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Homo floresiensis: a cladistic analysis

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ABSTRACT

The announcement of a new species, *Homo floresiensis*, a primitive hominin that survived until relatively recent times is an enormous challenge to paradigms of human evolution. Until this announcement, the dominant paradigm stipulated that: 1) only more derived hominins had emerged from Africa, and 2) *H. sapiens* was the only hominin since the demise of *Homo erectus* and *Homo neanderthalensis*. Resistance to *H. floresiensis* has been intense, and debate centers on two sets of competing hypotheses: 1) that it is a primitive hominin, and 2) that it is a modern human, either a pygmoid form or a pathological individual. Despite a range of analytical techniques having been applied to the question, no resolution has been reached. Here, we use cladistic analysis, a tool that has not, until now, been applied to the problem, to establish the phylogenetic position of the species. Our results produce two equally parsimonious phylogenetic trees. The first suggests that *H. floresiensis* is an early hominin that emerged after *Homo rudolfensis* (1.86 Ma) but before *H. habilis* (1.66 Ma, or after 1.9 Ma if the earlier chronology for *H. habilis* is retained). The second tree indicates *H. floresiensis* branched after *Homo habilis*.

Introduction

In 2004, a team of Indonesian and Australian researchers discovered human bones representing a number of individuals during an archaeological excavation in Liang Bua cave on the island of Flores in Indonesia (Brown et al., 2004). The hominin bones were in stratigraphic levels dated to between 13.4–10.2 ka and ~100 ka (Roberts et al., 2009); that is, they represent a population that existed for a period of approximately 76,000 years. A critically important component of the assemblage is a partially articulated skeleton, Liang Bua 1 (LB1), found at a depth of 6 m and bracketed by calibrated radiocarbon ages of 19–17.1 ka (Roberts et al., 2009).

Brown et al. (2004) announced the Liang Bua discoveries and attributed all the hominins to a new species, *Homo floresiensis*, based upon their assessment that its morphology comprises a number of primitive and derived features. The species is characterized by a small endocranial volume (417 cc: Falk et al., 2005) and short stature (106 cm: Brown et al., 2004) similar to *Australopithecus afarensis*, and robust limb bones similar to australopithecines in general. Unlike *Australopithecus afarensis*, however, the Liang Bua remains show more derived states such as reduced prognathism and facial height, along with smaller postcanine teeth. Indices of cranial shape, including maximum cranial breadth at the supramastoid region and a broad vault relative to height, reflect those for *H. erectus* (Brown et al., 2004).

These discoveries generated a robust body of papers, setting the stage for opposing views. Alternative interpretations include the possibility that the Liang Bua fossils represent a new hominin species, *H. floresiensis* (Brown et al., 2004; Morwood et al., 2004, 2005; Falk et al., 2005; Argue et al., 2006; Larson et al., 2007; Tocheri et al., 2007; Baab and McNulty, 2009), and that the holotype specimen, LB1, was a modern human, possibly afflicted with a pathological condition (Henneberg and Thorne, 2004; Jacob et al., 2006; Richards, 2006; Hershkovitz et al., 2007; Obendorf et al., 2008). These conflicting hypotheses are based on comparative analyses of the morphology of the bones with both archaic and modern *Homo*, typically using statistical methods to compare the Liang Bua bones with those of other hominins.

The morphological and morphometric analyses have contributed much to the debate about *H. floresiensis,* but have not conclusively resolved the controversy about the position of the species in human evolution. We, therefore, use a different tool, cladistic analysis, which has not yet been applied to resolving this problem. Cladistic analysis focuses on evolutionary relationships of species rather than using metric or morphological assessment of similarities and differences

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between species to resolve phylogenetic relationships. We test a range of phylogenetic hypotheses about the status of the *H. floresiensis* remains, recognizing these could show special affinities with a wide range of hominin taxa. Ultimately, we present two equally parsimonious hypotheses for the phylogenetic position of *H. floresiensis*. Most importantly, both hypotheses indicate that *H. floresiensis* was a very early species of *Homo* that survived on Flores until at least 17,000 years ago.

Background

Numerous studies have addressed the taxonomic status of *H. floresiensis*, beginning with Brown et al.'s (2004) announcement of the discovery, which designated LB1 the type specimen of a new species, *Homo floresiensis*. Originally, it was hypothesized that *H. floresiensis* was the end product of a long period of isolation for *H. erectus*, or possibly early *Homo*, involving a process known as insular dwarfism. Alternatively, the remains could represent the descendant of an unknown small-bodied and small-brained hominin, which had arrived earlier on Flores from the Sunda Shelf (Brown et al., 2004; Morwood et al., 2004). Later, Morwood et al. (2005) described new *Homo* material from the Liang Bua site: another mandible, tibia, and radius, as well as the right humerus and ulna of LB1. The humerus and ulna, along with the previously described femur, tibia, and pelvis, enabled Morwood et al. (2005) to estimate limb and body proportions for LB1. The humerus and ulna are long relative to femur length, with an estimated humerofemoral index ([humerus length $\times$ 100]/[femur length]) of 85.4 (equalling *A. afarensis* AL288-1) (Morwood et al., 2005). Although the postcrania of *H. erectus* are poorly known, body proportions for *H. erectus* probably approximate means for adult modern humans for most limb shaft proportions (Ruff and Walker, 1993; Haeusler and McHenry, 2004). Dmanisi materials also appear to be similar to *H. sapiens* (Lordkipanidze et al., 2007). Furthermore, limb bones are robust relative to length and differ from predictions for *H. sapiens* of similar body size. Specifically, femur robusticity falls in the range of *Pan paniscus* with humerus robusticity midway between *Pan paniscus* and *H. sapiens* (Morwood et al., 2005). Based on these observations, Morwood et al. (2005) concluded that *H. floresiensis* is not an allometrically scaled *H. erectus*. While it was not likely to be specially related to *H. erectus*, they agreed that it should be included in the genus *Homo*, although its genealogy remained uncertain (see also Baab and McNulty, 2009).

Argue et al. (2006) contributed a morphometric and morphological analyses of the LB1 cranium and postcranium using published data and descriptions of *H. floresiensis* to test the hypotheses previously presented for *H. floresiensis*. Specifically, they tested the following hypotheses: that LB1 represented a microcephalic modern human; a modern human pygmoid; an australopithecine; or a heretofore-unknown species of hominin. Their metric results clustered LB1 with archaic hominins, separating LB1 considerably from modern humans, including microcephalic modern humans. These morphological analyses provided absolutely no support for the hypothesis that the cranial and postcranial anatomy of LB1 represented a modern human, including a microcephalic or non-pathological modern human. Instead, *H. floresiensis* appeared to be a previously unknown early hominin that either evolved from a founder population of archaic *Homo*, or descended from an intermediate species between *Australopithecus* and early *Homo*. Argue and colleagues presented three scenarios for *H. floresiensis*, all invoking relatively early hominin diffusion from Africa.

An important and perplexing problem for analyses of *H. floresiensis* is its tiny cranial capacity, 417 cc, which falls well outside the range for archaic and modern *Homo* (Falk et al., 2005, 2009). Clearly, this became established as a key issue early in the debate (Henneberg and Thorne, 2004; Jacob et al., 2006; Martin et al., 2006). In response to this problem, Falk et al.'s (2005) analysis of LB1's virtual endocast using morphometric, allometric, and shape data concluded that it has derived frontal and temporal lobes and a lunate sulcus in a derived position. These brain characteristics are consistent with higher cognitive abilities. Further research established that LB1 has seven derived (in relation to apes) features including a caudally positioned occipital lobe, lack of a posteriorly-located lunate sulcus, caudal expansion of the temporal lobe, a lateral and rostral prefrontal cortex that appears derived compared with apes, an expanded orbitofrontal cortex, and an expanded Brodmann's area 10 (see Falk et al. [2009] for further description and interpretation). None of these traits is pathological, but many are in parts of the brain that were subject to selection during human evolution. Therefore, Falk et al. (2009) concluded that the tiny LB1 brain was neurologically reorganized in a manner consistent with later hominins, and suggested that neurological reorganization is an important factor in hominin brain evolution that is under-appreciated.

Analyses of individual bones of LB1 have provided further insights about the skeleton. Larson et al. (2007, 2009) examined the LB1 clavicle (LB1/5) and humerus (LB1/50), and the LB6 scapula. They showed that in the shoulder complex, *H. floresiensis* is similar to the 1.5 Ma *H. ergaster* skeleton, KNM-WT 15000, and did not have the same shoulder geometry and rotational ability as modern humans. They hypothesized that *H. floresiensis* retained a functional complex that characterized *H. ergaster*. The wrist bones of *H. floresiensis* also appear to be primitive. Tocheri et al. (2007) described three complete carpal bones from the left wrist of LB1; none show modern human features. Instead, the bones show a pattern found in all African apes as well as fossil hominins "that preserve the comparable wrist morphology and date before 1.7 Ma" (Tocheri et al., 2007: 1743). Jungers et al. (2009) provided a detailed description of the lower limb skeleton of *H. floresiensis*. They corroborated Brown et al.'s (2004) original observation that the degree of iliac flaring resembles that observed in the australopithecines, while the acetabulum is human-like. The length of the left femur (LB1/9; 280 mm) is close to the length of the reconstructed femur of *A. afarensis* AL288-1, and much shorter than any known modern human femur, including African pygmies and Andaman Islanders, although the intertrochanteric crest is strongly developed in comparison to AL288-1. Overall, Jungers et al. (2009) found that the *H. floresiensis* lower limb elements exhibit a mix of primitive and derived features not seen in either healthy or pathological modern humans.

Homo floresiensis appears to violate two dominant paradigms of human evolution. The first stipulates that the specimens from Dmanisi (1.77 Ma: Rightmire et al., 2006), who had modern body proportions (Lordkipanidze et al., 2007), were the earliest member of our genus to emerge from Africa and that the earliest hominins in East Asia are *H. erectus* (1.8 Ma: Swisher et al., 1994; Larick et al., 2001; or 1.1 Ma: Watanabe and Kadar, 1985; Pope, 1988). The existence of *H. floresiensis* in South East Asia, however, could indicate that a more primitive hominin emerged from Africa (Morwood et al., 2005; Argue et al., 2006). The second major paradigm, that *H. sapiens* was the sole remaining species of *Homo* since the demises of *H. erectus* in Asia and *H. neanderthalensis* in Europe around 30,000 years ago, is clearly contradicted by *H. floresiensis*. That a hominin species is hypothesized to have emerged in the Early Pleistocene and continued living, to the best of our knowledge, until the terminal Pleistocene, i.e., 1.3–1.8 m.yr. after its first appearance, and well after the arrival of *H. sapiens* in the region, is an extraordinary concept in palaeoanthropology.

These ideas offer profound challenges to human evolutionary paradigms. Thus, not unexpectedly, the attribution of the Liang Bua hominins to a new species has been challenged. The concept of another hominin species, particularly with a brain size outside the

Homo range, and existing at the same time as modern humans, is particularly vexing. In this light, several studies have concluded that *H. floresiensis* is indeed a modern human, its extreme short stature and small cranial capacity indicative of pathology. For example, Henneberg and Thorne (2004) concluded that LB1 represents a microcephalic modern human, based on comparisons of LB1 skull measurements with those of a 2000-year-old microcephalic skull from Crete (previously described by Poulianos [1975]). Microcephaly is a heterogeneous disorder characterized by a marked reduction of brain growth. It may also accompany other abnormalities, such as short stature and cognitive impairment (Mochida and Walsh, 2001). Jacob et al. (2006) and Martin et al. (2006) concurred that microcephaly was the most likely explanation for *H. floresiensis*. As noted, the hypotheses that *H. floresiensis* is either a microcephalic modern human or a new species was tested by Argue et al. (2006), and the hypothesis that LB1 is a microcephalic did not survive this testing (see also Falk et al., 2005, 2009).

Other authors have sought to address generalized differences between the Liang Bua remains and other hominin taxa. For example, Richards (2006) suggested that the LB1–LB9 individuals represent a *H. sapiens* population with a growth hormone deficiency that causes dwarfism. Hershkovitz et al. (2007) hypothesized that the skeletal remains of *H. floresiensis* had an autosomal recessive condition, Laron Syndrome, which is expressed in consanguineous families and causes short stature among other symptoms, and proposed that the Flores sample may represent a local, highly inbred *H. sapiens* population. A claim that *H. floresiensis* was part of a long-term population that suffered from cretinism resulting from an iodine deficiency causing thyroid malfunction and growth problems, has also been proposed (Obendorf et al., 2008).

These interpretations pose several problems. First, microcephaly and Laron syndrome are very rare conditions: the range of occurrence of microcephaly, for example, varies between populations, from 1/25,000 (Böök et al., 1953) to 1/2,000,000 births (Woods et al., 2005). One would expect that, even if an archaeological excavation revealed what would be a rare discovery, most of the other skeletal remains in the excavation would represent a normal, non-pathological, modern population. But no bones of modern human stature or morphology have been recovered from the Liang Bua excavations. The *absence* of modern-statured modern human bones is not explained by the microcephaly and Laron syndrome hypotheses. Further, it would seem most unlikely that a very rare pathology such as microcephaly or Laron's syndrome could be sustained for the 76,000 years that *H. floresiensis* lived on Flores. Obendorf et al. (2008), who proposed that the Liang Bua hominins represent a population suffering from cretinism, recognized that cretinism occurs in only a proportion of births, and that their hypothesis must explain the absence of normal statured *H. sapiens*. Like other analyses, theirs failed to present plausible explanations for this absence. The pathology-based hypotheses, then, do not account for several of the salient facts about *H. floresiensis*, are not supportable from this point of view, and we do not test these hypotheses further here.

The range of explanations for the unusual morphology of *H. floresiensis* includes the plausible hypothesis that the remains represent a morphological response to the "Island Rule" (see Brown et al., 2004; Morwood et al., 2005; Argue et al., 2006). The Island Rule stipulates that insular dwarfism of mammals may occur when a founder population reaches an island and becomes reproductively separated. In the case of *H. floresiensis*, the assumed founder population is *H. erectus*, the only known early hominin candidate in South East Asia. The assumed stature for *H. erectus* is generally considered to be similar to *H. sapiens*, based upon the almost complete sub-adult skeleton of a related species, *H. ergaster*, from Koobi Fora, Africa (KNM-WT 15000), whose height is estimated to be ~1.60 m (Ruff and Walker, 1993) although stature estimates from other postcranial remains attributed to *H. ergaster* are between 157–171 cm (females) and 180–181 cm (males) (McHenry, 1991). *H. erectus* cranial capacity is between 813–1059 cc (Sangiran crania: Holloway, 1981). That is, estimated stature and cranial capacity of *H. erectus* are far greater than for *H. floresiensis*. Lyras et al. (2009) argued for island dwarfing of *H. erectus*, but this clearly necessitates an ancestor-descendant phylogenetic relationship between *H. erectus* and *H. floresiensis*. This relationship cannot be supported based solely on Lyras et al.'s geometric morphometric comparisons of the LB1 skull with skulls of *H. sapiens*, Sangiran 17 (*H. erectus*), KNM-ER 1813 (*H. habilis*), and Sts 5 (*A. africanus*). However, they concluded that it was not possible to separate *H. floresiensis* from *H. erectus* and therefore the two species are likely to be related, interpreting this result to mean that *H. floresiensis* is a dwarfed descendant of *H. erectus*. However, their analysis, in fact, shows that *H. floresiensis* and *H. erectus* are *separated* on Principal Component Axis I (PC I), while *H. habilis* appears to be most similar to *H. floresiensis* on this axis (Lyras et al., 2009: Figure 3; cf. Baab and McNulty, 2009). On PC II, three hominins appear to cluster, including *H. floresiensis*, *A. africanus*, and *H. erectus* (Lyras et al., 2009: Figure 3). Therefore, their Principal Components Analysis fails to support the conclusion for exceptional phenotypic similarities between *H. floresiensis* and *H. erectus*, although a weighted pair-group cluster analysis based on Euclidean distances does group *H. floresiensis* with *H. erectus* specimen Sangiran 17.

Beyond Lyras et al.'s (2009) hypothesis and empirical results, the status of the "Island Rule" remains poorly established (Lawlor, 1982; Meiri et al., 2008). Meiri et al. (2008) found no evidence for a general rule: while there appear to be some clade-specific patterns in island rodents, carnivores, and lagomorphs, they found few significant factors affecting insular size. Insularity does not result in simple patterns of size evolution, and there is enormous variation in size evolution, rather than a general rule for morphological change in island environments. Island area, island isolation, species trophic level, and carnivore numbers do not appear to affect body size (Meiri et al., 2008). Other studies show that there are contradictory explanations for size reduction or increase in mammals on islands (see Sondaar, 1977; Heaney, 1978; Wassersug et al., 1979; Melton, 1982; Libois et al., 1993; Dayan and Simberloff, 1998). Consequently, the causes and effects of the "rule" on mammals are far from resolved. Nevertheless, as the hypothesis that *H. floresiensis* is a dwarfed form of *H. erectus* remains viable, the idea that *H. floresiensis* and *H. erectus* are sister taxa should be evaluated.

It is possible that the very short stature (106 cm: Brown et al., 2004) and tiny endocranial capacity (417 cc: Falk et al., 2005, 2009) in *H. floresiensis* could be affected by allometry. Gordon et al. (2008) recognized that their metric analyses of LB1, in which they found it to be similar to *H. erectus* (and, to a lesser extent, *H. habilis*), might be affected by scaling relationships for crania as small as LB1. They therefore scaled variables from 2,424 modern humans to the size of LB1 to assess the effects of scaling relationships on expected shape for crania of such a size. They found that the LB1 cranial shape is even more distinct from modern human cranial shape when scaling is considered, concluding that LB1 cannot lie within the shape range of nonpathological modern humans, regardless of whether or not scaling is taken into account. As LB1 did not resemble *H. sapiens*, Gordon et al. (2008) turned their attention to identifying the best fit between LB1 and scaled cranial shapes of other hominin groups. They found that LB1 most resembled non-Asian early hominin specimens D2700 (Dmanisi, Georgia) and KNM-ER 3733 (Koobi Fora, Kenya). That is, regardless of the potentially confounding issue of scaling, LB1 is significantly different from modern humans and similar to two archaic hominins.

Baab and McNulty (2009) also examined the relationship between cranial size and shape to test whether or not LB1's cranial morphology is consistent with the expected shape of a very small

specimen of *Homo*. They used 3D landmark data from a stereolithographic model of LB1 generated from a CT scan, and the same data were obtained from a sample of fossil and modern hominins and African apes. A standard PCA of the Procrustes coordinates of the neurocranium and facial landmarks was performed. Their results showed that the morphology of the LB1 cranium is consistent with the expected shape for a very small specimen of archaic *Homo* and quite distinct from the modern human sample. Their analysis supports the hypothesis that *H. floresiensis* was a diminutive representative of an early species of *Homo*.

Gilbert and Rossie (2007) addressed the issue of scaling in cladistic analyses. These authors presented a method to control for body size in cladistic analyses without the loss of phylogenetic information, performing Pearson correlation analyses of all isometrically size-adjusted shape characters against the geometric mean of all cranial measurements. Those characters that were found to be allometrically influenced were then subjected to a coding procedure aimed at offsetting the effects of allometry. They did not, however, address issues of scaling in cladistic character sets that comprise morphological traits rather than measurement data (we here use morphological traits). Just how scaling can be dealt with when morphological, rather than morphometric, characters are used is unclear, and we are not specifically addressing this issue here in our cladistic analyses.

In sum, a review of previous analyses reveals considerable uncertainty about the phylogenetic and biological status of *H. floresiensis*. Notably, previous analyses concentrate on metric data and approaches, leaving a major gap in our knowledge that could be addressed by cladistic studies. Therefore, the primary objective of this study is to test hypotheses about the phylogenetic relationships of *H. floresiensis* using cladistic analyses. The tests address the two major hypotheses. The first hypothesis is that *H. floresiensis* is a new species. Support for this hypothesis necessitates further tests of phylogenetic relations. In particular, we test whether: 1) the species is related to *H. erectus* as initially proposed by Brown et al. (2004); 2) it shared a common ancestor with a species of early *Homo* (Falk et al., 2005; Argue et al., 2006; Larson et al., 2007; Tocheri et al., 2007; Baab and McNulty, 2009); or 3) *H. floresiensis* shared an immediate common ancestor with *A. africanus* or *A. afarensis*, given that it has an endocranial volume, stature, and postcranial similarities to australopithecines (Brown et al., 2004; Jungers et al., 2009; Larson et al., 2009); and 4) it shared an immediate common ancestor with the hominin specimens from Dmanisi, to which Gordon et al. (2008) noted similarities. The main alternative hypothesis is that the Liang Bua remains represent those of exceptional or pathological modern humans (Henneberg and Thorne, 2004; Jacob et al., 2006; Richards, 2006; Hershkovitz et al., 2007; Obendorf et al., 2008).

Materials and methods

The comparative sample comprises character states from *H. floresiensis* (LB1 cranium and postcranium; LB6/4, a right clavicle), *H. erectus* (Sangiran 2, Sangiran 17, Trinil), *H. ergaster* (KNM-ER 3733 and KNM-ER 3883), a sample from Dmanisi (D2282, D2280, D2700), *H. rhodesiensis* (Kabwe 1), *H. habilis* (KNM-ER 1813, OH 24), *H. rudolfensis* (KNM-ER 1470), *A. africanus* (Stw 505, Sts 71, Sts 5), *A. afarensis* (AL444-2), *H. sapiens*, *Pan troglodytes*, and *Gorilla* (*Gorilla gorilla*, *Gorilla beringei*). *Pan troglodytes* and both species of *Gorilla* are used as outgroups to identify ancestral, or plesiomorphic, states for *Homo* (Table 1).

Our cranial character selection is a modified version of cranial character states used by Zeitoun (2000) in his cladistic analysis of *H. erectus*, and Lahr's (1996) coding scheme for human facial characters; in particular, we include characters available for *H. floresiensis*. We use 60 characters from the cranium, mandible, and postcranium. Fifty of these are cranial characters from the facial, frontal, temporal, parietal, nuchal, and basal regions; five are mandibular and dental characters (Brown et al., 2004); five are postcranial characters: humeral torsion (Groves, 1986; Larson et al., 2007; Lordkipanidze et al., 2007); palmar expansion complex (Tocheri et al., 2007: Figures 2 and 3); orientation of scapular spine; barglenoid angle (Larson et al., 2007); and postcranial proportions (Argue et al., 2006; Lordkipanidze et al., 2007) (Appendix 1). We intentionally omitted a character for cranial capacity. One of the main sources of contention in the competing models for *H. floresiensis* is its cranial size: if its small brain is due to a pathological variation within *H. sapiens*, or a result of insularity of a polymorphic variant of *H. erectus*, or if it is a primitive retention. This study will clarify this matter, and it is our view that brain size cannot be included in a study that tests its polarity.

Cranial characters were scored on both original specimens and casts. Scores for casts were crosschecked in the literature where there was any doubt about the expression of the character. For this purpose, we referred to Rak (1983), Tobias (1991a, b), Wood (1991), and Schwartz and Tattersall (2003). Characters for *A. afarensis* were obtained from Kimbel et al. (2004), with reference to casts (see Appendix 2).

Of the 60 characters, 10 are treated as ordered (2, 3, 51, 53, 54, 55, 56, 57, 58, 60); all other characters have only two possible states, or are not clearly directional in evolutionary terms, and any state can transform directly into another. All characters are equally weighted. Where a character presents more than one state in any given taxon, all observed states are included for that character in that taxon; such characters are treated as "uncertain" and PAUP* (Phylogenetic Analysis Using Parsimony) selects the variable state that minimizes tree length. Fossil hominin crania are rarely discovered intact. It is therefore inevitable that some character states will not be known for some specimens.

Cladistic analysis produces possible phylogenetic trees, called cladograms, which are branching diagrams that depict sister group relationships. The cladogram groups Operational Taxonomic Units (OTUs) into clusters called clades, and these represent hypotheses about relationships among OTUs. Cladistic analysis is based upon the total number of character changes necessary to support the relationship of OTUs in a tree. The shortest trees are those that account for the observed differences among taxa in the smallest number of evolutionary steps. They are the most parsimonious trees and are generally considered to present the best working hypotheses.

We used the PAUP* program Version 4.0b10 for Macintosh (Swofford, 2002) to perform our initial analyses. We had 12 OTUs, and we searched for the shortest tree or trees using the Heuristic algorithm. We performed a total of 10,000 searches using stepwise addition and the TBR swapping algorithm. These processes ensure that PAUP* performs extensive random replicate searches to obtain a good sampling of the tree space. PAUP holds trees in memory, and by performing branch swapping (TBR) on these trees, we increase the coverage of the tree space. We set the PAUP* parsimony settings to treat multistate taxa as polymorphic.

To explore competing hypotheses about OTUs, we transferred the shortest trees found using PAUP* to MacClade. MacClade (Maddison and Maddison, 1992) is an interactive environment for exploring phylogeny. In MacClade, OTUs can be manipulated to form clades and the resulting tree lengths can be observed, enabling statements about the strength (or otherwise) of the clade. To further test these artificially manipulated clades, we undertook a topology-dependent permutation tail probability test (T-PTP), which tests the support for clades, or sister taxa, shown in the cladogram (Faith and Cranston, 1991; Faith, 1991). This test is defined as the estimate of the proportion of times that a given clade can be found and

generated from permuted data to produce a tree as short as, or shorter, than the original tree. That is, it compares the degree of corroboration for the observed data to that expected by chance alone, so it is a test of monophyly of selected nodes. The null hypothesis, that the data in support of a given clade have no cladistic structure beyond that produced by chance, is rejected at the 0.05 level if fewer than 5 out of 100 of the trees have a length as short as, or shorter than, the cladogram, i.e., if the T-PTP result is 0.05 or less.

Our analyses are based upon 60 characters, of which cranial and mandibular characters comprise 89%. Cranial and mandibular shape changes, however, may be correlated with size, and these compounding effects of allometry might have affected the outcome of the cladistic analyses, especially as the LB1 cranium is so small compared to other hominins. A problem with dealing with allometry in analyses such as this is that we do not know *a priori* which characters might be influenced by size. Gilbert and Rossie (2007) used metric-based cladistic characters, and Gordon et al. (2008) used statistical methods when testing for scaling relationships. We, on the other hand, use qualitative characters such as the presence or absence of a trait, or the form of a trait.

Assumptions in cladistic analysis

We present the following assumptions that are inherent in cladistic analysis and follow with a short explanation about how we control for them.

First, the OTUs are real. We have largely followed current convention in delineating hominin taxa. We restrict our *H. habilis* sample to KNM- ER 1813 and OH 24, retaining KNM-ER 1470 as a separate taxon, *H. rudolfensis*, as there is debate about its attribution to *H. habilis*; this is to avoid the possibility of confounding our taxa by conflating what might be two species. We combine the character states for the three Dmanisi crania based upon Rightmire et al. (2006) who concluded that the Dmanisi group could be designated as a paeleodeme; the differences between the skulls probably relate to differences in physiological age and sexual dimorphism (Rightmire et al., 2006).

Secondly, changes in characters occur in lineages over time. This Darwinian principle can confound cladistics in cases where a continuous variation is observed within populations. In many cases, we coded for multiple states of a character, when the states "present" or "absent" were too restrictive. If more than one of these character states was observed within an OTU, we coded that character for all the states it presents (usually termed "multistate" or "polymorphic for that character").

Thirdly, any group of hominins is related by descent from a single common ancestor. Cladistics assumes a branching pattern of lineage splitting, preferably into two, although an unresolvable polytomy may result. Alternatively, branches that were once separated might well come together again (i.e., reticulation of populations); cladistics is not designed to deal with this situation.

Finally, characters are genetically independent of each other. We do not have a way of assessing genetic independence of characters, but bias may be minimized in an analysis by avoiding overemphasis on any given morphological feature (e.g., Cracraft, 1981; Fischer, 1981; Szalay, 1981; Strait et al., 1997).

The small number of specimens available in fossil studies almost always poses problems for cladists in that the full range of cranial morphological states may not be expressed in the sample. This is of particular importance when a species is represented by only few crania and a relatively small amount of other skeletal material, as is the case for *H. floresiensis*. It is unlikely that the discovered specimens express the full range of character states. In fact, all of our fossil hominin samples are small despite the inclusion of fragmentary specimens, because the fossil record for hominin taxa is relatively scant and it is unlikely that the full range of variation for each is expressed in any of these samples. The problem of limited sample populations is a problem faced by all palaeoanthropologists seeking to understand hominin phylogenetic relationships. On the positive side, cladistic analysis is flexible and testable, and should further specimens be found, or new or different characters identified, analyses can be repeated and hypotheses may be corroborated or reformulated.

The bootstrapping technique (Felsenstein, 1985) is the most commonly used method for assessing nodal support and has been used to estimate the statistical confidence of phylogenetic analyses since its introduction in 1985 (Zharkikh and Li, 1995). It is performed in PAUP* and involves random sampling with replacement of a set of characters until a replicate data set of the same size as the original data set is constructed. This replicate data set is subsequently analyzed, and a phylogenetic tree is reconstructed according to a specified search strategy. The results are summarized as a bootstrap consensus tree, and the frequency at which each clade is recovered is termed the bootstrap support (Mort et al., 2000). If a group shows up 95% of the time in the bootstrap analyses, then that group is considered to be statistically significant (Felsenstein, 1985), although Hillis and Bull (1993) have argued that bootstrap proportions of more than 70% indicate a strong probability that the clade is real and may, in fact, represent a probability of >90% support for the clade.

There may be problems with the bootstrapping technique, including the assumption that the characters in the data matrix represent a random sampling of all possible characters (Strait and Grine, 2004). Some of the original characters may not be sampled and are thus omitted, whereas other characters may be sampled more than once, and this, in effect, simulates weighting procedures (Trueman, 1993). It also assumes a large number of internally consistent characters so that the same clades will appear in most of the runs, but clades may well disappear if there are only a few synapomorphies supporting them. In fact, Hillis and Bull (1993) contended that bootstrap proportions are highly imprecise, except where the parametric values are near 0 and 1. Consequently, bootstrapping is neither an assessment of clade accuracy, nor a determination that clades are real. Nevertheless, it is customarily used in cladistics and we use it here in this analysis. Ten thousand bootstrap replicates are performed using the Heuristic search option and retention of groups of >50% frequency.

Results

The Heuristic algorithm found the two shortest trees comprised of 247 steps (Fig. 1). In one of the trees (Tree 1) *H. floresiensis* branches after *H. rudolfensis* and before *H. habilis*, in the other tree (Tree 2) it branches after *H. habilis*. There are differences between these trees within the configuration of the later *Homo* OTUs, and their internal phylogenetic structure is unresolved. In Tree 2, Dmanisi forms a clade with *H. ergaster*, and *H. sapiens* forms a clade with *H. rhodesiensis* to which *H. erectus* is a sister taxon. The T-PTP value for the Dmanisi/*H. ergaster* clade is, however, $p = 0.11$, and for the *H. sapiens*/*H. rhodesiensis* clade the T-PTP value is $p = 0.16$; the null hypothesis, that these clades formed by chance alone, is not refuted. The clade comprising *H. rhodesiensis*, *H. sapiens*, and *H. erectus*, however, has a T-PTP of $p = 0.03$, suggesting statistical support. The larger clades in both trees, comprising *H. sapiens*, *H. rhodesiensis*, *H. erectus*, *H. ergaster*, Dmanisi, *H. habilis*, and *H. floresiensis* have a T-PTP of $p = 0.003$. This larger branch is therefore supported: it is the internal arrangement that is unresolved.

The bootstrap analysis (Fig. 2) shows that the clades, or the single nodes, in the trees are not supported by many characters (Appendix 3). Bootstrapping, however, assumes equal rates of change and an intermodal change of 20% or less of characters. These conditions are arguably unrealistic for well-defined phylogenies. For well-

Table 1
Comparative sample included in this study.

Specimen	Original/Cast/Reference	Curatorial Institution	Original Site	Date	Species
Sangiran 2, Sangiran 17, Trinil	Original	Forschungsinstitut Senckenberg, Frankfurt, Germany (Sangiran 2); Geological Museum, Bandung, Indonesia (Sangiran 17); National Museum of Natural History, Leiden, Holland (Trinil)	Indonesia	c. 1.8 Ma–c. 50 ka	*H. erectus*
KNM-ER 3733, KNM-ER 3883	Original	Kenya National Museum, Nairobi, Kenya	East Africa	1.8 Ma, 1.55–1.6 Ma	*H. ergaster*
D2280, D2282, D2700	Casts; Rightmire et al. (2006)	Georgian State Museum, Tbilisi, Georgia	Georgia	1.8 Ma	Possible affinities: *H. erectus*, *H. georgicus* (Gabounia et al., 2002), *H. ergaster*
KNM-ER 1813, OH 24	Casts; Wood (1991) (KNM-ER 1813)	Australian National University (ANU), Canberra, Australia	East Africa	1.7–1.88 Ma	*H. habilis*
KNM-ER 1470	Casts; Wood (1991)	Australian National University (ANU), Canberra, Australia	East Africa	1.88 Ma	*H. rudolfensis*
Sts 5, Sts 7, Stw 505	Casts	Australian National University (ANU), Canberra, Australia	South Africa	2.8–2.3 Ma	*A. africanus*
AL444-2	Kimbel et al. (2004)		Awash River Tributary, Ethiopia	3.0 ± 0.02 Ma	*A. afarensis*
H. floresiensis: LB1	Original	National Archaeological Research Centre, Jakarta, Indonesia	Flores, Indonesia	18 ka (luminescence dates of 35 ± 4 ka and 14 ± 2 ka)	*H. floresiensis*
H. floresiensis postcranial material: right humerus LB1/50; clavicle LB1/5; right scapula LB6/4; 3 carpals of LB1 left wrist	Larson et al. (2007); Tocheri et al. (2007)	National Archaeological Research Centre, Jakarta, Indonesia	Flores, Indonesia	LB1: 18 ka (luminescence dates of 35 ± 4 ka and 14 ± 2 ka), LB6/4: 15.7–17.1 ka	*H. floresiensis*
Kabwe	Original	National History Museum, London, UK	Zimbabwe	Unknown	*H. rhodesiensis*
H. sapiens (6 males, 5 females)	Original	Australian National University (ANU), Canberra, Australia	Indonesia (2), India (1), Africa (1), Egypt (1), "Caucasoid" (1), New Guinea (3), Polynesia (3), Japan (Ainu) (3)	Modern	*H. sapiens*
Chimpanzees (2 males, 2 females)	Original	Australian National University (ANU), Canberra, Australia; Australian Museum, Sydney, Australia	Unknown	Modern	*P. troglodytes*
Gorilla (2 males, 2 females)	Original	Australian National University (ANU), Canberra, Australia; Australian Museum, Sydney, Australia	Gabon, Cameroon	Modern	*G. gorilla*, *G. beringei*

supported clades, bootstrap values will almost always underestimate both accuracy and repeatability. While the bootstrap method shows no support for any clade in this analysis, the T-PTP tests also show no support for Dmanisi/*H. ergaster* or *H. sapiens*/*H. rhodesiensis* clades.

Homo floresiensis has four possibly uniquely derived characters in this analysis (the character state might occur in taxa that are not included in this analysis, so we cannot say categorically that a given state is uniquely derived for *H. floresiensis*). These traits include: 1) obelionic depression (Character 7; State 2); 2) no postglenoid process (Character 17; State 2); 3) the orifice of incisive canal is on a plane with 2nd premolar (Character 40; state 4); and 4) P_4 Tomes root (Character 60; State 1).

We transferred the two trees produced by PAUP* into the MacClade interactive environment to explore alternative phylogenies for *H. floresiensis*. We tested possible sister taxon relationships by manoeuvring *H. floresiensis* to form a clade with each of the other OTUs, observed tree lengths for each test, and performed T-PTP for each resulting clade. From these analyses we can establish if *H. floresiensis* is likely to be sister taxon to *H. erectus*, *H. ergaster*, Dmanisi, *H. habilis*, *H. sapiens*, *A. africanus*, or *A. afarensis*.

Test for a phylogenetic relationship between H. floresiensis *and* H. erectus

The original hypothesis for *H. floresiensis* was that it was the end product of a long period of isolation of *H. erectus* (Brown et al., 2004), keeping in mind modified versions of this hypothesis in light of further information (Morwood et al., 2005). Lyras et al. (2009) later revived this hypothesis, proposing that *H. floresiensis* may have been related to *H. erectus* but had been subjected to insular dwarfism. In contrast to this hypothesis,

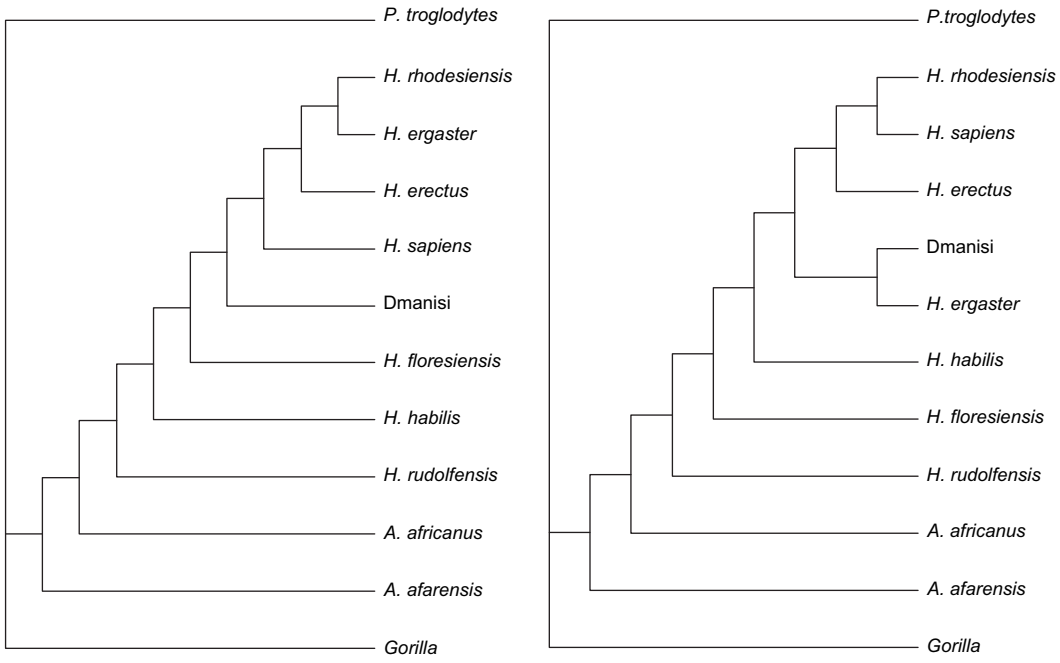

Figure 1. Two shortest trees found using PAUP* program Version 4.0b10 for Macintosh (Swofford, 2002) performed using 10,000 searches. Tree 1, left; Tree 2, right.

H. floresiensis fails to form a clade with *H. erectus* in the PAUP* analysis (Fig. 2).

When MacClade is used to manoeuvre *H. floresiensis* into a clade with *H. erectus*, the length of Tree 1 is 252 steps and the length of Tree 2 is 253 steps (Fig. 3) These are 5 and 6 steps longer than the shortest tree ($L = 247$), respectively. That is, they represent less parsimonious phylogenies than those represented by the shortest trees (Fig. 1). The T-PTP for the *H. floresiensis*/*H. erectus* clade is $p = 0.53$; the clade is not supported and it is unlikely that *H. floresiensis* and *H. erectus* shared a common ancestor.

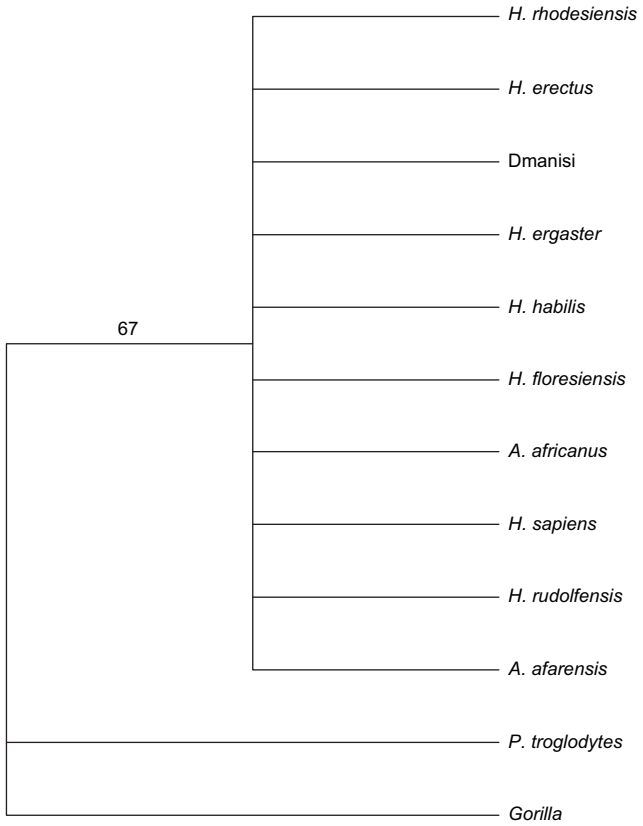

Figure 2. Bootstrap analysis PAUP* program Version 4.0b10 for Macintosh (Swofford, 2002) performed using 10,000 searches.

Test for a phylogenetic relationship between H. floresiensis *and* H. sapiens

H. floresiensis has been attributed to *H. sapiens* with or without pathology (Henneberg and Thorne, 2004; Jacob et al., 2006; Martin et al., 2006; Richards, 2006; Obendorf et al., 2008). In the PAUP* cladistic analysis (Fig. 2), the only phylogenetic relationship between *H. sapiens* and *H. floresiensis* is that they are within the *Homo* branch.

The tree lengths are 5 and 4 steps longer, respectively, than the shortest trees ($L = 247$) when *H. floresiensis* and *H. sapiens* are constrained (Fig. 4), and the T-PTP for the *H. floresiensis*/*H. sapiens* clade is $p = 0.39$; the clade is not supported. We conclude that *H. floresiensis* and *H. sapiens* did not share an immediate common ancestor.

Test for a phylogenetic relationship between H. floresiensis *and the Dmanisi hominins*

In analyses that consider Dmanisi hominins, tree 1 is 8 steps longer ($L = 255$) than the shortest tree ($L = 247$). Although Tree 2 is only 2 steps longer ($L = 249$) than the shortest tree, the T-PTP for the *H. floresiensis*/Dmanisi clade is $p = 0.37$; the null hypothesis that the clade would come together *only by chance* is not refuted (Fig. 5).

To our knowledge, it has not been proposed that *H. floresiensis* is phylogenetically related to *H. habilis*, *H. rudolfensis* (to which it is close in the PAUP* analysis), or to the australopithecines. We nevertheless explored these possibilities, given that *H. floresiensis* and the australopithecines share certain postcranial characters (Brown et al., 2004; Jungers et al., 2009; Larson et al., 2009). We have included *A. africanus* and *A. afarensis* to represent *Australopithecus*.

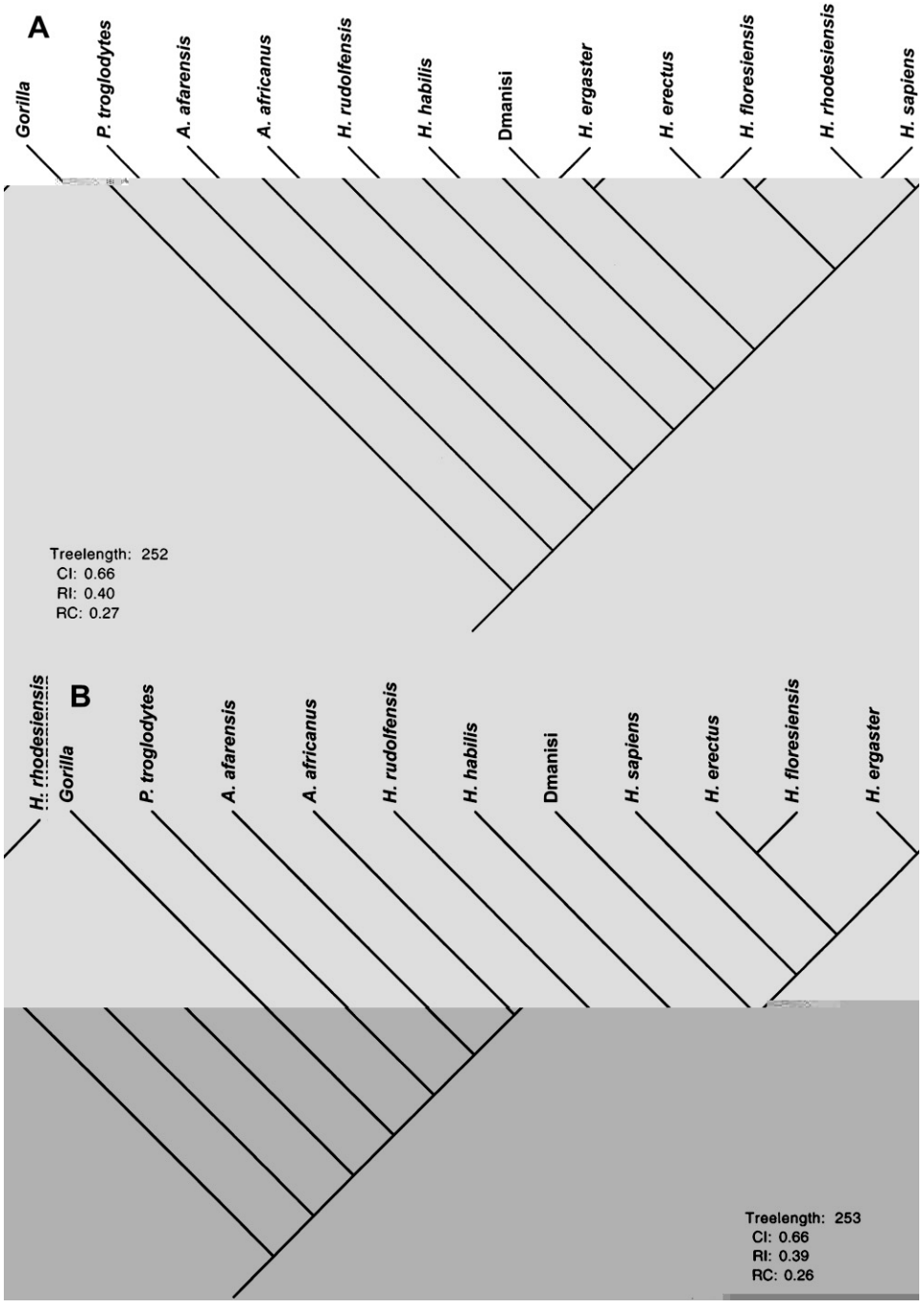

Figure 3. Test for *H. floresiensis* and *H. erectus*. (A) Tree 1: Tree length (*L*) 252; Consistency Index (CI) 0.66; Retention Index (RI) 0.40; Rescaled Consistency Index (RC) 0.27. (B) Tree 2: $L = 253$; $CI = 0.66$; $RI = 0.39$; $RC = 0.26$.

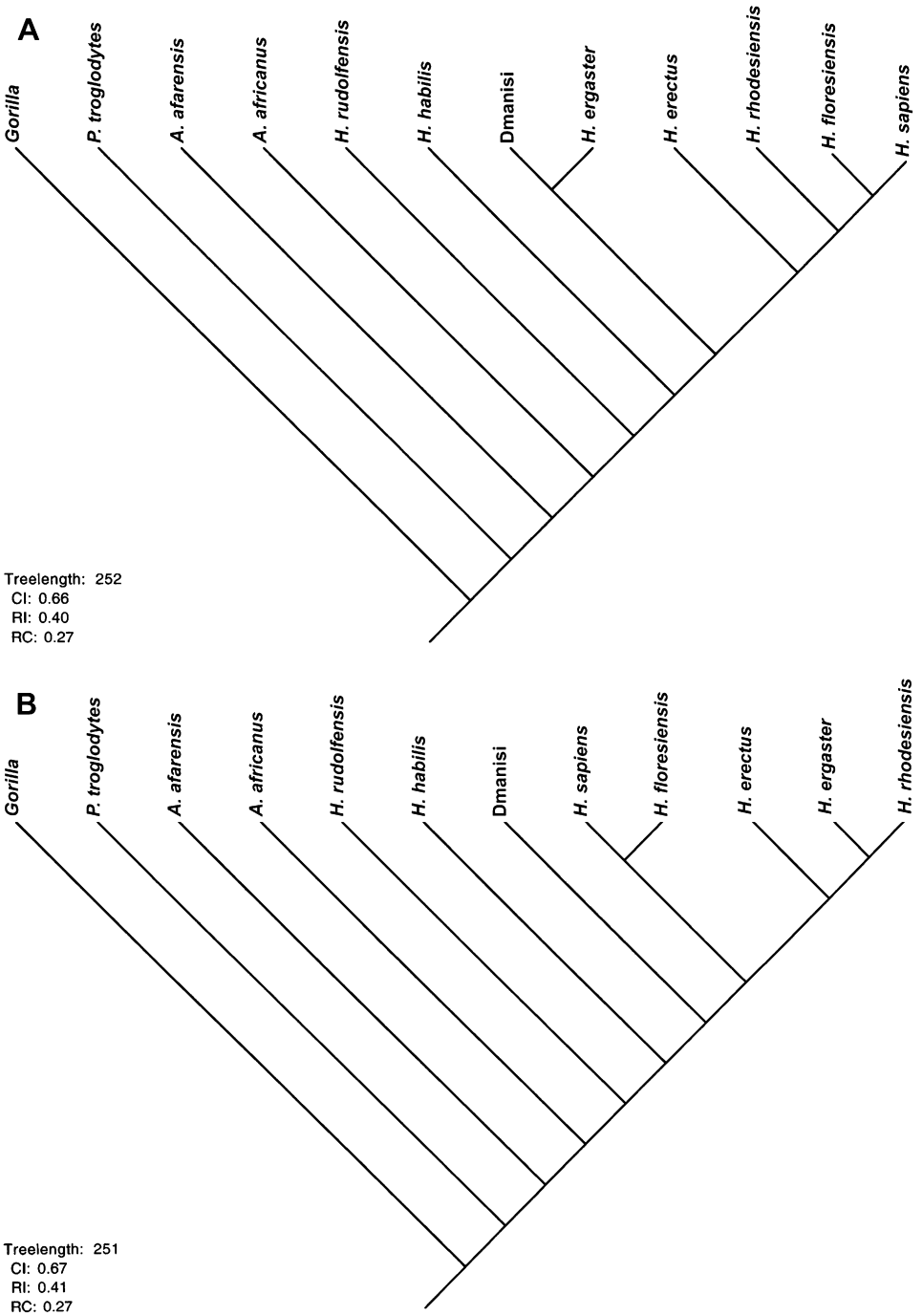

Figure 4. Test for *H. floresiensis* and *H. sapiens*. (A) Tree 1: $L = 252$; CI = 0.66; RI = 0.40; RC = 0.27. (B) Tree 2: $L = 251$; CI = 0.67; RI = 0.41; RC = 0.27.

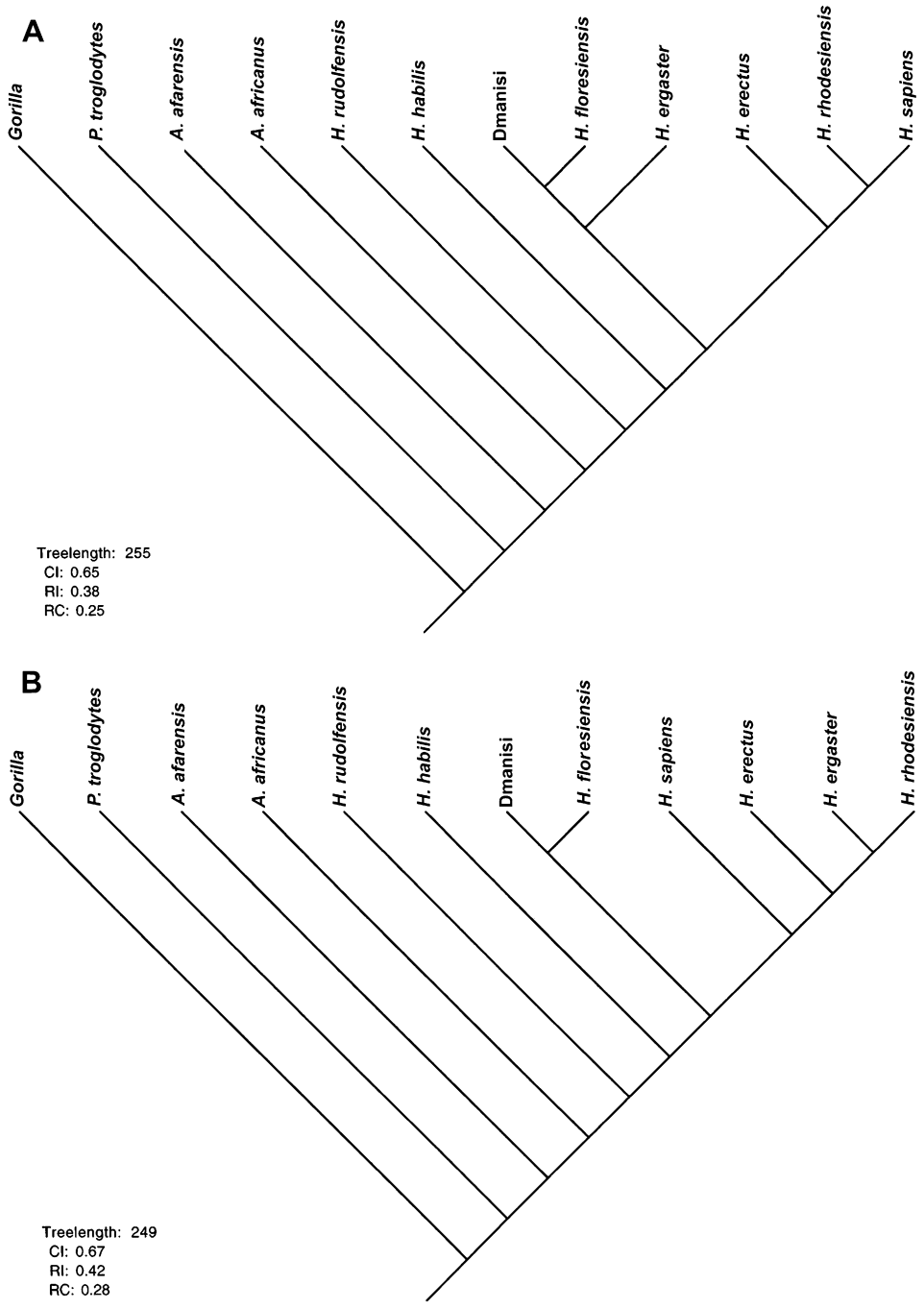

Figure 5. Test for *H. floresiensis* and the Dmanisi group. (A) Tree 1: $L = 255$; CI = 0.65; RI = 0.38; RC = 0.25. (B) Tree 2: $L = 249$; CI = 0.67; RI = 0.42; RC = 0.28.

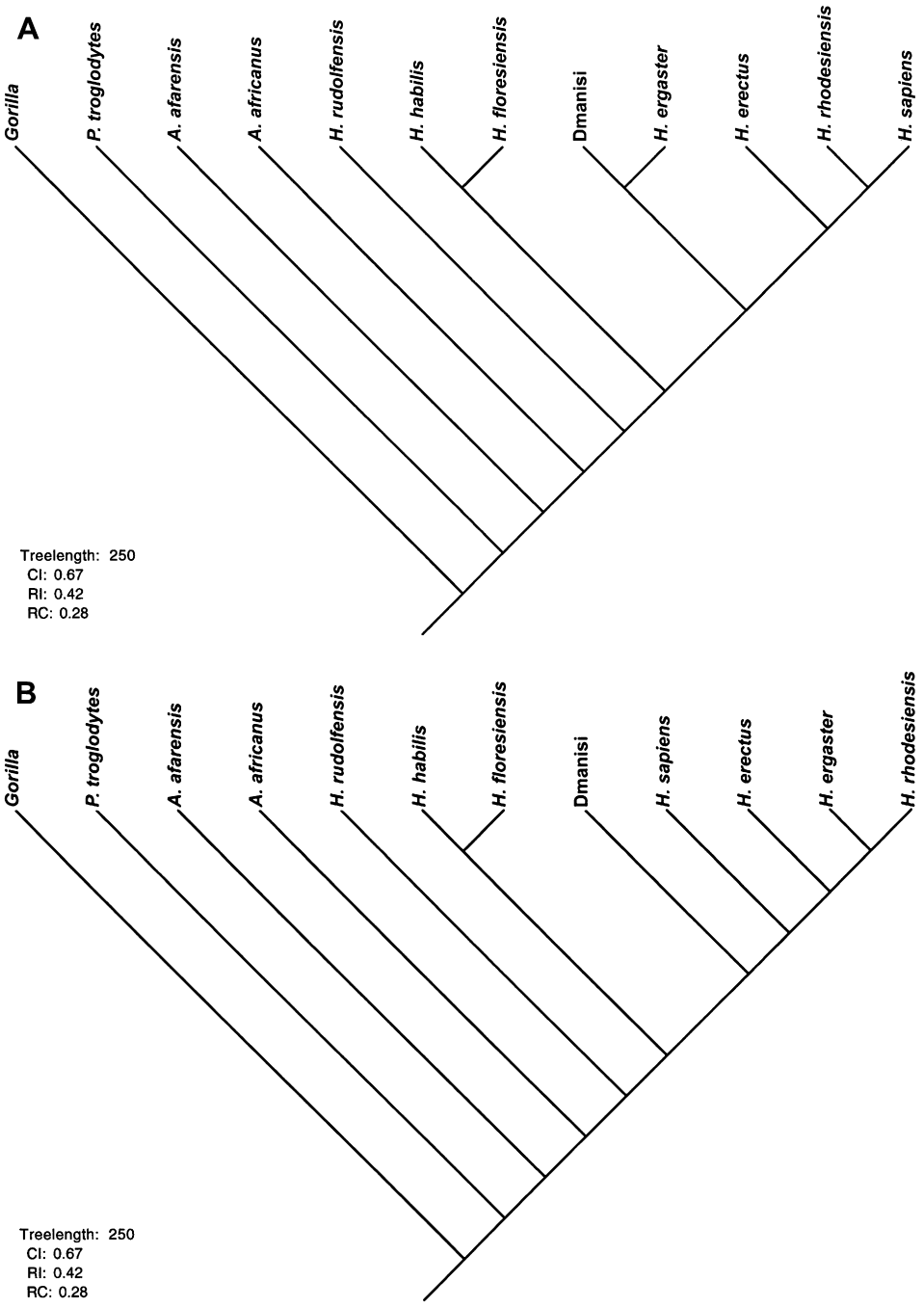

Figure 6. Test for *H. floresiensis* and *H. habilis*. (A) Tree 1: $L = 250$; CI = 0.67; RI = 0.42; RC = 0.28. (B) Tree 2: L = 250; CI = 0.67; RI = 0.42; RC = 0.28.

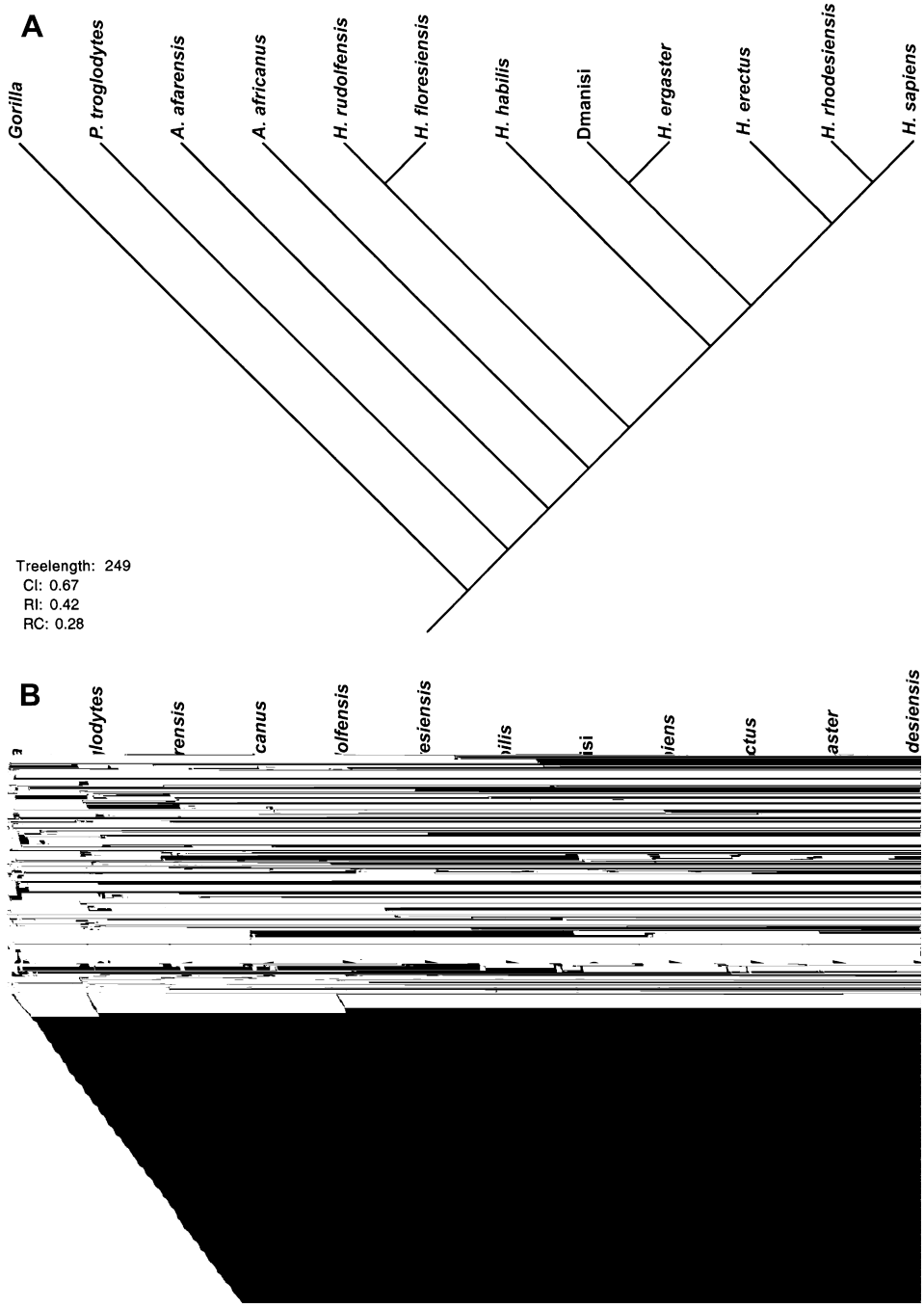

Figure 7. Test for *H. floresiensis* and *H. rudolfensis*. (A) Tree 1: $L = 249$; CI = 0.67; RI = 0.42; RC = 0.28. (B) Tree 2: $L = 250$; CI = 0.67; RI = 0.42; RC = 0.28.

Test for a phylogenetic relationship between H. floresiensis *and* H. habilis

In both cases for this test, the tree lengths are $L = 250$, 3 steps longer than the shortest tree ($L = 247$) (Fig. 6). The T-PTP is $p = 0.49$. This, too, is an unsupported phylogeny.

Test for a phylogenetic relationship between H. floresiensis *and* H. rudolfensis

The trees evaluating a possible relationship between these taxa are two and three steps longer ($L = 250, 249$) than the shortest tree (Fig. 7). The T-PTP, however, is $p = 0.32$, indicating that the clade could be a consequence of chance alone.

Test for a phylogenetic relationship between H. floresiensis *and* A. africanus *or* A. afarensis

For representations of a *H. floresiensis*/*A. africanus* clade, the tree lengths are 4 steps longer than the shortest tree and the T-PTP is $p = 0.52$; when *H. floresiensis* is manoeuvred to form a clade with *A. afarensis*, tree lengths are 10 and 11 steps longer than the shortest tree ($L = 247$), and the T-PTP is $p = 0.87$. Phylogenies in which

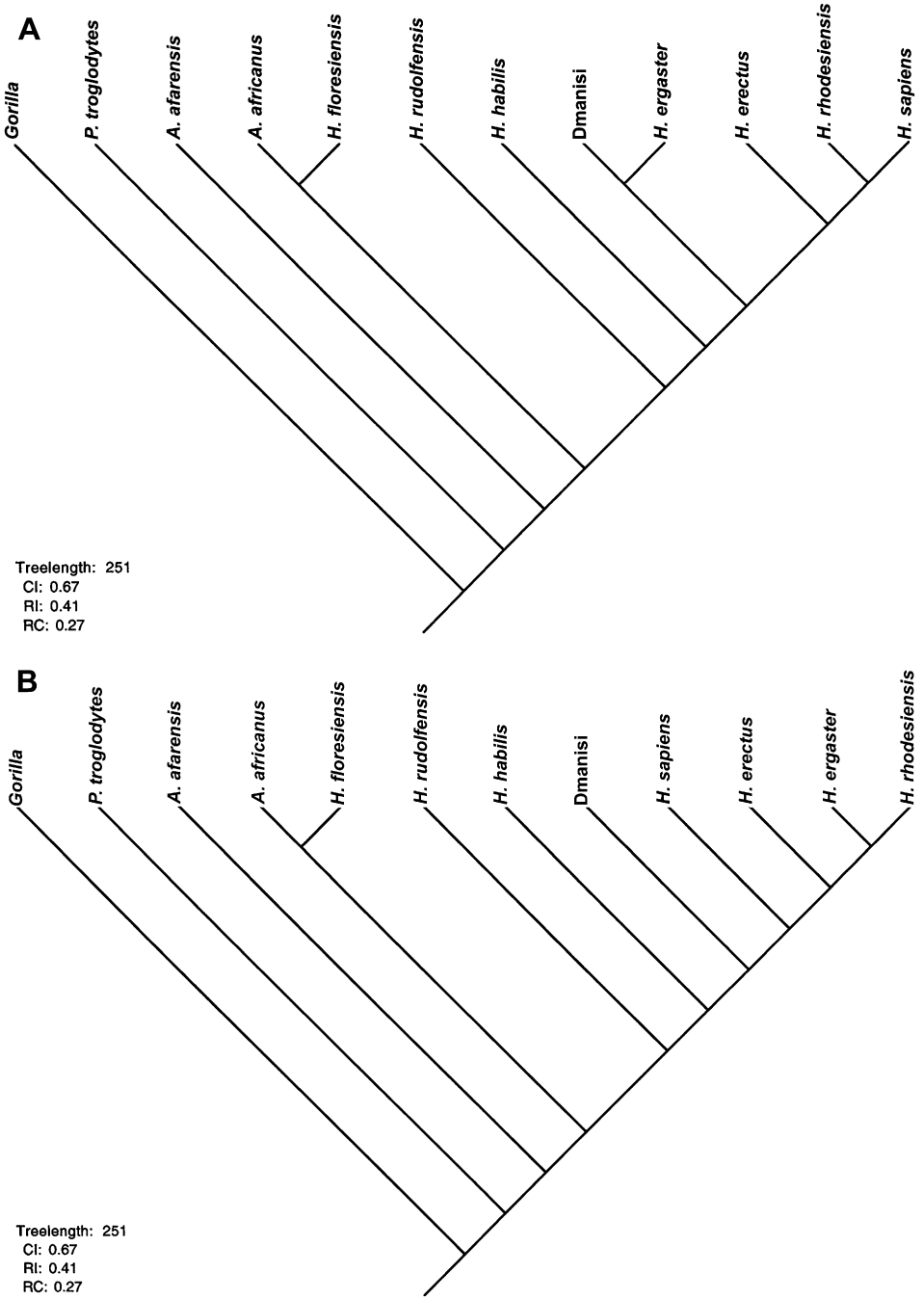

Figure 8. Test for *H. floresiensis* and *A. africanus*. (A) Tree 1: $L = 251$; CI = 0.67; RI = 0.41; RC = 0.27. (B) Tree 2: $L = 251$; CI = 0.67; RI = 0.41; RC = 0.27.

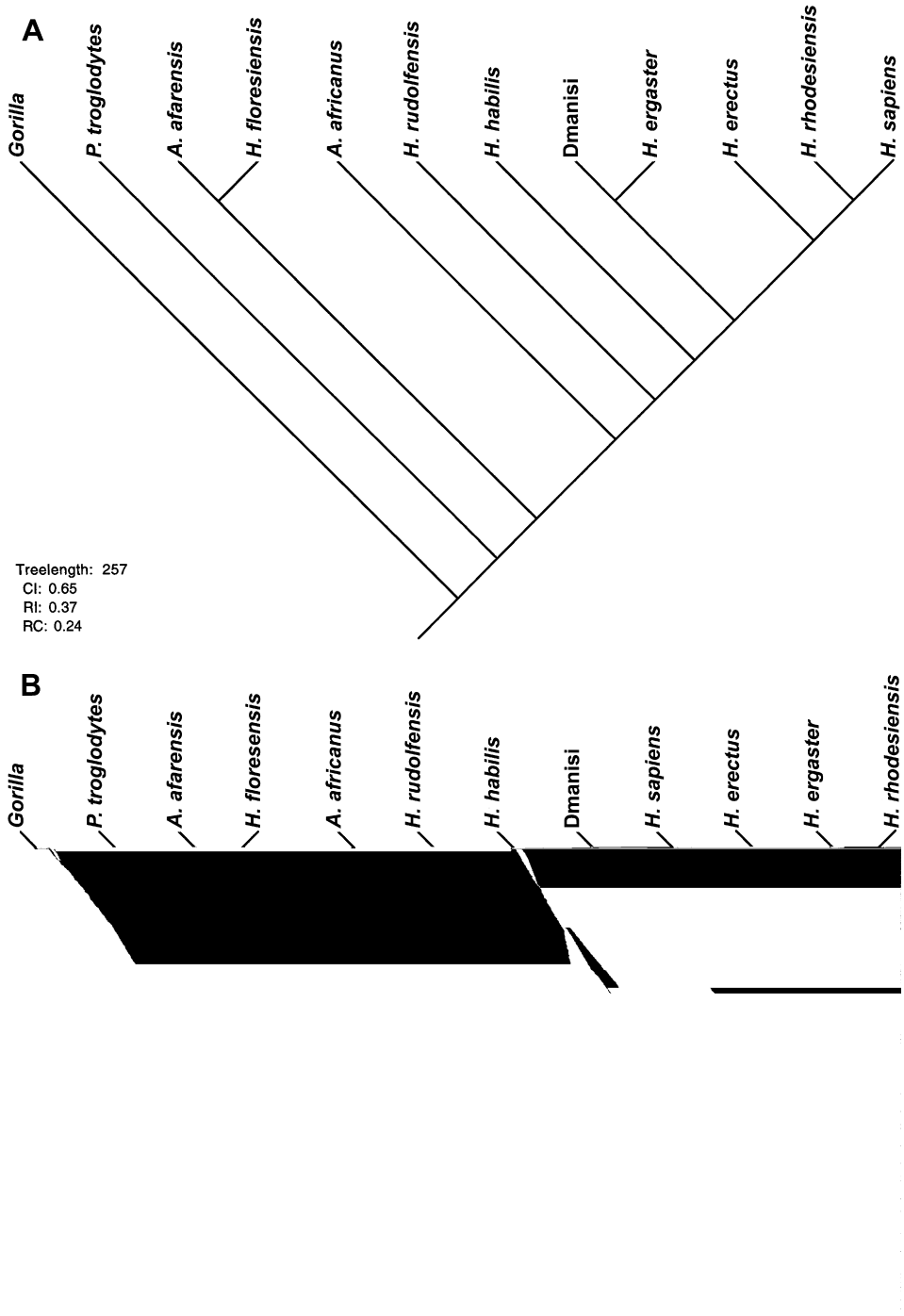

Figure 9. Test for *H. floresiensis* and *A. afarensis*. (A) Tree 1: $L = 257$; CI = 0.65; RI = 0.37; RC = 0.24. (B) Tree 2: $L = 258$; CI = 0.65; RI = 0.36; RC = 0.23.

H. floresiensis is sister taxon to either *A. africanus* or *A. afarensis* are unsupportable (Figs. 8 and 9).

Discussion

The objective of this analysis was to test a wide range of hypotheses about the phylogenetic status of the Liang Bua fossil remains. Specifically, we tested whether or not *H. floresiensis* shared an ancestor with a founder population of archaic *Homo*, or descended from a species intermediate between *Australopithecus* and early *Homo* (Falk et al., 2005; Argue et al., 2006; Larson et al., 2007; Tocheri et al., 2007). In addition, we tried to determine if *H. floresiensis* is phylogenetically related either to *H. erectus* (Lyras et al., 2009) or to *H. sapiens* (Henneberg and Thorne, 2004; Jacob et al., 2006; Martin et al., 2006; Richards, 2006; Obendorf et al., 2008). We also accounted for numerous other possible phylogenies.

Most importantly, the shortest trees produced in our PAUP* cladistic analysis support two hypotheses. Tree 1 leads us to hypothesize that *H. floresiensis* is an early member of the genus *Homo* that evolved after *H. rudolfensis* and before *H. habilis*. Tree 2 also leads us to hypothesize that *H. floresiensis* is an early member of the genus *Homo*, but that it evolved after *H. habilis*. Moreover, *H. floresiensis* apparently does not share a unique common ancestor with (i.e., is not a sister taxon to) any OTU in the analysis. Taken together, these

findings suggest that *H. floresiensis* is a late surviving species of *Homo* that evolved either in the Late Pliocene or in Early Pleistocene.

This crucial conclusion has major implications for our understanding of the evolution of our genus. More specifically, our results strongly imply that a very early member of the *Homo* lineage diffused from Africa to Indonesia. This taxon survived on Flores until between 13.4–10.2 ka at the very least (Roberts et al., 2009). We cannot say exactly when diffusion occurred, but we can make several testable predictions about this event. It could have been either after the last known appearance of *H. rudolfensis* (if *H. floresiensis* appeared at this time; refer to Tree 1). Alternatively, the diffusion event could have occurred after the latest appearance of *H. habilis* (if *H. floresiensis* appeared at this time; refer to Tree 2). Several specimens, including KNM-ER 1470, KNM-ER 1501, and KNM-ER 1502 (*H. rudolfensis*) were found in the Koobi Fora Tuff (Findlater, 1978: Figure 2.5; Leakey et al., 1978) which is dated to 1.868 ± 0.007 Ma (McDougall and Brown, 2006). That is, the last known appearance of *H. rudolfensis* could be dated to 1.861 Ma. The *H. habilis* specimen KNM-ER 1813 is dated to ~1.65 Ma, and KNM-ER 1505 is dated to 1.75 Ma (Gathogo and Brown, 2006); the last known appearance of *H. habilis*, then, is likely to be ~1.65 Ma, or 1.9 Ma, if the earlier chronology (Feibel et al., 1989) for *H. habilis* is retained. In other words, *H. floresiensis* may have emerged either after ~1.8 Ma (or 1.9 Ma) or after ~1.65 Ma. We do not know when it arrived in South East Asia, only that its earliest appearance at Liang Bua could be as late as ~100 ka (Roberts et al., 2009).

Our hypotheses would predict a greater range of hominin variation during the Early Pleistocene than hitherto has been conceptualized by hypotheses of human evolution. *H. floresiensis* has an extremely small stature (106 cm: Brown et al., 2004), similar to the "Lucy" specimen of *A. afarensis* (105 cm: McHenry, 1992) and a little shorter than *A. africanus* (estimated between 110–134 cm: McHenry, 1991), and a small cranial capacity estimated at 417 cc (Falk et al., 2005, 2009), which is within the *A. afarensis* range of 343 cc (AL 333-45; Falk, 1987) to 500 cc (AL 444-2; Johanson and Edgar, 1996). The cranial capacity and stature of *H. floresiensis* fall outside the known ranges for *Homo*, taking the size of *H. habilis*, the earliest species of *Homo*, as a "Rubicon," or immutable lower limit, for the stature and cranial capacity (600 cc: Leakey et al., 1964) for our genus. *H. floresiensis* has, however, been placed in *Homo* (Brown et al., 2004) and our analyses strongly support its placement within this genus. To place a hominin with a cranial capacity of 417 cc in *Homo* might be considered a very challenging proposal, but Falk et al. (2005, 2009) have shown that LB1's brain had expanded temporal lobes and prefrontal cortex relative to fossil hominins, implying the capacity for higher cognitive processes.

Those who oppose *H. floresiensis* as a new species interpret LB1 as a modern human, typically focusing only this one specimen, sometimes invoking pathology (but sometimes not) (Henneberg and Thorne, 2004; Jacob et al., 2006; Richards, 2006; Hershkovitz et al., 2007; Obendorf et al., 2008). Our cladistic analyses show no evidence that *H. floresiensis* and *H. sapiens* share a unique common ancestor. Specifically, tree lengths are considerably longer when such a clade is interjected, and the T-PTP test does not support *H. floresiensis* and *H. sapiens* as sister taxa or sister OTUs. Just as importantly, *H. floresiensis* has several characters that are, to our knowledge, never observed in *H. sapiens*. Specifically, *H. floresiensis* presents internal mandibular buttressing comprising a sub-alveolar plane with inferior and superior transverse tori (Brown et al., 2004) lacking external mandibular buttressing. *H. sapiens* mandibular buttressing is on the external symphysis only, never internally, and takes the form of a chin; the chin has a distinctive inverse "T" formed by a raised central keel that flows into a distended inferior margin. Furthermore, all *H. sapiens* have this (Schwartz and Tattersall, 2000) regardless of any degree of projection or retrenchment of the chin. *Homo floresiensis* also has marked, sharp ridges and relatively deep longitudinal furrows in the palate; strongly developed nasal pillars; supraorbital and occipital tori; the cranium is widest at the biauricular region, while the cranium of *H. sapiens* is widest at the parietals; and relatively long arms in relation to legs, outside the range of modern humans (Brown et al., 2004; Argue et al., 2006). As our cladistic analysis shows, *H. floresiensis* and *H. sapiens* are unlikely to be sister taxa, and *H. floresiensis* poseses characters that are not found in *H. sapiens*. On this basis, we strongly reject the hypothesis that *H. floresiensis* is *H. sapiens*, either with or without pathology.

Our results also have important implications for the hypothesis that *H. floresiensis* resulted from island dwarfing of *H. erectus* (Lyras et al., 2009). For this hypothesis to be sustained in the cladistic analysis, *H. floresiensis* and *H. erectus* would be expected to form sister OTUs with T-PTP support. In other words, the analyses must demonstrate that they share a common ancestor. *H. floresiensis*, however, does not form a clade with *H. erectus*. In fact, the trees are considerably longer when the two taxa are constrained to form a clade, producing a less-parsimonious phylogeny than represented by the shortest trees, and lacking T-PTP support. We conclude, then, that H. *floresiensis* and *H. erectus* did not share a common ancestor and *H. floresiensis* is unlikely to be a dwarfed form of *H. erectus*.

Despite some morphological similarities of *H. floresiensis* with *Australopithecus*, *H. floresiensis* does not share an immediate common ancestor with either *A. africanus* or *A. afarensis*. The trees in which *H. floresiensis* was maneuvered to form a clade with each of these australopithecine species are also considerably longer than the most parsimonious one, and again, lack T-PTP support. Finally, we tested for possible phylogenetic relationships between *H. floresiensis* and *H. rudolfensis*, *H. habilis*, and the hominins from Dmanisi, but again, the relevant trees were longer than the most parsimonious trees, and unsupported.

Conclusions

Based on rigorous cladistic analyses, we propose that *H. floresiensis* evolved in the Late Pliocene or Early Pleistocene. The first of our two equally parsimonious trees suggests that *H. floresiensis* branched after *H. rudolfensis* (represented by KNM-ER 1470) but prior to the divergence of *H. habilis* (represented by KNM-ER 1813 and OH 24). Alternatively, our results are equally supportive of *H. floresiensis* branching after the emergence of *H. habilis*. Our results sustain *H. floresiensis* as a new species (Brown et al., 2004; Morwood et al., 2005) and favor the hypothesis that *H. floresiensis* descended from an early species of *Homo* (Falk et al., 2005; Argue et al., 2006; Larson et al., 2007; Tocheri et al., 2007). We find no evidence of close phylogenetic relations to *H. sapiens*, and reject the idea that the Liang Bua remains represent a pathological modern human. Importantly, we also are unable to link *H. floresiensis* phylogenetically to *H. erectus*, rejecting the hypothesis that the small enigmatic bones resulted from insular dwarfing of *H. erectus*. It is surely time we accepted the reality of *H. floresiensis* as a species and seek answers to the questions that this species poses, not least of which is: who were its ancestors?

Acknowledgments

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Appendix. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jhevol.2009.05.002.

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