et al., 2009; Berger et al., 2015

	3=variable			
Relative development of the mastoid process in norma lateralis	0=mastoid does not project below the base 1=variable 2=mastoid projects below the base	L	O	Argue et al., 2009
Extension of the pre-glenoid planum	0= no pre-glenoid planum precedes the glenoid cavity 1= pre-glenoid planum precedes the glenoid cavity 2=variable	L	U	Arguet et al (2009)
Space between the tympanal and anterior of mastoid process	0=posterior part of tympanal joins anterior part of mastoid process 1=variable between 0 and 2 2= "split" 3= variable between 0 and 4 4= wide space	L	O	Argue et al., 2009
Anteroposterior width of mandibular fossa	0=narrow 1=variable 2=wide	L	O	Argue et al., 2009
Height of the articular eminence relative to the posterior wall of the glenoid fossa	0=slope is shorter 1=similar 2=intermediate between 1 and 3 3=higher	L	O	Argue et al., 2009

Deepness of digastric fossa	0=not deep 1=variable 2=deep	L	O	Argue et al., 2009
Importance of the deepness between entoglenoid process and tympanic plate	0= fused 1=groove 2=space 3=variable (0 & 1) 4=variable (1 & 2)	L	U	Argue et al., 2009
Anterior wall of glenoid fossa	0=oblique 1=almost vertical 2=variable	L	U	Argue et al., 2009
Inferior projection of the entoglenoid process compared to that of the tuberculum zygomaticum anterior	1= entoglenoid projects to a greater extent than the tuberculum anterior 2= variable 3=entoglenoid is similar to tuberculum zygomaticum anterior in degree of inferior projection	L	O	Argue et al., 2009; Berger et al., 2015
Relative position of the entoglenoid process to the tuberculum zygomaticum anterior	0=entoglenoid process is at the same level as the tuberculum zygomaticum 1=variable between level and posterior 2=entoglenoid process is posterior to the tuberculum zygomaticum 3=entoglenoid process is very	L	O	Argue et al., 2009

	posterior to the tuberculum zygomaticum			
Inferior projection of the entoglenoid process and the tuberculum zygomaticum compared to the tuberculum articulare	0=very large interior projection relative to the tuberculum zygomaticum articulare 1=variable 2=large interior projection relative to the tuberculum zygomaticum articulare 3= small interior projection relative to the tuberculum zygomaticum articulare	L	O	Argue et al., 2009
Anteroposterior convexity of the tuberculum articulare	0=tuberculum articulare is flat/straight in norma lateralis 1=variable between flat and small round arc 2=tuberculum articulare forms a large round arc 3=the tuberculum articulare forms a small round arc	L	O	Argue et al., 2009

Continuity between the pre-glenoid planum and the posterior slope of the tuberculum articulare	0=the two are continuous 1=there is an angulation between them 2=variable	L	U	Argue et al., 2009
Inferior projection of the entoglenoid process compared to the sphenoid border/edge	0=entoglenoid process projects inferiorly to a greater extent than the sphenoid 1=variable 2=the entoglenoid process is equivalent in inferior projection to the sphenoid edge 3=the entoglenoid process is less projected than the sphenoid edge	L	O	Argue et al., 2009
Does the postglenoid process extend out beyond the tympanic?	0=does not overlap the tympanal 1= intermediate between 0 and 2 2= overlaps the tympanal 3= intermediate 2 and 4 4=rudimentary or no postglenoid process	L	O	Argue et al., 2009
Profile of the nasal saddle and nasal roof	1=flat nasal bones 2=slightly raised nasals, forming a curve 3=nasals forming well-defined curve, ranging in size from medium to large 4= deep angled nasal bones forming a pinched nose	L	U	Argue et al., 2009

Condition of the margo limitans	1= forms a sill 2=forms a smooth curve 3=includes a prenasal groove 4=variable (1 & 2) 5=variable (2 & 3)	L	U	Argue et al., 2009
Condition of the facies anterior of the maxilla/alveolar process	1=inflated/puffy 2=well filled out 3=sunken 4=forms a flat surface	L	U	Argue et al., 2009
Presence of jugum alveolar	1=there is no jugum alveolar 2= intermediate between 1 and 3 3= it forms a narrow ridge 4=it forms a broad and prominent ridge	L	O	Argue et al., 2009
Presence of sulcus infraorbitalis	1= none 2=narrow 3=wide	L	U	Argue et al., 2009
Zygomaticoalveolar crest	1=relatively straight 2=variable (1 & 3) 3=curved 4=forms an arc 5=variable (4 & 6) 6=forms an arch	L	O	Argue et al., 2009; Berger et al., 2015
Shape of clivus nasoaveolaris mediolaterally	1= convex 2=flat 3=concave	L	U	Argue et al., 2009; Berger et al., 2015

Location and Direction of orifice of incisive canal	1=immediately posterior to incisors 2=on a plane with canines 3=on a plane with 1st premolar 4=on a plane with 2nd premolar 5=variable	L	U	Argue et al., 2009; Berger et al., 2015
Condition of the supraorbital margin	1= thick, rounded and not demarcated from roof of orbit 2=thick with an edged crest not demarcated from roof of orbit 3= is an edged crest demarcated from the roof of orbit 4= is thin with an edged crest and demarcated from roof of orbit 5=variable (2 & 4) 6= variable 3 & 4)	L	U	Argue et al., 2009; Berger et al., 2015
Condition of infraorbital margin of orbits	1=sharp, high line dividing floor of the orbit from facial portion of the malar 2=relatively rounded orbital margin but raised in relation to floor of the orbit 3=pronounced rounding of the inferior lateral border which is leveled with the floor of the orbit 4=variable	L	U	Argue et al., 2009

Tympanic trough	0=absent 1=variable 2=present	L	O	Argue et al., 2009
Metopic keeling	1=present on frontal posteriorly 2= variable 3=present for all frontal 4=not present	L	O	Argue et al., 2009; Berger et al., 2015
Sagittal keeling on first half of parietal	0=absent 1=present	L	U	Argue et al., 2009; Berger et al., 2015
Presence of occipital torus	0=absent 1=variable 2=present	L	O	Argue et al., 2009
Presence of juxtamastoid eminence	0=absent 1=variable 2=present	L	O	Argue et al., 2009; Berger et al., 2015
Presence of Glaserian fissure	0=absent 1=variable 2=present	L	O	Argue et al., 2009
Tuberculum linearum	0=absent 1= variable 2=present	L	O	Argue et al., 2009
Length of nuchal dominates over length of occipital	0=no 1=variable 2=yes	L	O	Argue et al., 2009

Postcranial proportions	0=radiofemoral index <60 1=radiofemoral index 61-80 2=radiofemoral index >80	L	O	Argue et al., 2009
Humeral torsion	0=very low 1=low 2=high	L	O	Argue et al., 2009
Palmar Expansion complex	0=absent 1=intermediate 2=full complex	L	O	Argue et al., 2009
Orientation of scapular Spine	0= 20 - 40 degrees 1= 41-60 degrees 2= > 60	L	O	Argue et al., 2009
Bar-glenoid angle	0= <135 degrees 1=136-150 degrees 2=>150	L	O	Argue et al., 2009
Mandibular corpus robusticity	0=thin/gracile 1=intermediate 2=thick/robust	L	O	Argue et al., 2009
relative molar area	0=small 1=intermediate 2=large	L	O	Argue et al., 2009
Symphyseal region	0=no mental protuberances and retreats 1= variable 2=no mental protuberance and vertical 3=mental protuberance present	L	O	Argue et al., 2009

Internal symphyseal buttressing	0=prominent superior and inferior transverse tori 1=superior and inferior tori moderate to weak 2=no transverse tori	L	U	Argue et al., 2009
P4 root morphology	0=two root 1=Tomes root 2=single root	L	O	Argue et al., 2009
Length of Clavicle		N	O	Lordkipanidze et al., 2007; Larson et al., 2009; Will and Stock, 2015; Niskanen and Junno 2009;
Glenocoracoid angle		N	O	Lordkipanidze et al., 2007
Humerus length		N	O	Lordkipanidze et al., 2007; Pontzer et al., 2010; Will and Stock, 2015 ; Richmond et al., 2002; Hartwig-Scherer and Martin, 1991;
Diameter of Humeral Midshaft A-P		N	O	Lordkipanidze et al., 2007; McHenry and Brown, 2008; Will and Stock, 2015; Sankhyan et al., 2012;
Diameter of Humeral Midshaft M-L		N	O	Lordkipanidze et al., 2007; Will and Stock, 2015; Sankhyan et al., 2012;

Width of Humeral Trochlea		N	O	Larson et al., 2009
Depth of olecranon fossa		N	O	McHenry and Brown, 2008; Larson et al., 2009; Walker and Leakey, 1993
Diameter of olecranon fossa M-L		N	O	McHenry and Brown, 2008; Larson et al., 2009; Trinkaus, 2012; Di Vincenzo et al., 2015
Width of medial pillar of olecranon fossa		N	O	McHenry and Brown, 2008; Larson et al., 2009; Trinkaus, 2012
Width of lateral pillar of olecranon fossa		N	O	McHenry and Brown, 2008
Distal length of medial epicondyle AP length		N	O	McHenry and Brown, 2008; Larson et al., 2009
Hamate mc2 articulation angle on capitate		N	O	Orr et al., 2013
Hamate mc3 articulation angle on capitate		N	O	Orr et al., 2013
Mc2 mc3 articulation angle on capitate		N	O	Orr et al., 2013
Hamate hamulus length		N	O	Orr et al., 2013

Capitate-triquetrum articulation angle on hamate		N	O	Orr et al., 2013
Capitate-mc4 on articulation angle on hamate		N	O	Orr et al., 2013
Capitate mmc-5 articulation angle on hamate		N	O	Orr et al., 2013
Mc4-mc 5 articulation angle on hamate		N	O	Orr et al., 2013
Iliac height		N	O	Dart., 1949; Jungers et al., 2009a; Sankhyan et al., 2012;
Maximum iliac breadth		N	O	Jungers et al., 2009a; Niskanen and Junno, 2009; Morbeck and Zihlman, 1989
Thickness of iliac crest at tubercle		N	O	Jungers et al., 2009a;
Sciatic notch to anterior inferior iliac spine		N	O	Jungers et al., 2009a; Hager, 1996
Ischial length		N	O	Jungers et al., 2009a; Johanson et al., 1982; Mchenry, 1975; Lewton, 2015
Length of ischial shank (edge of acetabulum to edge of tuberosity)		N	O	Jungers et al., 2009a; Johanson et al., 1982

Robusticity of iliac pillar 0=weak/none 1=robust		L	U	Jungers et al., 2009a;
Acetabulum size		N	O	Dart, 1949; Jungers et al., 2009a; Johanson et al., 1982; Pycraft, 1930; Walker and Leakey, 1993; Zihlman et al., 2008; Lewton, 2015
Depth of acetabulum		N	O	Jungers et al., 2009a; Pycraft, 1930; Walker and Leakey, 1993; Rose, 1984;
Length of auricular surface		N	O	Dart, 1949; Jungers et al., 2009a; Rightmire, 1990; Rose, 1984;
Width of auricular surface		N	O	Dart, 1949; Jungers et al., 2009a;
Femoral length		N	O	Lordkipanidze et al., 2007; Johanson et al., 1982; Pontzer et al., 2010; Mchenry and Corruccini, 1978; Jungers et al., 2009a; Lovejoy, 1978; Day, 1971
Femoral midshaft diameter A-P		N	O	Lordkipanidze et al., 2007; Kennedy, 1984; Mchenry and Corruccini, 1978; Pycraft, 1930; Rightmire, 1990; Jungers et al.,

				2009a; Haeusler and McHenry, 2004
Femoral midshaft diameter M-L		N	O	Lordkipanidze et al., 2007; Kennedy, 1984; Mchenry and Corruccini, 1978; Rightmire, 1990; Jungers et al., 2009a; Haeusler and McHenry, 2004
Femoral midshaft circumference		N	O	Rightmire, 1990; Jungers et al., 2009a; Richmond et al., 2002; DeSilva, 2009; Hartwig-Scherer and Martin, 1991
Femoral neck shaft angle		N	O	DeSilva et al., 2013; Johanson et al., 1982; Pycraft, 1930; Jungers et al., 2009a; Lovejoy, 1978
Femoral medial condylar breadth		N	O	Lordkipanidze et al., 2007; Mchenry and Corruccini, 1978
Femoral lateral condylar breadth		N	O	Lordkipanidze et al., 2007
Platymeric index (ratio of the anterior-posterior diameter of the femur to its lateral diameter multiplied by 100)		N	O	DeSilva et al., 2013; Kennedy, 1984; Mchenry and Corruccini, 1978; Jungers et al., 2009a; Day and Molleson, 1976; Grine et al., 1995;

Pilastric index (ratio anterior-posterior length to the transverse breadth multiplied by 100)		N	O	Kennedy, 1984; Jungers et al., 2009a; Day and Molleson, 1976; Grine et al 1995;
Length of less trochanter on femur		N	O	Jungers et al., 2009a
Width of lesser trochanter on femur		N	O	Jungers et al., 2009a
Femoral bicondylar angle		N	O	DeSilva et al., 2013; Tardieu and Trinkaus, 1994
Femoral head diameter		N	O	Johanson et al., 1982; Kennedy 1984; Mchenry and Corruccini, 1978; Pycraft, 1930; Jungers et al., 2009a; Day and Molleson, 1976; Ward et al., 2015; Lovejoy, 1978; Grine et al., 1995;
Femoral condylar notch width		N	O	Pontzer et al., 2010; Mchenry and Corruccini, 1978
Tibial length		N	O	Lordkipanidze et al., 2007; Pontzer et al., 2010; Will and Stock, 2015
Tibial midshaft diameter A-P		N	O	Lordkipanidze et al., 2007

Tibial midshaft diameter M-L		N	O	Lordkipanidze et al., 2007
Tibial angle of torsion		N	O	Lordkipanidze et al., 2007
Tibial angle of inclination		N	O	Lordkipanidze et al., 2007; DeSilva, 2009
AP diameter of malleolus articular surface		N	O	Jungers et al., 2009a
Talar head torsion angle		N	O	Lordkipanidze et al., 2007
Hourglass shape of pedal phalanges		N	O	Jungers et al., 2009a
Fleshy foot size		N	O	Jungers et al., 2009b
Ulna max length		N	O	Will and Stock, 2015; Mchenry et al., 2007
Maximum length of radius		N	O	Will and Stock, 2015; Niskanen and Junno, 2009;
Maximum diameter of radial head		N	O	Will and Stock, 2015; Niskanen and Junno, 2009; Dobson, 2005;
Humeral circumference		N	O	Will and Stock, 2015; Hartwig-Scherer and Martin, 1991
Total epicondylar breadth		N	O	Will and Stock, 2015
Maximum diameter of talar facet of		N	O	Will and Stock, 2015

distal tibia A-P				
Maximum length of talus		N	O	Will and Stock, 2015; Gebo, 1992
Length of talar head		N	O	Will and Stock, 2015; Gebo, 1992
M-L diameter of trochlear surface at midpoint		N	O	Will and Stock, 2015
Max width of talus		N	O	Will and Stock, 2015; Gebo, 1992
Femoral bicondylar width		N	O	Will and Stock, 2015
Diameter of subtrochanteric shaft M-L		N	O	Will and Stock, 2015
Diameter of subtrochanteric shaft A-P		N	O	Will and Stock, 2015
Femoral neck length		N	O	Will and Stock, 2015
Femoral bicondylar width		N	O	Will and Stock, 2015
Diameter of of medial condyle M-L		N	O	Will and Stock, 2015
Humeral capitulum height		N	O	Di Vincenzo et al., 2015
Bar glenoid angle		N	O	Larson, 2007;
Axillo-spinal angle		N	O	Larson, 2007;

Humeral torsion		N	O	Larson, 2007;
Metatarsal V length		N	O	Zipfel et al., 2009
Maximum length of ulna		N	O	Will and Stock, 2015; Mchenry et al., 2007; Hlusko et al., 2015
Length of ulnar styloid		N	O	Hlusko et al., 2015

**Table 3. Synapomorphies within selected clades**

<b>Clade</b>	<b>Trait</b>	<b>Description</b>
<i>H. floresiensis/Au. africanus</i>	Distal length of medial epicondyle AP length Acetabulum Size Metatarsal V length Orientation of Scapular Spine	Relatively long medial epicondyle Mid-size acetabulum Relatively long metatarsal V Between 41° and 60°
<i>H. floresiensis/Au. africanus/H. rudolfensis/Au. afarensis</i>	Fleshy foot size Bar-glenoid angle Internal symphyseal buttressing  Height of articular eminence relative to posterior wall glenoid fossa Continuity of supramastoid crest Palmar Expansion	Relatively long fleshy foot size Relatively low bar-glenoid angle Prominent superior and inferior transverse tori  Articular eminence is shorter relative to the posterior wall of the glenoid fossa Continuity with temporal line present No palmar expansion complex
<i>Dmanisi/H. erectus/H. ergaster/H. sapiens</i>	Femoral head diameter Tibial angle of torsion	Mid-size femoral head diameter Low talar torsion

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