



News and Views

A new cladistic analysis of *Homo floresiensis*

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Introduction

Argue et al. (2009) recently presented a cladistic analysis of *Homo floresiensis* in relation to eight fossil hominids and *Homo sapiens*. They state, “Our results sustain *H. floresiensis* as a new species ... and favor the hypothesis that *H. floresiensis* descended from an early species of *Homo*.” They reject alternative hypotheses that *H. floresiensis* is a pathological modern human or a dwarf form of *Homo erectus*. They consider but reject six further hypotheses of a sister-relationship between *H. floresiensis* and each other fossil species in their sample.

I contend that the analysis presented by Argue et al. (2009) is insufficient to sustain their main phylogenetic conclusions. Their data matrix contains too little hierarchical signal to give confidence that either of their ‘best-fit’ trees matches the history of *Homo*, and they assume, wrongly, that when a data set contains no evidence in favor of a given phylogenetic hypothesis it must contain evidence against that hypothesis. I present an alternative visualization of their data that does not rely on the assumption that all terminal taxa are strictly hierarchically related, and show that some parts of their conclusions but not their preferred position of *H. floresiensis* are supported by the data.

Analysis

Characters and character-states for eight species of *Homo* and two *Australopithecus*, with *Pan* and *Gorilla* as outgroups, were described by Argue et al. (2009) but a data matrix was not presented.

I have reconstructed their 60-character matrix (Supplementary Online Material of this paper) from the descriptions given, and although small differences in tree search results show that this reconstruction does not exactly reproduce their matrix these differences have no material bearing on the present paper.

Argue et al. found two most-parsimonious trees at length 247 steps by heuristic tree search in PAUP 4.0b10 (Swofford, 2002). The reconstructed matrix gives one of those trees by an exact search strategy (branch-and-bound) at length 242. Argue et al. reported a bootstrap score of 67% for the branch connecting the ingroup and outgroup. A bootstrap on the reconstructed matrix (1000 replicates) gave a score 63%. This difference is immaterial and no doubt reflects the undocumented differences between the two data matrices. Since no other branch has a score of 50% or higher, the ingroup is completely unresolved in the bootstrap consensus tree under either analysis.

Argue et al. employed two additional analytical tools. In one they took their best-fit tree, changed the position of *H. floresiensis* and reported the increase in tree length. In the other they conducted TPTP tests (Faith and Cranston, 1991) on species pairs representing some alternative positions for *H. floresiensis*. The first procedure was flawed in two ways. The reported tree length difference was not tested for statistical significance, and the increase in tree length was biased upward because the tree topology was not re-optimised following each change in position of the focal species. The method when applied to the reconstructed matrix gives comparable results. For example, if *H. floresiensis* is made sister to *H. erectus* tree length increases by 5 steps. Argue et al. correctly state this is a “less parsimonious phylogeny”, as it must be because it is not the most-parsimonious tree for their data, but in fact it is not significantly less parsimonious than their best-fit tree. A Templeton test, in PAUP, for the difference in fit of two trees to given data shows that any tree within 18 steps of a most-parsimonious tree is not significantly less parsimonious than that tree. Only a tree on which *Pan* was separated from *Gorilla* could have that many steps. This test reinforces the bootstrap result. As would be expected when there is no bootstrap support for any ingroup branching pattern, any alternative tree is not significantly less parsimonious than the best-fit tree.

Failure to re-optimise the tree when *H. floresiensis* is moved will overstate the length difference in some cases. For example, when *H. floresiensis* is made sister to *H. erectus* two steps could be saved by rearranging other taxa, and the best tree for the new position of *H. floresiensis* is three not five steps longer than the best tree overall

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(PAUP branch-and-bound search with topological constraint enforced). However, even without this refinement none of the alternative hypotheses examined by Argue et al. is close to being significant. The greatest length increase is seven steps.

The second procedure used by Argue et al. TPTP, was computed correctly but its results were entirely misinterpreted. The variant of TPTP that Argue et al. used addresses the question “Is there more evidence *in favor* of a test clade than might occur by chance alone?” Argue et al. considered, in turn, placing *H. floresiensis* sister to *H. erectus*, *H. sapiens*, the Dmanisi hominids, *Homo habilis*, *Homo rudolfensis*, *Australopithecus africanus* or *Australopithecus afarensis*. In every case their TPTP result indicates no excess of evidence in favor of that relationship. The TPTP scores reported by Argue et al. range from 0.32 to 0.87. A score as low or lower than 0.05 would be significant. Tests using the reconstructed matrix confirm those results.

Argue et al. misinterpreted this lack of evidence *for* a clade to mean there is evidence *against* that clade. There is no such evidence in their data. A distribution of tree length differences is two-tailed, but each score falls towards the centre of the relevant distribution, no score lies in the opposite tail. Using the reconstructed data I ran TPTP tests of the so-called ‘reverse direction’ variant of TPTP. This asks, “Is there more evidence *against* the test clade than might occur by chance alone?” The results were TPTP scores in the range 0.67–0.12, none was below 0.05. To further examine the proposition that none of these hypotheses can be rejected, within a cladistic parsimony framework and using the reconstructed data, I conducted a PTP test (Faith, 1991). This test asks “Is there greater hierarchical structure somewhere (anywhere) in these data than

might occur by chance alone?” Structure was present when all twelve taxa were included (1000 randomizations, PTP score 0.021) but not when analysing the ingroup alone (1000 randomizations, PTP score 0.223). This again is consistent with the bootstrap result, but it goes a little further. Not only is there no statistical support for the best-fit tree, there is not even a trend in that direction.

An alternative view

Lack of support for a parsimony best-fit tree can result from the absence of information or from data conflict. Character conflict can arise due to convergent evolution or else from reticulation events (hybridization or introgression). Reticulate histories are difficult to model. However, data conflict can be visualized. The program Splitstree (Huson and Bryant, 2006, 2007) offers several visualization methods. One limitation of Splitstree, relevant to the present case, is that the program cannot deal with taxa that are polymorphic for morphological characters. To circumvent this limitation I replaced each polymorphic taxon with three monomorphic variants. In the first, each polymorphism was coded at its lowest numerical value (according to the coding scheme developed by Argue et al.) The second used the highest numerical value, and in the third alternate polymorphisms were coded at their lowest or highest value. This, of course, does not cover the entire range of observable possibilities for any given species, and some combinations among these exemplars may be either impossible or not yet observed, but this range of codings is sufficient to indicate the region of Splitstree graph space in which each species might be found.

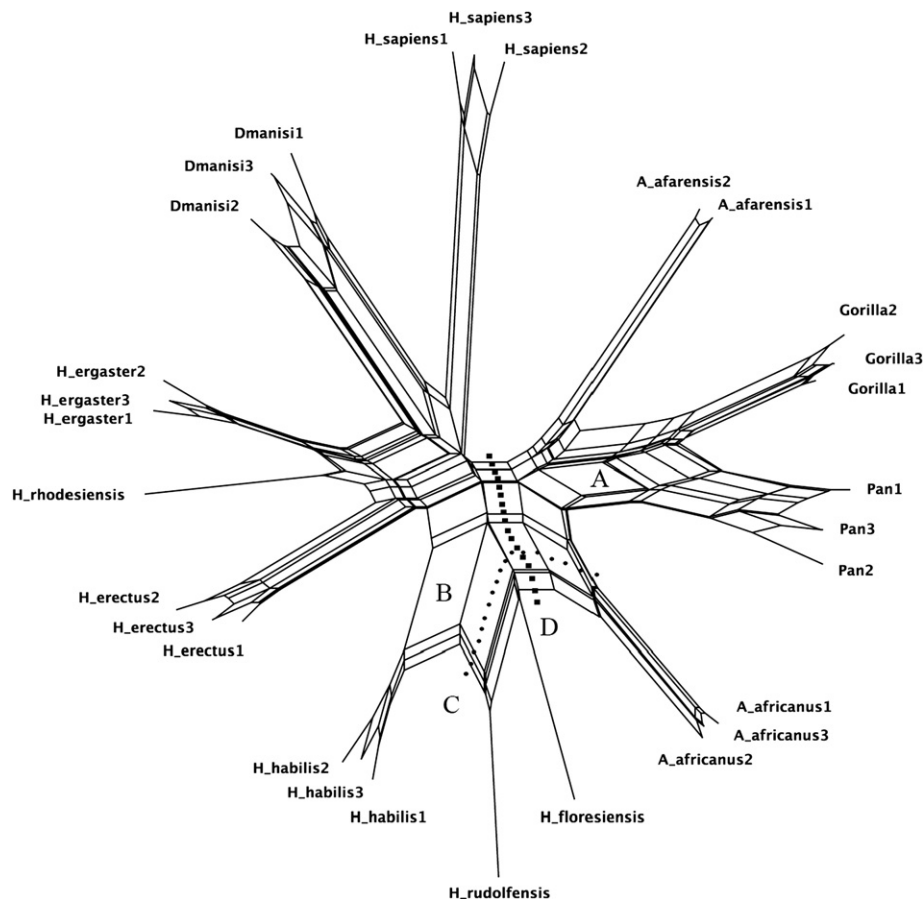


Figure 1. Splitstree graph (NeighborNet method) from the reconstructed and monomorphically recoded data matrix.

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