

Correspondence

Primate evolution – in and out of Africa

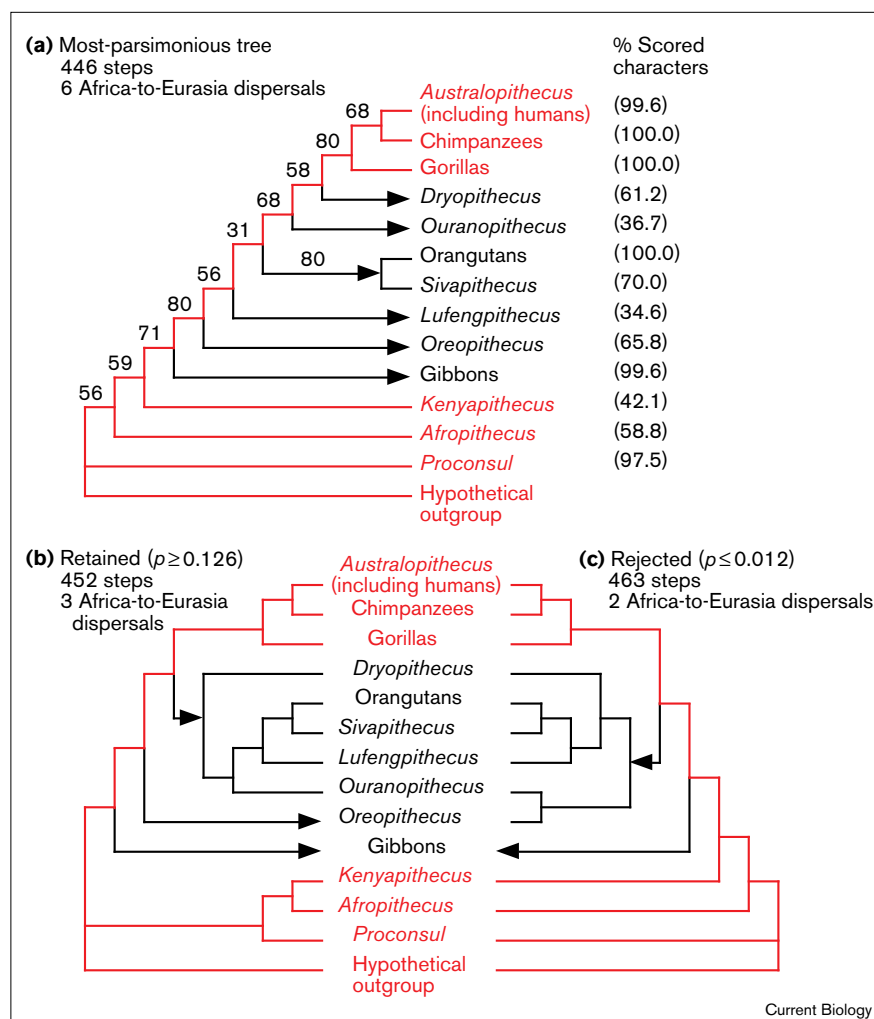
Comments from
Michael M. Miyamoto*
and Timothy S. Young†

Stewart and Disotell [1] have controversially proposed that the hominoid lineage dispersed from Africa to Eurasia about 20 million years ago, and that the common ancestor of human, chimpanzee and gorilla returned to Africa within the past 10 million years. Their model relied on the phylogeny shown in Figure 1a to estimate the minimum number of migrations under two different scenarios: dispersals only from Africa to Eurasia (scenario A); or dispersals in both directions (scenario B). Scenario B is strongly supported by the phylogeny because it requires only two dispersals to explain the distributions of extant and fossil hominoids. Scenario A invokes a minimum of six dispersals to explain hominoid distributions.

This phylogeny was derived by synthesis of molecular data for living hominoids and morphological data for both extant and fossil groups. The hominoid phylogeny of Begun *et al.* [2] was emphasized, as it incorporated 240 cranial and post-cranial characters for the same extant and fossil genera as considered by Stewart and Disotell. Relationships among extant hominoids are well established and not in dispute [3], but many questions persist about the positions of the extinct genera, because of the fragmentary nature of their morphological data (Figure 1). To what extent is the controversial model of Stewart and Disotell based on an unreliable estimate of hominoid phylogeny [4]?

To address this question, we have re-analyzed the 240 morphological

Figure 1



Parsimony analyses of 240 morphological characters for extant and extinct hominoids [2]. (a) The single most-parsimonious phylogeny for these data; this is the same tree found by Begun *et al.* [2] and emphasized by Stewart and Disotell [1]. It requires six Africa-to-Eurasia dispersals under scenario A. (b,c) Shortest phylogenies that require three (b) and two (c) dispersals under scenario A (with each of these trees invoking only two dispersals under scenario B). There are one and seven additional trees of 452 and 463 steps, with three and two 'out of Africa' dispersals, respectively (the other alternative of 452 steps is in Figure 3 of [2]). All parsimony analyses were completed with version 4.0d64 of PAUP*. Post-*Australopithecus* movements by humans

have not been considered. Extinct genera are in italics; arrows track dispersals from Africa to Eurasia; Eurasian groups are black, African taxa are red, and the same colours apply to their ancestors under scenario A. In (a), numbers next to internal branches correspond to bootstrap scores with 2,000 pseudosamples; parenthetical values indicate the percentages of morphological characters, out of 240, scored for each genus. The bootstrap scores provide another measure of character support for each group [5]. Of greatest importance with regard to the % scored is that all extinct genera, except *Australopithecus* and *Proconsul*, are $\leq 70\%$ complete, with *Kenyapithecus*, *Lufengpithecus*, and *Ouranopithecus* known for only 35–42% of their characters.

characters of Begun *et al.* [2] and have identified all of the shortest trees with four, three, two or one dispersal(s) under scenario A (Figure 1):

parsimony analyses show that these are 448, 452, 463, and 492 steps long, respectively (2, 6, 17 and 46 steps longer than the most-parsimonious

phylogeny, respectively). The two phylogenies of 452 steps, each requiring three dispersals out of Africa, are not significantly worse than the most-parsimonious tree, according to their Templeton tests of character support ($p = 0.126$ and 0.227 for the two comparisons, $\alpha = 0.05$, two-tailed testing [5]). The same conclusion applies to the four phylogenies of 448 steps, with four dispersals. The eight trees of 463 changes, with two dispersals, are significantly worse than the most-parsimonious phylogeny ($p = 0.002$ – 0.012), as is the one tree of 492 steps with one dispersal.

Although these results re-emphasize that the Stewart and Disotell model is most-parsimonious and requires the fewest dispersals, the evidence for this model cannot be regarded as conclusive, as there are trees of insignificantly longer length which invoke only one or two extra migrations under scenario A (e.g. see Figure 1b). Retaining these trees forces one to consider whether a single inferred migration is enough to convincingly reject scenario A in favor of scenario B.

The failure of the morphological data to distinguish between the most-parsimonious phylogeny and these alternatives can be most easily attributed to the large numbers of missing data for most extinct genera [3,4]. There remains a critical need for more complete specimens of known fossil genera. With more complete material, gaps in the morphological matrix can be filled, allowing the assignment of these fossil genera to the hominoid phylogeny with greater certainty and permitting more precise estimates of the number and timing of hominoid dispersals 'out of and into Africa'.

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Address: Department of Zoology, University of Florida, Gainesville, Florida 32611, USA.
E-mail: *miyamoto@zoo.ufl.edu;
†tasyoung@zoo.ufl.edu

Comments from Carol Ward

The model of catarrhine evolution presented by Stewart and Disotell [1] highlights the roles of parallelism and competitive exclusion in shaping adaptations in various lineages. It is interesting to note that for most of the time that monkeys were predominantly terrestrial, apes were abundant and arboreal. In Africa, about the time colobines became increasingly arboreal, the gorilla, chimp and human lineages appeared, and hominids became terrestrial bipeds. In Asia, arboreal monkeys appeared about the time fossil apes disappeared.

Arboreality in its various forms appears to have evolved at different times and rates in different lineages. Old World monkeys were largely terrestrial for most of their evolutionary history, with many returning to the trees only recently. Re-invasion of an arboreal niche seems to have happened after the divergence of Asian and African colobine lineages. Shared arboreal traits among colobines, then, must represent independent evolutionary acquisitions, suggesting that mechanical requirements of an arboreal lifestyle select for predictable morphological changes given a similar ancestral form.

Hominoids have always been predominantly arboreal, even in the earliest parts of the lineage. The only fossil hominoid that has been interpreted as displaying any apparent adaptations to part-time terrestriality is *Kenyapithecus* [6]. It would also be surprising if *Proconsul major* and *Gigantopithecus* sp. were not at least partly terrestrial, due to their gorilla-like body sizes. The rest were generalized, above-branch arboreal creatures. Below-branch arboreal specializations probably originated with the modern ape clade. Fossil evidence suggests, however, that the extreme adaptations seen in extant apes were only 'completed' independently in the gibbon/siamang ancestor, in orangutans, at least once in

the African ape and human clade, and perhaps again in the early Miocene ape *Morotopithecus*. Like the apparent parallelisms seen in colobines, this supports the hypothesis that evolution produces similar morphologies under similar selective regimes in closely related primates.

Address: Department of Anthropology and Department of Pathology and Anatomical Sciences, 107 Swallow Hall, University of Missouri, Columbia, MO 65211, USA.
E-mail: anthward@showme.missouri.edu

Comments from Adrienne L. Zihlman* and Jerold M. Lowenstein†

What is missing from the synthesis reported by Stewart and Disotell [1] is a study of the comparative anatomy and locomotor behavior of living apes, evidence that may further strengthen their hypothesis.

The paradox in interpreting ape evolution is that the Asian apes, belonging to the older hominoid lineage, are dependent upon continuous forest canopy. Their younger African cousins, chimpanzees and gorillas, are equally at home in the trees and on the ground. Knuckle-walking accommodates weight-bearing on their long forelimbs and their massive hindlimbs approach those of quadrupedal, terrestrial Old World monkeys [7].

As global cooling occurred in the Miocene, the Asian forests contracted, the Himalayas rose, and the Tethys Sea shrank. These environmental changes probably contributed to the extinction of Miocene ape genera, such as *Sivapithecus* in Asia and Europe [8]. One of the survivors may well have been the ancestor of the gorilla and the chimp, anatomically equipped to travel quadrupedally between discontinuous forests and to radiate into new habitats. Presumably the ancestor, like the living gorilla and chimp, was able to survive outside of primary

rain forest; gorillas in fact seem to prefer secondary forests, and chimpanzees survive in deciduous forests.

The more specialized anatomy of gibbons and orangutans, the small size of the former and the extreme joint flexibility of the latter, has evidently evolved during the millions of years since they diverged from their common ancestor with each other and with their earlier and later African relatives. Further discussion is needed on the timing, as a gibbon branch at 13–14 million years ago, rather than 18 million years ago, would seem to better accommodate the anatomical data.

The weakest link in Stewart and Disotell's scenario is the fossil record. Although Miocene fossil apes exist in Eurasia and Africa, limited evidence of their locomotor anatomy shows little affinity with living apes. For the time of the supposed re-migration into Africa during the past 8–10 million years, the fossil cupboard is virtually bare. We nevertheless congratulate Stewart and Disotell for presenting a well-defined and testable model.

Addresses: *Social Sciences 1, University of California Santa Cruz, Santa Cruz, CA 95064, USA. †Department of Nuclear Medicine, California Pacific Medical Center, San Francisco, CA 94115, USA. E-mail: *zihlman@cats.ucsc.edu; †jlowen@itsa.ucsf.edu

Comments from Colin Groves

The new model proposed by Stewart and Disotell [1] is controversial, but it is an ideal scientific hypothesis: it is testable, and it is supported by the discovery of new specimens of a long-known East African fossil, now named *Morotopithecus*, and its redating at more than 20 million years ago. The new material shows clear affinities with modern hominoids, in a way which *Proconsul* and *Afropithecus* do not, confirming that these two genera form separate lineages [9]. The more diverse the early African hominoid

group turns out to be, the more support there is for the Stewart and Disotell model. On the other hand David Pilbeam has queried the once seemingly unassailable orangutan affinities of *Sivapithecus* [10], and such a proposal would argue against the model. Among the new research that may be stimulated by the hypothesis, I would like to see work to determine the real affinities of Asian fossils including *Sivapithecus*, *Indopithecus* and *Gigantopithecus*, and new investigations of the late Miocene fossils of southern Europe, *Graecopithecus* and *Ankarapithecus*, which could probably fit into either scenario.

Address: Department of Archaeology and Anthropology, The Australian National University, Canberra 0200, Australia.

Comments from Herbert Covert

There are some potential problems with Stewart and Disotell's [1] analysis that need to be considered before the results are considered to be compelling. The most vexing is the overly simplistic biogeographic approach. In their Figure 2, such Eurasian forms as *Oreopithecus*, *Dryopithecus*, *Lufengpithecus*, *Ouranopithecus* and *Sivapithecus* are included. While each is known from Eurasian localities, it would be more accurate to note that some are from Western Europe, others central Europe, one from the Indian subcontinent, and one from eastern Asia. In fact, only *Lufengpithecus* is known from geographic localities within 1,500 km of the range of modern Asian apes.

To make this analysis more meaningful, the authors should divide Eurasia and Africa into three or four regions and repeat the analysis. For example, Eurasia might simply be divided into Europe, Western Asia and Eastern Asia, and Africa divided into Saharan Africa, East Africa, West Africa and southern Africa. The authors would then be treating biogeographic data at a level

of detail approaching that with which they treat the morphological and molecular data.

Address: Department of Anthropology, C.B. 233, University of Colorado, Boulder, Colorado 80309-0233, USA.

Caro-Beth Stewart* and Todd R. Disotell† respond:

We thank the authors of the above letters for their thoughtful comments, and wish to make a few comments in response. Foremost, we encourage the authors to perform the various analyses that they suggest here. Given that all of the data matrices used in our analyses have been explicitly presented in the literature, anyone can test various evolutionary hypotheses by reanalyzing these data, recoding them or adding new characters as they see fit.

For example, Miyamoto and Young present an elegant illustration of how Swofford's computer program, PAUP* [11], can be used to statistically test various evolutionary hypotheses about hominoid evolutionary relationships and dispersal patterns. They present a reanalysis of the dataset of Begun *et al.* [2], the main one we used for our placement of the hominoid fossils in the primate evolutionary tree. We applaud Miyamoto and Young for taking our study one step further, and showing how rigorous phylogenetic analysis can be performed to rule out alternative evolutionary hypotheses. They have set a new standard in the field of paleoanthropology.

Covert rightly suggests that more sophisticated biogeographical analyses could be performed to better understand the details of primate dispersal patterns. We chose to focus on the simple, traditional dichotomy between Africa and Eurasia for several reasons. Importantly, the water and desert that have separated Africa and Eurasia during most of evolutionary history have presented major barriers to primate dispersal between

these land masses. Thus, the major dispersal events between Africa and Eurasia are the first that need to be studied before more sophisticated analyses are performed.

Whether multiple dispersals out of Africa should be considered more or less likely than one dispersal out of and another back into Africa depends, in part, on the locomotor behavior of the migrant species, as discussed originally by Sarich and Cronin [12] and here by Ward, Zihlman and Lowenstein. We note that the common ancestor of the modern African apes was most likely a semi-terrestrial quadruped, as are gorillas and chimpanzees (and young humans). Similarly, the fossil colobine *Mesopithecus* is believed to have been semi-terrestrial. So both of the ancestral primate groups that we propose dispersed about 10 million years ago were probably capable of quadrupedal, terrestrial locomotion through suboptimal, thinly-forested environments.

The longer trees that Miyamoto and Young present have implications for the divergence date of the orangutan and African ape lineages, one of the most important and hotly-contested dates in primate evolution. It is often claimed that calibration of this key divergence date relies solely on the placement of *Sivapithecus* on the orangutan lineage, but this is not true. Any hominoid fossils that cluster with either the African ape or orangutan clade are relevant to this divergence date, as we previously explained. In Figure 1b above, for example, *Dryopithecus* and *Ouranopithecus* are found to cluster with the orangutan clade, rather than with the African apes, as they do in the most parsimonious tree (Figure 1a above); either of these placements suggests that the African ape and orangutan lineages diverged before the earliest appearance of these fossil hominoids. Indeed, the placement of any of these Eurasian hominoid fossils on either the orangutan or African ape lineages precludes this key divergence date from being as recent as

8.6 million years ago, as proposed by Kumar and Hedges [13] based on analysis of a few unidentified proteins. Thus, this key divergence date does not rely solely on the phylogenetic position of *Sivapithecus*.

Groves points out the controversy surrounding *Sivapithecus*, which derives from relatively recent discoveries of a few postcranial bones that are thought to belong to this genus. Few paleoanthropologists contest the detailed likeness of the *Sivapithecus* face and palate to that of the orangutan, but the arm bones display a curious mix of ape and monkey-like features that suggest a quadrupedal locomotor pattern unlike that seen in the arboreally-committed orangutans. Some authors, notably Pilbeam [10], have taken these postcranial features to imply that *Sivapithecus* may not be uniquely related to the orangutan lineage. Importantly, however, parsimony analysis of the Begun *et al.* [2] data matrix indicates that *Sivapithecus* does branch with orangutans, and with a respectively high bootstrap support of 80% (Figure 1a, above). This placement suggests that the *Sivapithecus*-like ancestor was more terrestrial than are orangutans, a locomotor behavior that would have more easily allowed their dispersal into southeast Asia.

We also agree with these authors that more — and more complete — fossil primates need to be included in computer-aided parsimony analyses. Sadly, more complete fossils do exist for some of the genera shown in these trees, but they have not yet been made available for such analyses. Due in part to logistical difficulties, some paleontologists do not allow access to ‘their’ fossils by many other researchers in the field; nor do all present explicit data matrices that can be reanalyzed, challenged or augmented. These situations are unacceptable in modern science. We call for a change in the culture of paleoanthropology, such that all relevant specimens can be examined by other researchers and all data used to infer evolutionary hypotheses must be explicitly presented. Modern imaging

and computer technologies will allow the acquisition and storage of three-dimensional images of fossils, making the primary data widely available.

Addresses: *Department of Biological Sciences, University at Albany, State University of New York, 1400 Washington Avenue, Albany, New York 12222, USA.

†Department of Anthropology, New York University, 25 Waverly Place, New York, New York 10003, USA.

E-mail: *c.stewart@albany.edu;

†todd.disotell@nyu.edu

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