



The phylogenetic position of *Morotopithecus*

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Abstract

The phylogenetic relationship of the Ugandan Miocene hominoid *Morotopithecus bishopi* to fossil and living hominoids remains to be determined. In a cladistic approach to this question, we used three published Miocene character sets as the basis of a phylogenetic analysis: J. Hum. Evol. 29 (1995) 101; Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations, 1997, 389. Because these datasets often describe the same anatomy using different characters and states, three different datasets were created to reflect these alternatives. In addition, new postcranial characters describable in *Morotopithecus* were added to each of the above datasets and a fourth dataset was created using only postcranial characters. The most parsimonious tree(s) recovered in all analyses consistently placed *Morotopithecus* as a sister taxon to the extant great apes, with *Hylobates* sister to this clade. *Morotopithecus* was also consistently more derived than *Proconsul*, *Afropithecus*, and *Kenyapithecus* (as defined prior to the description of *Equatorius*), but less derived than *Oreopithecus*, *Sivapithecus* (only craniodentally) and *Dryopithecus*. These results imply that *Morotopithecus* is more derived than *Hylobates*. However, gibbons are believed to have branched off by at least 18 Ma while *Morotopithecus* is dated at >20.6 Ma. Possible explanations include: (1) the dating of the *Morotopithecus* material is too old; (2) the *Hylobates* divergence time has been underestimated; (3) the great ape condition, and not that of *Hylobates*, is primitive for hominoids; (4) the similarities of *Morotopithecus* and great apes are homoplasies. Given current evidence, the first possibility is unlikely, but it is not possible to choose definitively between the latter three possibilities. This conclusion is supported by the fact that despite the consistencies of the analyses, the addition of *Morotopithecus* and the use of different characters had a large effect on the placement of other Miocene taxa. This raises questions as to the robustness of the connections between Miocene taxa and extant hominoids since different results can be achieved by changing either a few characters, or by adding a single taxon. Many of the characters used to estimate phylogeny may need to be reassessed before a reliable assessment of the phylogenetic position of *Morotopithecus* can be achieved.

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Introduction

Hominoid fossils from two early Miocene localities (>20.6 Ma) near the Moroto volcano in

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the Karamoja District, Uganda have been assigned to a new genus and species of Miocene hominoid, *Morotopithecus bishopi* (Gebo et al., 1997). This new designation is based on a combination of previously known craniodental and vertebral specimens with new femoral and scapular material (Fig. 1a–d). The craniodental features of *Morotopithecus* are generally primitive whereas some of the postcrania exhibit features associated with orthogrady and suspension that resemble the condition found in extant apes (Sanders & Bodenbender, 1994; Gebo et al., 1997; MacLatchy & Pilbeam, 1999; MacLatchy et al., 2000).

Previous phylogenetic analysis of *Morotopithecus* craniodental material has placed the taxon near the base of the hominoid radiation, sister to all living hominoids (Begun & Güleç, 1998). This interpretation is consistent with the dating of *Morotopithecus* fossil material and the divergence time of the hominoids as inferred from multiple genetic datasets (Caccone & Powell, 1989; Sibley et al., 1990; Kumar & Hedges, 1998). However, the newly described postcranial specimens have never been included in any formal phylogenetic analysis. Given the importance of postcrania to alternative hypotheses of hominoid evolution and the relative scarcity of diagnostic postcranial material in the ape fossil record, the addition of these data to a phylogenetic analysis could yield interesting insights.

For example, the phylogenetic placement of *Morotopithecus* based on currently available data depends heavily on whether its postcranial similarities to living hominoids are homologous or homoplastic. If the similarities are synapomorphic with living hominoids, then younger Miocene hominoids (e.g., *Sivapithecus*, *Proconsul*, *Afropithecus* and *Kenyapithecus*) that lack such features either “re-evolved” a more pronograde quadrupedalism, or are more distantly related to extant hominoids than is *Morotopithecus*. If the similarities are homoplastic, it would bolster claims that hominoid postcranial similarities are convergent (e.g., Larson 1998). A phylogenetic analysis including all of the *Morotopithecus* material may therefore illuminate not only the relationship of this taxon to other living and fossil apes but also may help to discriminate between these alternative hypotheses of ape evolution.

In addition, the analysis of *Morotopithecus* can serve to illustrate how character and taxa selection may affect the robusticity of results derived from these data. Debate about Miocene ape phylogenetics has produced a number of competing hypotheses concerning the specific affinities of fossil apes to living apes (Andrews & Martin, 1987; Schwartz, 1990; Andrews, 1992; Begun, 1992; Moyà-Solà & Köhler, 1995; Begun et al., 1997; Cameron, 1997; Harrison & Rook, 1997; Begun & Güleç, 1998; Andrews & Bernor, 1999). These differences are partially due to disagreements about how anatomy should be described as characters and which taxa are included in analyses.

In this paper we address the following issues:

1. Using previously published character sets, what is the phylogenetic position of *Morotopithecus*?
2. How does adding *Morotopithecus* to published hominoid morphological datasets affect previously inferred phylogenies?
3. What effect do missing characters or different character partitions have on our interpretation of Miocene hominoid relationships?
4. What effect, if any, does the analysis of *Morotopithecus* have on assessing the likelihood of hominoid postcranial parallelism?

Data

In order to sample the most variation in character description, we chose to derive our character list from three published sources (Begun et al., 1997; Moyà-Solà & Köhler, 1995; Cameron, 1997), and from our own analysis of the *Morotopithecus* postcranium. However, these three datasets often differ in their description of the same anatomical regions. In order to avoid any pre-judgement of which character description is “better”, we created three different datasets (described in detail below) to reflect these alternatives and analyzed them individually. Because Begun et al.’s complete dataset is the most comprehensive list of hominoid characters and taxa, we used it as the basis for all of our analyses. Characters from

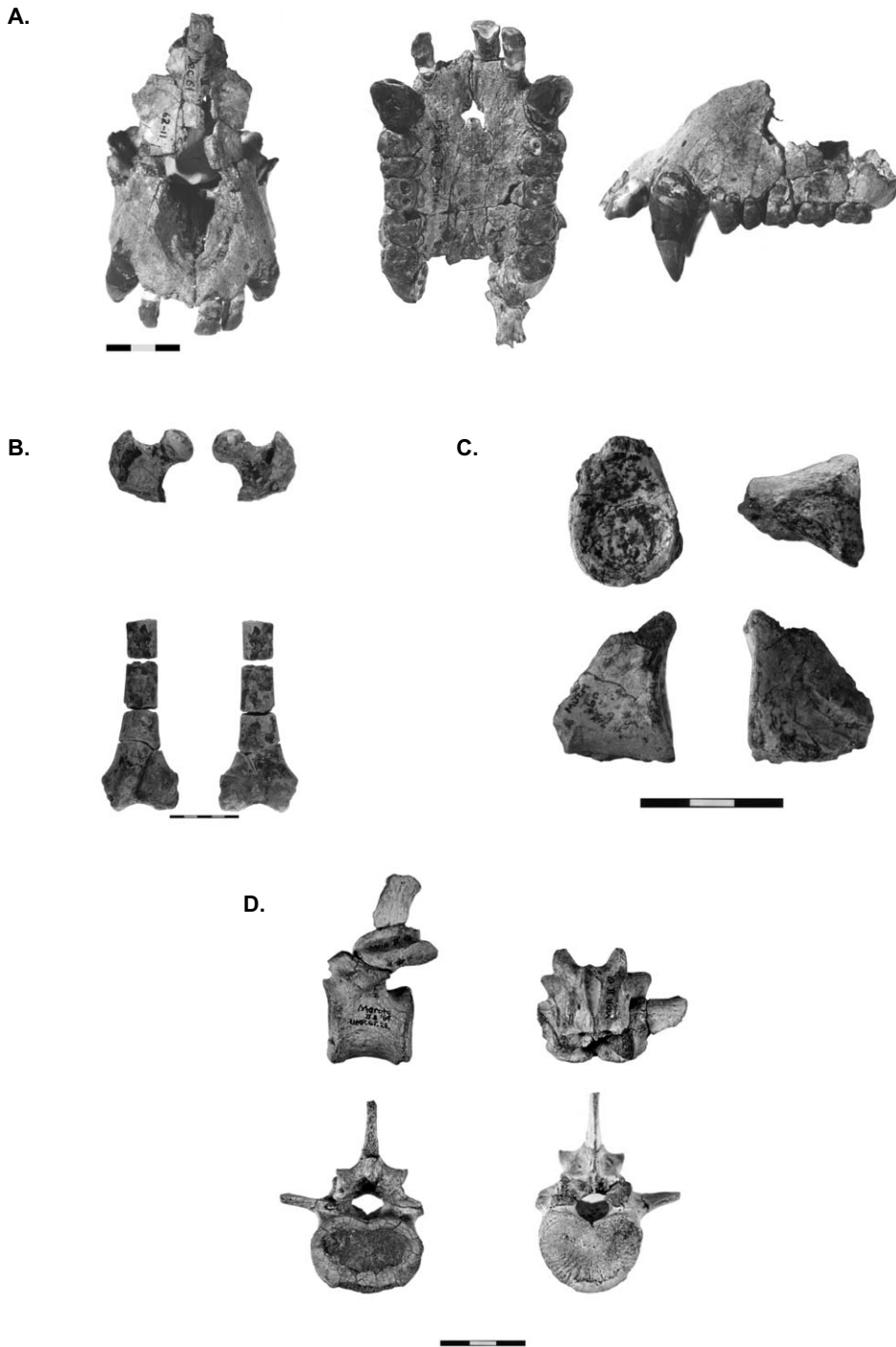


Fig. 1. *Morotopithecus* craniodental and postcranial remains. A. Craniodental remains UMP 62.11: (from left to right) front, inferior and medial views. B. Proximal and distal femur MUZM 80: anterior (left) and posterior (right) views of the right femur. C. Scapula fragment MUZM 60: (clockwise from upper left) medial, inferior, ventral, and dorsal views. D. Lumbar vertebra UMP 67.28: (clockwise from upper left) lateral, dorsal, caudal, and cranial views. All scalebars in centimeters.

Moyà-Solà & Köhler and Cameron that are represented in *Morotopithecus* were then added to this base dataset, replacing any Begun et al. character that described the same anatomy (Fig. 2). In addition, for all three datasets new characters were added where *Morotopithecus* anatomy was not describable using published characters. In particular, postcranial characters describable in *Morotopithecus* were added (see Appendix A). A fourth dataset was created using only postcranial characters.

In addition to *Morotopithecus*, the following taxa were included in our analysis: *Australopithecus*, *Pan*, *Gorilla*, *Pongo*, *Hylobates*, *Proconsul*, *Afropithecus*, *Kenyapithecus*, *Lufengpithecus*, *Sivapithecus*, *Oreopithecus*, *Dryopithecus*, and *Ouranopithecus* (*Graecopithecus*). Although in our analyses *Kenyapithecus* was synonymous with that in Begun et al. (1997), Ward et al. (1999) have proposed that the sample represented by this genus is paraphyletic. They argue *Kenyapithecus* can be divided into two genera based on both site location and anatomy: material from Fort Ternan is maintained in *Kenyapithecus wickeri* while fossils from the Tugen Hills and elsewhere can be attributed to a new taxon named *Equatorius africanus*. Ishida et al. (1999) further recognize a third genus that is represented by *Kenyapithecus* material from Samburu, a taxon they name *Nacholapithecus*. To account for these taxonomic differences, we also performed analyses of all datasets with both pre-Ward et al. (1999) *Kenyapithecus* (hereafter referred to as “*Kenyapithecus*”) and with the sample divided into *Equatorius africanus* and *Kenyapithecus sensu stricto*. *Nacholapithecus* was not included in these analyses because we did not have access to casts of the material. Likewise, Cameron (1997) proposed *Dryopithecus* could be divided based on geographic region: *Hispanopithecus* represents the Spanish material and *Rudapithecus* represents the Hungarian sample. Although this taxonomic arrangement has not been widely accepted in the literature, we accepted its use when analyzing Cameron’s characters (see below).

Following these criteria, four different combinations of characters and taxa were created:

- 1a Begun et al.’s (Begun et al., 1997) complete character list (71 cranial, 43 dental, 125 postcranial, 1 life history) with the addition of our postcranial characters (13 characters) and the taxon *Morotopithecus* (253 characters and 15 taxa, total). The effect of *Kenyapithecus/Equatorius* was also considered in a separate analysis.
- 1b Same as 1a but using only characters represented in *Morotopithecus* (84 characters).
- 2a Characters from Moyà-Solà & Köhler (1995) that are represented in *Morotopithecus* were added to [1], with conflicts resolved by removing similar Begun et al. characters (15 taxa, 10 characters added and 18 removed; 245 characters total) (Fig. 2). The effect of *Kenyapithecus/Equatorius* was also considered in a separate analysis.
- 2b Same as 2a but using only characters represented in *Morotopithecus* (67 characters).
- 3a Characters from Cameron (1997) that are represented in *Morotopithecus* were added to [1], with conflicts resolved by replacing similar Begun et al. characters (16 taxa, 20 characters added and 19 characters removed; 255 characters total) (Fig. 2). The taxon *Rudapithecus* (= *Dryopithecus* from Rudabánya, Hungary) was added, and Cameron’s *Hispanopithecus* (= *Dryopithecus* from Spain) was represented by *Dryopithecus*. The effect of *Kenyapithecus/Equatorius* was also considered in a separate analysis.
- 3b Same as 3a but using only characters represented in *Morotopithecus* (89 characters).
- 4 Postcranial characters from Begun et al. and additional postcranial characters created by us. *Ouranopithecus* and *Lufengpithecus* were not included in this dataset because they were represented by very few postcranial characters (three and five, respectively) and these characters did not overlap significantly with the characters represented in other fossil taxa. The effect of *Kenyapithecus/Equatorius* was also considered in a separate analysis.

Character states for *Morotopithecus* were coded by comparison of casts to samples of extant and fossil hominoid skeletal material housed in the

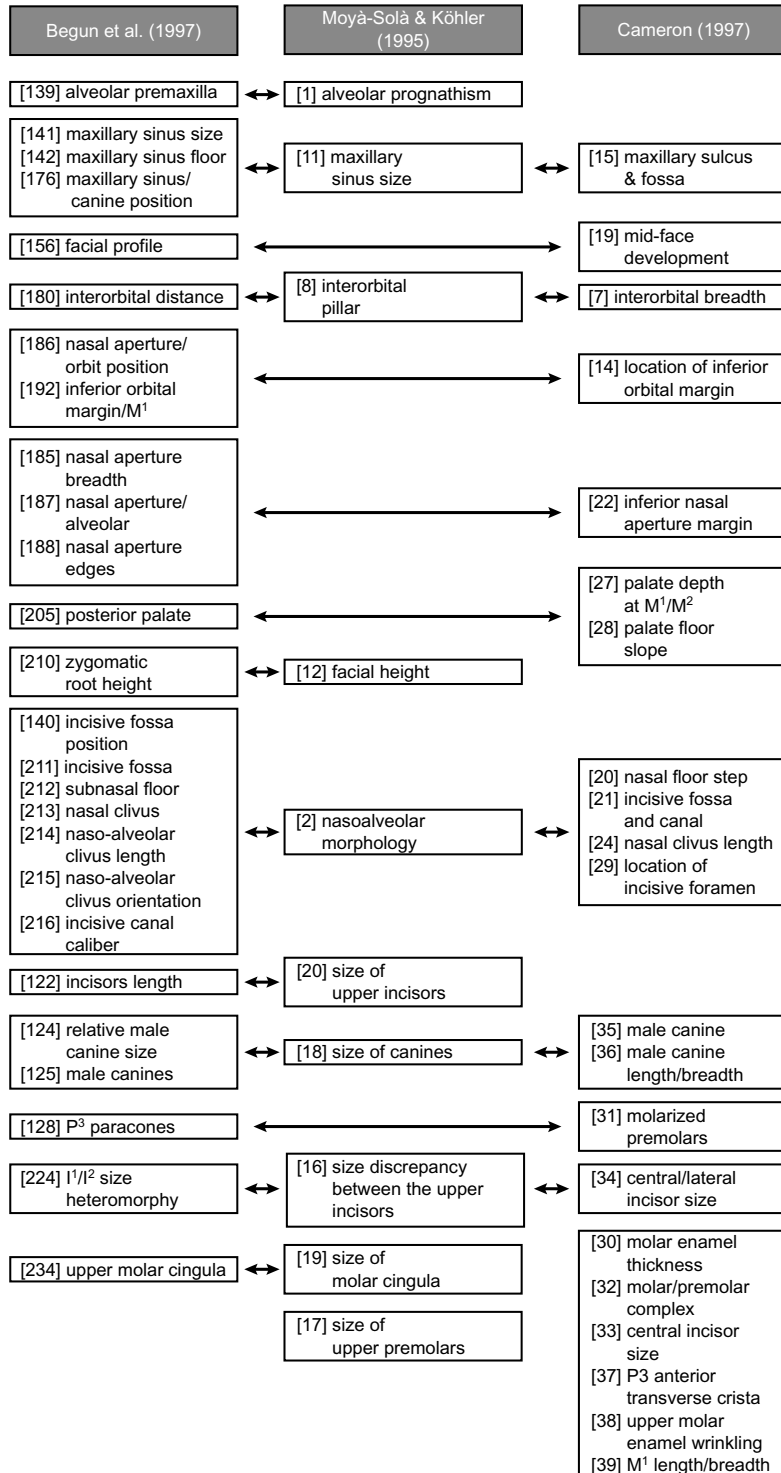


Fig. 2. Differences in cranial and dental description and number of characters for the three datasets considered in the text.

Peabody Museum, Harvard University (see Appendix B).

Analyses

Parsimony analyses of these datasets were performed in PAUP* (Swofford, 2002) using a heuristic search method of 1000 random replicates, and resolution of ambiguous nodes via ACCTRAN (Farris, 1970). All most-parsimonious trees were saved. If more than one most-parsimonious tree was found, a 50% majority-rule consensus tree (MRCT) was computed. Bootstrap estimates (heuristic search, 1000 random replicates) were performed for datasets 1a, 2a, 3a, and 4 (Felsenstein, 1985). Character state distributions for the most-parsimonious or majority-rule consensus trees were inspected in MacClade 3.07 and compared to those from alternative phylogenies and to investigate suboptimal tree arrangements (Maddison & Maddison, 1992).

Results

Analysis of dataset 1a recovered nine most-parsimonious trees (MPTs), and analyses of datasets 2a and 3a recovered one MPT each (Fig. 3b, Fig. 4b, Fig. 5b). All analyses consistently placed *Morotopithecus* as a sister taxon to the extant great apes, with *Hylobates* sister to this clade. To make *Morotopithecus* a sister taxon to all living hominoids requires eleven additional steps using datasets 1a and 3a, and fourteen additional steps using dataset 2a. *Morotopithecus* was also consistently more derived than *Proconsul*, *Afropithecus*, and “*Kenyapithecus*” but less derived than *Oreopithecus*, *Sivapithecus*, *Lufengpithecus*, *Ouranopithecus* and *Dryopithecus*. Bootstrap support for the position of *Morotopithecus* was consistently high (73–96%) (Fig. 6a–c).

The use of alternate characters and the addition of *Morotopithecus* yielded consistent differences from Begun et al.’s original tree. For example, analyses 1–3a all supported a primitive hominoid clade containing *Afropithecus*, “*Kenyapithecus*”, and *Proconsul* (Figs. 3–5b). But the major differ-

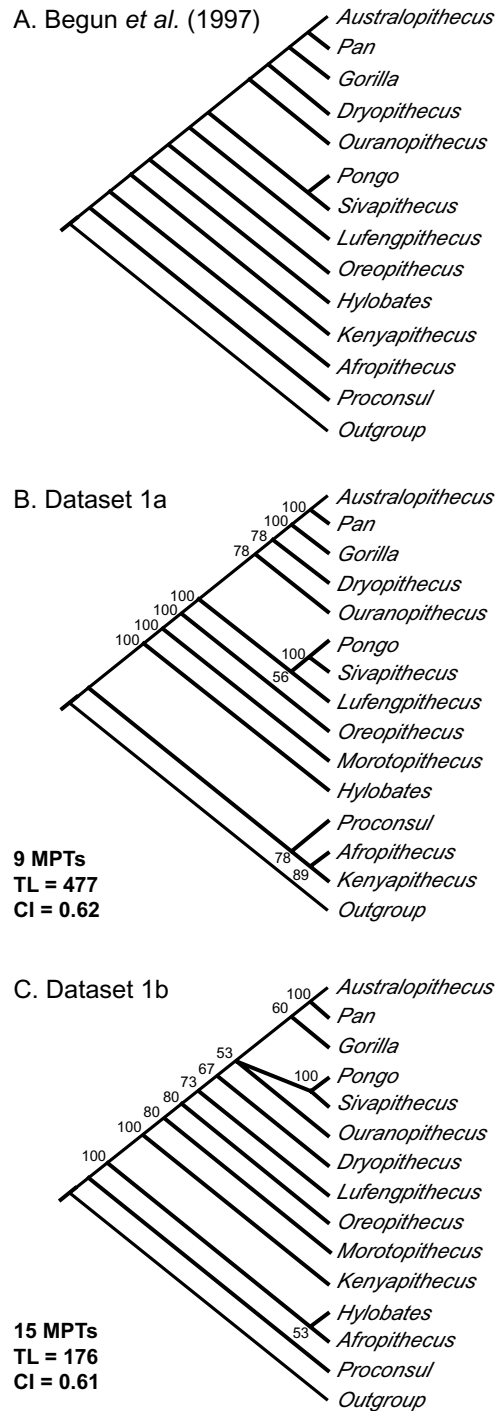


Fig. 3. a–c: Results from the phylogenetic analysis of Begun et al. (1997) including *Morotopithecus*.

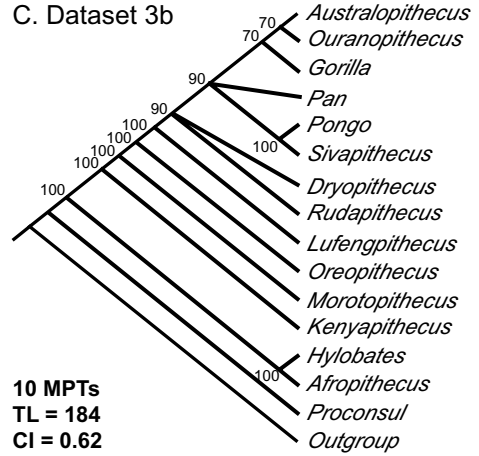
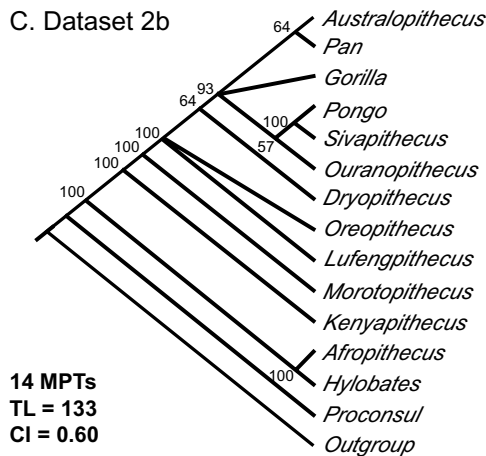
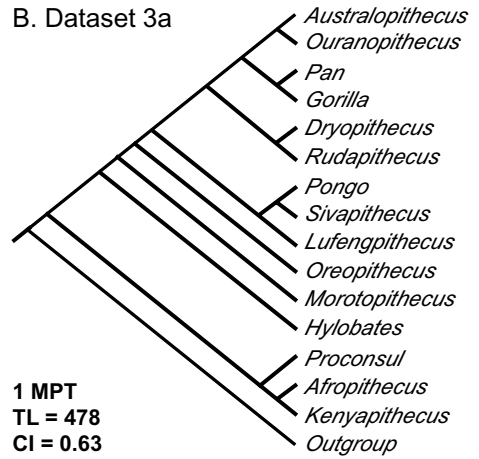
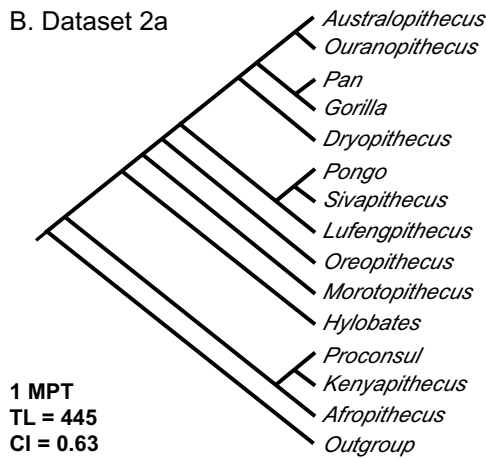
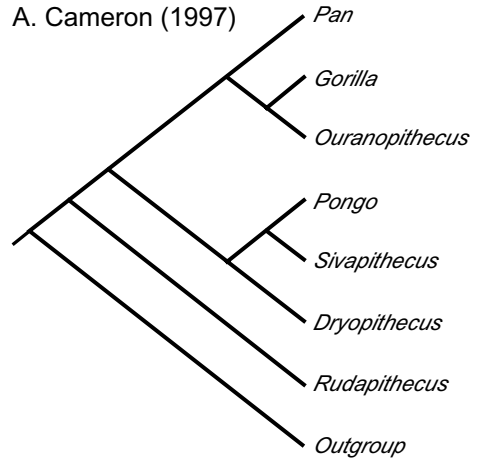
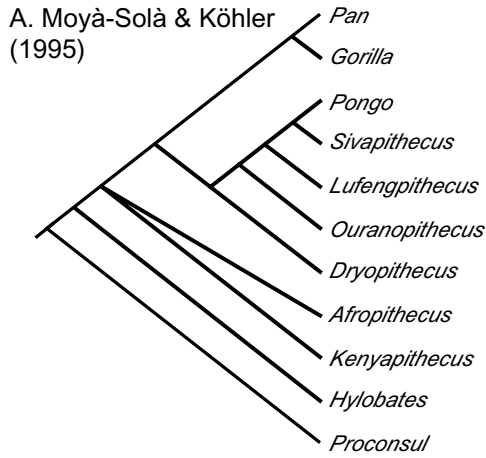


Fig. 4. a–c: Results from the phylogenetic analysis of Moyà-Solà & Köhler (1995) including *Morotopithecus*.

Fig. 5. a–c: Results from the phylogenetic analysis of Cameron (1997) including *Morotopithecus*.

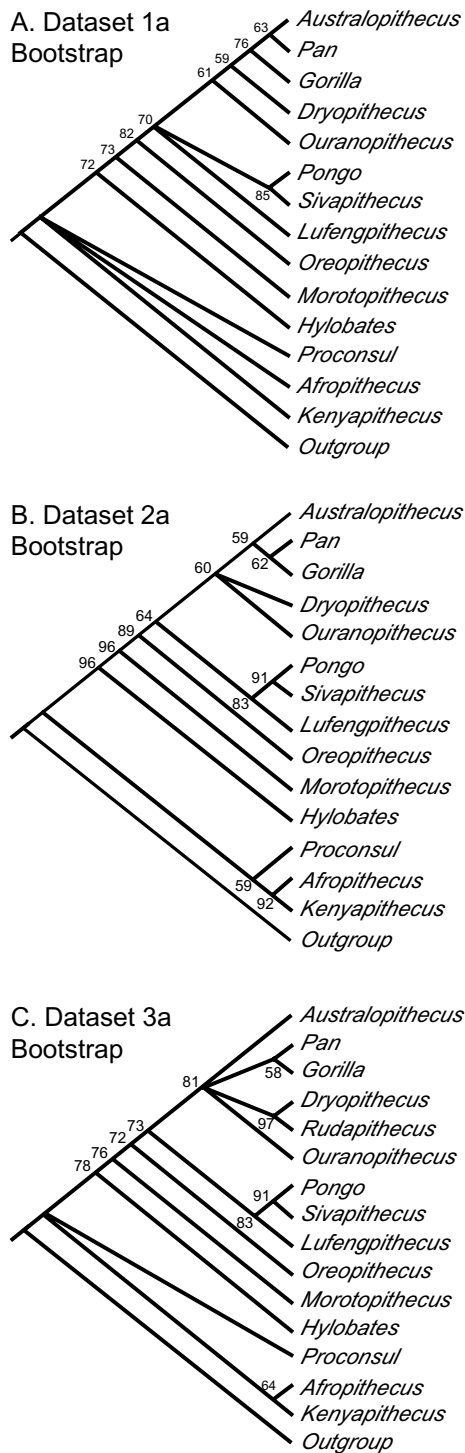


Fig. 6. a–c: Results from the bootstrap analyses of Dataset 1–3b and including *Morotopithecus*.

ence between the branching pattern of trees from analyses 1a, 2a, and 3a is the positioning of *Ouranopithecus* as sister to either the African apes or *Australopithecus*. This result parallels the findings of two of the original unaltered datasets. [Begun et al. \(1997\)](#) placed *Ouranopithecus* as sister to the African apes (supported by Analysis 1a), and [Cameron \(1997\)](#) placed *Ouranopithecus* within the African ape clade (supported by analysis 3a). [Moyà-Solà & Köhler \(1995\)](#) placed *Ouranopithecus* in the *Pongo* clade, however in Analysis 2a *Ouranopithecus* is linked to *Australopithecus* as in [Cameron \(1997\)](#). The positioning of *Lufengpithecus* as part of the *Pongo*–*Sivapithecus* clade is another consistent although not strongly supported difference from [Begun et al.’s \(Begun et al., 1997\)](#) preferred tree (5/9=56% of the trees, and an additional tree places *Lufengpithecus* sister to African apes). This relationship was supported by the analyses of [Moyà-Solà & Köhler \(1995\)](#), while *Lufengpithecus* was not included in [Cameron’s \(1997\)](#) original analysis.

The use of only the characters found in *Morotopithecus* in analyses 1b, 2b and 3b again consistently placed *Morotopithecus* as sister to the great apes (Figs. 3–5c). However, these analyses differ from 1a, 2a and 3a, and are consistently similar to each other in placing *Afropithecus* as sister to *Hylobates* or the great apes, and “*Kenyapithecus*” and *Dryopithecus* sister to the great apes. Analyses 1b, 2b and 3b differ in the placement of *Lufengpithecus* and *Ouranopithecus*, but in a manner consistent with analyses 1–3a. In contrast to Analysis 2a, Analysis 2b places *Ouranopithecus* in the *Pongo* clade. This result is similar to [Moyà-Solà & Köhler’s](#) preferred tree.

Analysis of postcranial characters in dataset 4 recovered 15 most-parsimonious trees, and the majority-rule consensus tree places *Morotopithecus* as sister to the great apes in 80% (=12/15) of the trees (60% of the trees placed *Morotopithecus* more primitive than *Oreopithecus*, and 20% as sister to or more derived than *Oreopithecus*) (Fig. 7a). In the majority-rule consensus tree, *Morotopithecus* was more derived than all other Miocene taxa with the exception of *Oreopithecus*. Bootstrap support was equivocal, with neither *Morotopithecus*, *Sivapithecus*, *Dryopithecus*, nor *Hylobates* being more

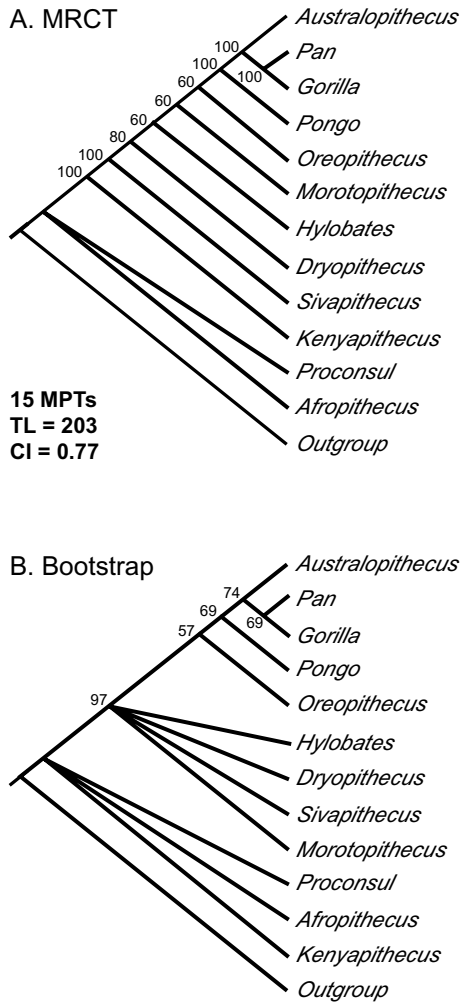


Fig. 7. a–b: Results from the phylogenetic and bootstrap analysis of postcranial characters only.

derived in over 50% of the bootstrap replicates (Fig. 7b).

The use of alternative genera (e.g., *Equatorius*/*Kenyapithecus* or *Hispanopithecus*/*Rudapithecus*) did not have a major effect on the outcome of the maximum parsimony analyses (results not shown). Both *Equatorius*/*Kenyapithecus* and *Hispanopithecus*/*Rudapithecus* were sister taxa in the majority of MPTs which suggests separate genera are not cladistically supported by these

datasets. The exception to this result was that in analyses including *Equatorius*/*Kenyapithecus* but using only characters found in *Morotopithecus*, *Equatorius* was linked with more primitive hominoids (i.e., *Proconsul* and *Afropithecus*) whereas *Kenyapithecus* was more derived and typically linked to *Lufengpithecus*. This supports the contention of Ward et al. (1999) that *Kenyapithecus* is more derived than *Equatorius*. However, it is important to remember that this result is produced only by using a reduced character matrix, suggesting that the characters used are critical to this result. Related to this point is that in the bootstrap analyses of all datasets including *Equatorius*, early to middle Miocene taxa (*Proconsul*, *Afropithecus*, *Equatorius*, *Kenyapithecus*, and *Morotopithecus*) could not be linked in >50% of the replicates to any derived taxa. This was also true of some later Miocene taxa (*Lufengpithecus* and *Oreopithecus*). This result likely reflects the effect of breaking a samplewise well-represented “*Kenyapithecus*” into two partially overlapping genera, and demonstrates that choice of characters (here randomly chosen by the bootstrap analysis algorithm) can seriously affect the robusticity of phylogenetic results.

Discussion

The phylogenetic positioning of *Morotopithecus* in all of the analyses suggests it is a primitive member of the great ape clade, and not a more primitive sister taxon of the crown hominoid clade as previously suggested (Gebo et al., 1997; MacLatchy et al., 2000). However, *Morotopithecus* is dated at >20.6 Ma, while inferences derived from molecularly-derived trees and calibrated using fossil dates indicate later dates for the branching of gibbons from the other hominoids: 14.3 Ma (Kumar & Hedges, 1998), 14.9 Ma (Stauffer et al., 2001), 17.4 Ma (Sibley et al., 1990), 17.8 Ma (Caccone & Powell, 1989), or 18 Ma (Goodman et al., 1998). Thus, even the oldest date for the hylobatid split (18 Ma) is significantly younger than *Morotopithecus*. Below are several possible explanations.

Scenario 1: the phylogenetic position of Morotopithecus is correct but the dating of the specimens is too old

Early radiometric dates for Moroto localities I (the scapula site) and II (the femur/vertebrae/palate site) estimated ages of older than 12–14 Ma (Bishop et al., 1969), while faunal comparisons yielded an estimate of 17.5 Ma (Pickford et al., 1986). Basalt samples stratigraphically overlying the fossil sediments collected in 1995 were analyzed to reveal a significantly older date, that of >20.6 Ma (Gebo et al., 1997). This older date has not been accepted by Pickford and co-workers who have recently revised their faunal estimates for both Moroto I and II to between 15 and 17 Ma (Pickford et al., 1999). While we recognize that the Moroto II lava sample was weathered and revealed disturbed argon systematics in the initial steps, it settled to a plateau-like release with an age of 20 Ma. In addition, the Moroto I lava sample was characterized by a single apparent age plateau across the entire gas release (Gebo et al., 1997). Thus, we think the radiometric dating to be very strongly supported, and that the absolute faunal dates (which consider Moroto I and II to be equivalent in age) need to be reevaluated.

Scenario 2: the Hylobates divergence date based on fossil-calibrated molecular clock estimates has been underestimated

As mentioned previously, numerous genetic analyses show that the split of the hylobatids from the other extant hominoid lineages occurred from anywhere as early as 14 Ma to as late as 18 Ma (mean 15.4 Ma) (Fig. 8) (Caccone & Powell, 1989; Sibley et al., 1990; Goodman et al., 1998; Kumar & Hedges, 1998; Stauffer et al., 2001). Most of these dates were calculated by calibrating the hominoid–cercopithecoid divergence at 23–25 Ma, and thus are predicated on the accuracy of this estimate. This calibration point is sometimes justified by its approximation of the Oligocene–Miocene boundary (e.g., Stauffer et al., 2001), but more often the date results from rounding up the date of the oldest hominoid or cercopithecoid (e.g., Caccone & Powell, 1989). *Proconsul* is typically cited as the

oldest hominoid, but the stratigraphically oldest site where it occurs is Meswa Bridge (Andrews et al., 1981), which is not securely dated radiometrically, although it is probably older than 20 Ma. The next oldest *Proconsul* sites are Songhor and Koru at 19.5 Ma. *Kamoyapithecus*, a late Oligocene catarrhine, is radiometrically dated at 24–27.5 Ma (Boschetto et al., 1992) but its hominoid affinities are uncertain (Leakey et al., 1995). The oldest cercopithecoid, *Victoriapithecus/Prohylobates* is from Napak (~19 Ma), but it is not securely dated (radiometric dates range from 6.7 to 30+ Ma (Bishop et al., 1969)). The next oldest specimens come from Buluk (>17 Ma, radiometric date (Leakey, 1985)) and Wadi Moghara (17–18 Ma, faunal date (Miller, 1999)). This leaves *Morotopithecus* as the best dated and oldest undoubted hominoid or cercopithecoid at >20.6 Ma.

However, because the middle and late Oligocene record is so fossil poor, it is wise to use other calibration points to test this estimate since we have no way of knowing if the hominoids diverged 1, 5 or 10 Ma prior to *Morotopithecus*. Using widely accepted paleontological calibration points for early eutherian mammals of ca 100 Ma, a number of studies have converged on a hominoid–cercopithecoid divergence of ~20–25 Ma (Dene et al., 1976; Sarich & Cronin, 1976; Bailey et al., 1991; Goodman et al., 1998). Nei & Glazko (2002) calculated a date of 23.5 Ma using the divergence of primates and artiodactyls at 90 Ma as a calibration point. Kumar & Hedges (1998) interpolated a divergence time of 23 Ma using a combination of much older calibration points for birds and mammals (310 Ma) and cite the correspondence to the Oligocene–Miocene epoch boundary as support for the overall goodness of fit of this estimated date.

The 23–25 Ma calibration date for the divergence time of hominoids and cercopithecoid monkeys is therefore compatible with the fossil record, and is supported by genetic-based interpolations using early mammalian calibration points, as well as with the Kumar & Hedges (1998) estimate of 23 Ma using a much older calibration point for mammals and birds. Estimates for the *Hylobates* divergence fall within the range of 14 to 18 Ma,

Ma	Caccone & Powell (1989)	Sibley <i>et al.</i> (1990)	Goodman <i>et al.</i> (1998)	Kumar & Hedges (1998)	Stauffer <i>et al.</i> (2001)
6	Chimp	Chimp	Chimp Gorilla	Chimp Gorilla Orangutan	Chimp Gorilla
8	Gorilla	Gorilla			
10					Orangutan
12	Orangutan	Orangutan	Orangutan	Gibbon	Gibbon
14					
16					
18	Gibbon	Gibbon	Gibbon		
20	<i>Morotopithecus</i>	<i>Morotopithecus</i>	<i>Morotopithecus</i>	<i>Morotopithecus</i>	<i>Morotopithecus</i>
22				OWM	*OWM
24	*OWM	*OWM	OWM		
26					
63			*Primates		
310				*Birds-Mammals	

Fig. 8. Timing of splitting events in hominoid evolution from multiple datasets.

which would support *Morotopithecus*' appearance before *Hylobates* diverged.

There is reason to be cautious however. It is important to note that the analyses cited in Fig. 8 estimate the chimpanzee-hominid divergence at between 5.4–6.0 Ma with a mean of 5.6 Ma, a date that is younger than the earliest probable hominid *Sahelanthropus* dated at between 6–7 Ma (Brunet *et al.*, 2002). We tested whether this difference has an effect on the timing of the *Hylobates* divergence by recalibrating the Fig. 8 datasets using a hominid divergence time of 7 Ma (Fig. 9). The recalculated divergence times for *Hylobates* range from 18.5–22.0 Ma with a mean of 20.5 Ma and suggest a scenario in which *Hylobates* diverged before

Morotopithecus cannot be definitively ruled out, especially when errors are included.

Two points should be emphasized here. First, older *Hylobates* divergence times push back the hominoid–cercopithecoid split to between 29–31 Ma (mean 30.1 Ma). Second, if we accept the earlier dates derived from the 7 Ma hominid calibration, the range of errors indicates it is impossible to distinguish with certainty whether *Hylobates* divergence estimates predate or post-date *Morotopithecus*.

In sum, current genetic-fossil tree calibrations suggest that hylobatids diverged close to the divergence time of *Morotopithecus*, and too close to determine exact branching order with confidence.

Ma	Caccone & Powell (1989)	Sibley <i>et al.</i> (1990)	Goodman <i>et al.</i> (1998)	Kumar & Hedges (1998)	Stauffer <i>et al.</i> (2001)
6	*Chimpanzee	*Chimpanzee	*Chimpanzee	*Chimpanzee	*Chimpanzee
8			Gorilla	Gorilla	Gorilla
10	Gorilla	Gorilla		Orangutan	
12					
14					
16	Orangutan	Orangutan	Orangutan		Orangutan
18				Gibbon	
20					Gibbon
22	<i>Morotopithecus</i> Gibbon	Gibbon/Moroto	Gibbon/Moroto	<i>Morotopithecus</i>	<i>Morotopithecus</i>
24					
26					
28					
30			OWM	OWM	
32	OWM	OWM			OWM

Fig. 9. Recalibration of genetic datasets using a hominid divergence time of 7 Ma.

But we are cognizant that future fossil finds and/or more genetic data could make choosing between alternatives easier. Regardless, *Morotopithecus*' basal location in hominoid evolution indicates that both a reassessment of *Hylobates* postcranial primitiveness and of the earliest appearance of some aspects of the great ape ancestral morphotype is warranted.

Scenario 3: the hylobatid condition is not primitive for hominoids

The basal location of *Morotopithecus* relative to the splitting of the hominoid lineages yields interesting implications for the reconstruction of

ancestral hominoid morphotypes. For example, *Hylobates*' morphology is often considered to be primitive for the hominoids (e.g., Tuttle, 1975; Moyà-Solà & Köhler, 1996; Begun *et al.*, 1997). But if *Morotopithecus* is older than or broadly contemporary with the hylobatid divergence, and its similarities are homologous with the great apes, then *Hylobates*' morphology would likely not be reflective of the ancestral hominoid morphotype unless following a large-bodied stage all apes passed through a small-bodied brachiator phase and then reevolved large body size. The alternative is that hylobatids are dwarfed versions of a large-bodied ancestor. This might be supported if large-bodied siamangs are reflective of the primitive

crown hylobatid form (Groves, 1972). However, analyses of multiple independent genes demonstrate siamangs are not the first crown hylobatid to diverge (Zehr, 1999).

Hylobates as an autapomorphic lineage is not a new proposition. For example, Cartmill (1985) noted that the wrist morphology and disproportionate forelimb elongation of hylobatids may be a result of specialization for acrobatic locomotor habits, and that the widespread distribution of ape-like anatomical traits in slow-climbing arboreal mammals suggests brachiation may not be primitive for hominoids. Shea (1986) argued that the narrow hylobatid scapula is not primitive but rather a secondary adaptation for quick movement overlain on a hominoid-wide ability to circumduct at the shoulder while suspending. A reanalysis of putative derived postcranial characteristics of the hominoid postcranium also supports a scenario in which *Hylobates* is specialized, demonstrating that it is morphologically divergent compared to the great apes (Young, 2003). Small body size and some morphological features of hylobatids could be interpreted as secondarily-derived adaptations related to moving quickly through the canopy. The primitive condition for apes may then be closer to a larger-bodied, slow-moving, and more cautious arboreal suspensor (Gebo et al., 1997).

Scenario 4: the similarities of Morotopithecus and great apes are homoplasies

The postcranial similarities of *Morotopithecus* to the great apes suggest the possibility that the ancestral hominoid morphotype was more great ape-like in the shoulder and lower back. These similarities are interpreted by some as hominoid synapomorphies representing either a past (e.g., in the gorilla) or present dependence on orthogrady and suspension (Sarmiento, 1987; Pilbeam, 1996, 1997). However, others have questioned whether the postcranial similarities of living apes are indeed homologous (Begun, 1992, 1993; Begun et al., 1997; Larson, 1998). Until the description of *Proconsul* postcrania in the 1960s it was assumed that the common ancestor of living apes was postcranially ape-like rather than monkey-like (Tuttle, 1975). That is, it was a suspensory form

with many adaptations of the torso (broad and shallow thorax, short lumbar region, wide pelvis) and limbs (long and limber) for hanging and swinging below branches (Walker, 1997). With additional discovery came the recognition that *Proconsul* is non ape-like (Rose, 1993, 1994), and the idea that at least some hominoid postcranial features evolved in parallel became more common. But current interest in parallelism among the great apes stems primarily from the recovery of material attributed to *Sivapithecus*, a fossil ape that shares a number of derived facial features with *Pongo* and suggest a close phylogenetic link (Pilbeam et al., 1980). However, *Sivapithecus* lacks critical suspensory features in its postcranium, suggesting it is not related to the crown hominoid radiation (Pilbeam, 1996).

Because the facial similarities of *Sivapithecus* and *Pongo* are generally considered to be homologies (but see Pilbeam [1996] for a cautionary view), similarities in the hominoid postcranium have been increasingly interpreted as parallelisms. For example, Larson (1998) argued that within-hominoid postcranial variability and overlap with ateline and non-suspensory primate genera was supportive of homoplasy. Begun (1993) argued living hominoid similarities could be parallelisms based on his analysis of *Dryopithecus* phalangeal morphology. If some of the suspensory features that unite hominoids are indeed homoplastic, *Morotopithecus* must have evolved its suspensory features independently of the other apes. However, it has not been demonstrated that the features which link *Morotopithecus* to the great apes are homoplastic in the living apes. Analyses investigating the homology of great ape postcranial similarities are needed to help clarify this problem.

Which scenario?

The first scenario is unlikely. The first appearance of *Morotopithecus* is well-supported by radiometric dating. The second scenario is also unlikely, however it cannot be definitively ruled out until better calibration dates are available. Which of the two remaining scenarios is the best explanation of our results? One method for discriminating this

type of question is an *a posteriori* character analysis of phylogenetic results (Lauder, 1994). However, our results reveal several important caveats that make choosing between the alternative scenarios problematic.

Despite consistencies in our results, factors such as the use of different character descriptions for the same anatomy, the presence or absence of characters, and the use of different subsets of data did have an effect. These factors are not uncommon and likely affect every analysis that includes fossil taxa and/or analyzes hard-tissue morphology (Sarich, 1993; Pilbeam, 1996). Indeed, disagreement about character choice is standard practice in morphological phylogenetics (Kluge, 1983; Schwartz, 1984; Andrews & Martin, 1987; Groves, 1986; Cartmill, 1994; Collard & Wood, 2000), and, as Cartmill (1982) has empirically demonstrated for a primate case, these choices can lead to very different phylogenetic conclusions. These facts raise important questions about the criteria used to select and discriminate among characters, and on the robustness of conclusions derived from phylogenetic analyses that include partially-represented fossil material.

Results from the analysis of *Morotopithecus* confirm the effect of character choice on phylogenetic results. In analyses 1a, 2a, and 3a only ~8–10% of the characters were changed in order to reflect alternative character choices. These relatively small changes were enough to affect the positioning of two taxa: *Lufengpithecus* and *Ouranopithecus*. Importantly, these changes were consistent with differences in the choice of characters between the original datasets (i.e., unaltered Begun et al., Moyà-Solà & Köhler, and Cameron). For example, Begun et al. and Moyà-Solà & Köhler describe the nasoalveolar region with different characters (Fig. 10), and the phylogenetic tree supported by these characters is different. Begun et al.'s characters support a *Sivapithecus*–*Pongo* clade with *Dryopithecus* linked to African apes and humans, whereas Moyà-Solà & Köhler's characters support a *Pongo* clade including *Sivapithecus*, *Lufengpithecus* and *Dryopithecus*.

An alternative interpretation of these results might be that differences were confined to two poorly known taxa, whereas other taxa are more

consistently located. A case in point is *Dryopithecus*, which is sister taxon to the African apes in all analyses even though the alternative characters came from datasets that support its inclusion in the *Pongo* clade. *Ouranopithecus* and *Lufengpithecus* are represented by very limited fossil material compared to *Dryopithecus* and correspondingly have fewer characters described (87 and 83 characters, respectively, compared to 147 in *Dryopithecus*) (Begun et al., 1997). Consequently, replacing characters will have a larger effect on those taxa that are not as “character rich”, even if the total number of characters replaced is small. For example, in Analysis 2a, ten characters were added, and 19 were removed. Of the 87 characters represented in *Ouranopithecus*, 16 were changed (=18.4%). In contrast, 16 *Dryopithecus* characters were changed out of 147 (=10.9%). This result would seem to indicate that increased fossil representation is the answer to increasing the reliability of phylogenetic results.

But there is reason to believe this is not a complete solution. First, although more fossil material would help, examples from better-represented fossil groups suggest that it is no panacea. Hominids are well-sampled (Klein, 1999), particularly relative to their true abundance in the total fauna (Behrensmeyer, 1976), yet there are still significant debates involving phylogeny that ultimately can be tied to differences in how characters are described and selected (Lieberman et al., 1996; Strait et al., 1997). Even in essentially “perfect” samples of extant taxa there are significant debates. For example, disagreement about the relationships of extant hominoids based on morphological characters is well-documented (Schultz, 1930; Simpson, 1963; Kluge, 1983; Schwartz, 1984; Groves, 1986; Andrews & Martin, 1987). Although molecular analyses (e.g., Ruvolo, 1997) eventually proved one of the “contenders” correct (i.e., Groves, 1986), and others have followed with morphological datasets congruent with this result (e.g., Begun et al., 1997), the inability to reach a consensus illustrates the lack of tools for deciding which characters give the “true” signal (i.e., homology). This is especially difficult problem in fossil analyses where the “true” phylogeny can never be known for certain.

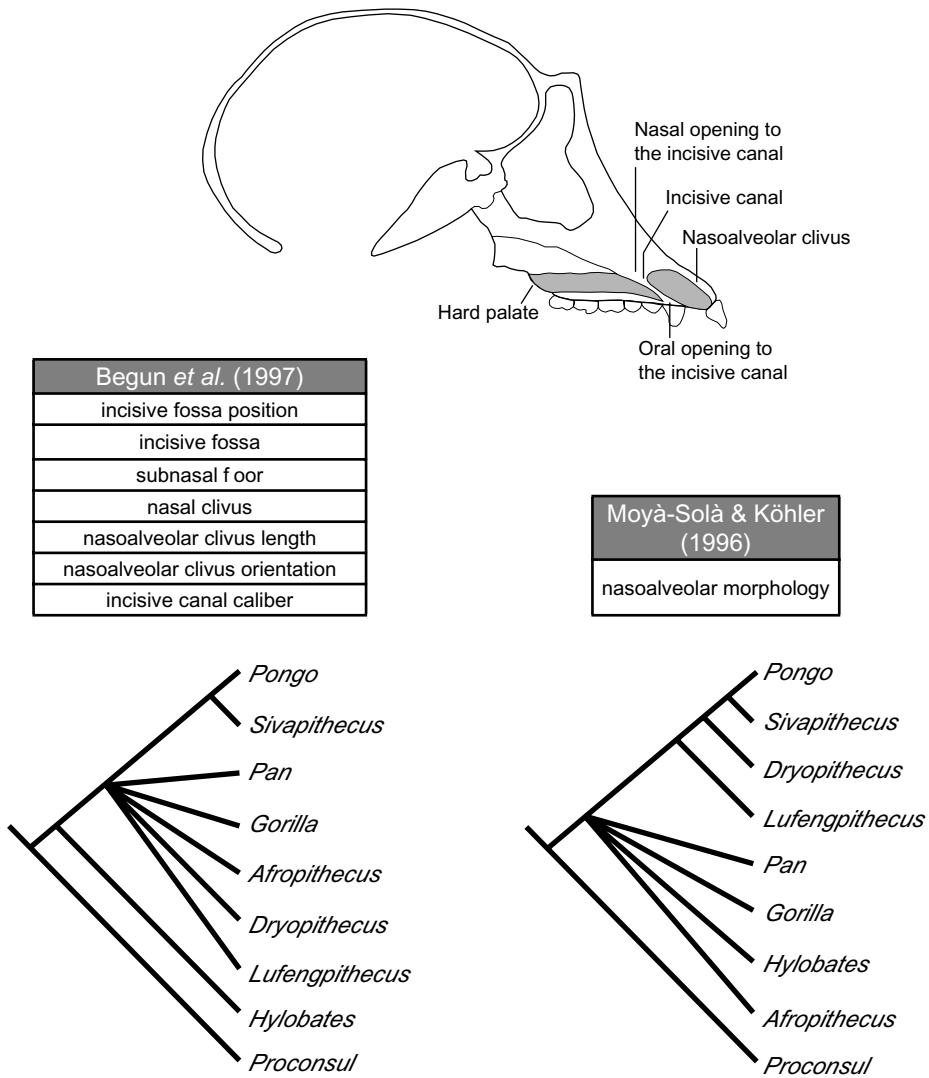


Fig. 10. An example of the effect of alternative descriptions of morphology on phylogenetic results. Begun *et al.* (1997) describe the nasoalveolar region (diagram shown at top) with seven characters, whereas Moyà-Solà & Köhler (1995) describe the same anatomy with one character. These characters support different phylogenetic trees (shown at bottom). Top illustration modified from Kelley (1992).

A second important point is that differences between our analyses stem from more than fossil representation, but also the number of characters described in the original datasets. Characters from Begun *et al.*'s analysis outnumber those of Moyà-Solà & Köhler and Cameron by roughly 20 to 1. Any signal from Begun *et al.* will therefore tend to swamp those of the smaller datasets. Despite this

disparity, analyses 1a, 2a, and 3a show that even small disagreements about character description can lead to different phylogenies. *Dryopithecus* is represented by more characters in Begun *et al.* than for Moyà-Solà & Köhler so it is not surprising that there is little change in its position despite important differences in opinion. This then brings up the question of whether larger datasets should

be trusted more just because they are larger. In other words, how many characters should be used in a phylogenetic analysis, and which ones?

This question takes on special importance here because a critical factor in deciding between alternative scenarios is whether the postcranial similarities of *Morotopithecus* and living apes represent a “true” phylogenetic signal. Analysis 4 demonstrates that when only postcranial characters are included, there are major changes in how the tree is structured: *Oreopithecus* is always more derived than either *Dryopithecus* or *Sivapithecus*, and *Sivapithecus* is not paired with *Pongo*. This character conflict has been noted before (Ward, 1997; Pilbeam, 1997; Pilbeam & Young, 2001). Although postcranial and craniodental characters are equally represented in the Begun et al. dataset, it is easy to imagine how reducing or increasing characters in one region or another could seriously alter the results (e.g., a dataset that emphasizes craniodental over postcranial will give much different results than vice versa).

Analyses 1b, 2b, and 3b demonstrate that a similar effect occurs when using only those characters represented in a fossil to generate phylogenetic results. Although compared to Analyses 1–3a the positioning of *Morotopithecus* does not radically change with respect to *Hylobates* and the great apes, there are notable changes in the positioning of *Afropithecus* (sister to *Hylobates* in half the analyses), *Kenyapithecus* (more derived than *Hylobates*), and *Dryopithecus* (sister to the African apes in 1b, and sister to the great apes in 2b and 3b). This suggests that representation of a fossil taxon can seriously affect one’s results.

Together these analyses show how different characters or subsets of data can produce different phylogenetic results. Unfortunately, few objective criteria have been put forward for determining which character description or type of character is more likely to be phylogenetically reliable (Lieberman, 1999; Lovejoy et al., 1999). Ultimately, our inability to assess the likelihood of character homology or homoplasy *a priori* compromises *a posteriori* analyses. Because it is unclear at this time which characters are homologous or homoplastic we are therefore unable to choose with confidence one scenario over another.

Conclusions

Phylogenetic analyses of new and previously discovered material attributed to *Morotopithecus* suggest that it is a primitive member of the great ape clade. This finding is consistent even with the use of alternate character descriptions, with postcranial characters only, or with characters found in *Morotopithecus* only. However, this finding is inconsistent with the dating of *Morotopithecus* at >20.6 Ma, and the molecular estimates of the divergence of hylobatids at 18 Ma or less. Thus, a pre-hylobatid phylogenetic position for *Morotopithecus* cannot be ruled out. Instead, this result suggests that some aspects of the great ape condition may have evolved much earlier than previously thought. If great ape similarities found in *Morotopithecus* are homologous, *Morotopithecus* may be a better representative of the ancestral morphotype of the hominoids than *Hylobates*. An alternative is that postcranial similarities between great apes and *Morotopithecus* are the result of homoplasy.

However, deciding between these scenarios is made difficult by our lack of tools for assessing the phylogenetic reliability of different characters, types of characters, or even character descriptions. This problem manifests itself in the multiple characters available to describe the same anatomy, and leads to a lack of robusticity in phylogenetic results. As has been shown in other fossil and living taxa (e.g., Lieberman et al., 1996; Strait et al., 1997), Miocene hominoids are sensitive to all of these factors. *Proconsul*, *Afropithecus*, *Kenyapithecus*, and *Lufengpithecus* were sensitive to the inclusion of *Morotopithecus* and the addition of new postcranial characters. *Lufengpithecus* and *Ouranopithecus* were sensitive to the use of alternate character descriptions taken from published datasets. *Sivapithecus* and *Dryopithecus* were sensitive to the use of only postcranial characters. And *Dryopithecus*, *Lufengpithecus*, *Kenyapithecus* and *Afropithecus* were sensitive to the use of only those characters represented in *Morotopithecus*.

These results reconfirm that character selection can play a large role in phylogenetic analyses (Cartmill, 1982, 1994), and with the Miocene hominoids in particular (Pilbeam, 1996, 1997).

Either because of methodological reasons such as poor character description, or because of biological reasons such as homoplasy, not all alternative character descriptions of anatomy are of equal phylogenetic value (Lieberman, 1999; Collard & Wood, 2000). Unfortunately, it is not clear which characters give the *right* answer for the *right* reasons because there are no criteria for selecting one morphological character over another (Pilbeam, 1996). Although the characters used in our analyses consistently support a single position for *Morotopithecus*, depending on how the dataset is arranged the conclusions concerning relationships of other Miocene taxa are either different or weakened. This creates doubt about our ability to assess which characters portray a “true” signal of homology and consequently which scenario is more likely. Determining whether *Morotopithecus* represents an early example of rampant postcranial parallelism or the earliest appearance of a suspensory ancestral ape body-plan will therefore require a better understanding of how to distinguish morphological homoplasy from homology.

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Appendix A.

New postcranial characters, states, and distribution in primates

Character		State	Condition present in
Glenoid curvature	0	glenoid is very curved craniocaudally and flatter dorsoventrally	all primate quadrupeds, <i>Pliopithecus</i>
	1	glenoid is moderately and uniformly curved along both craniocaudal and dorsoventral axes	all extant hominoids, <i>Ateles</i> , <i>Oreopithecus</i> , <i>Morotopithecus</i>
Size of femoral head relative to mid shaft diameter	0	small	primitive catarrhines, including <i>Proconsul</i> and <i>Morotopithecus</i>
	1	expanded	living apes, <i>Dryopithecus</i>
Presence of hypotrochanteric fossa	0	absent	gibbons, <i>Morotopithecus</i>
	1	present	great apes, <i>Dryopithecus</i>
Linea aspera ridge up to or above lesser trochanter	0	absent	gibbons, <i>Morotopithecus</i> , <i>Dryopithecus</i>
	1	present	great apes
Buttressing of intercondylar notch	0	no buttressing	gibbons, <i>Proconsul</i>
	1	buttressing	<i>Sivapithecus</i> , <i>Dryopithecus</i> , <i>Morotopithecus</i> , great apes
Popliteal groove	0	shallow	gibbons, <i>Proconsul</i>
	1	deep	<i>Sivapithecus</i> , <i>Morotopithecus</i> , great apes
Gluteal ridge	0	absent	gibbons
	1	present	<i>Morotopithecus</i> and great apes

Character	State	Condition present in
Distal femur shaft shape	0 round	gibbons and <i>Proconsul</i>
	1 AP flattened	great apes, <i>Dryopithecus</i> , <i>Morotopithecus</i>
Ventral keeling	0 present	<i>Proconsul</i> and cercopithecoids
	1 absent or reduced	all living apes, <i>Morotopithecus</i>
Spooling of lumbar centrum	0 present	<i>Proconsul</i> and cercopithecoids
	1 absent or reduced	all living apes, <i>Morotopithecus</i>
Hollowing of lumbar centrum	0 present	<i>Proconsul</i> and cercopithecoids
	1 absent or reduced	all living apes, <i>Morotopithecus</i>
Spinous process inclination	0 cranially inclined	<i>Proconsul</i> and cercopithecoids
	1 caudally inclined	all living apes, <i>Morotopithecus</i>
Transverse process inclination	0 ventrally inclined	<i>Proconsul</i> and cercopithecoids
	1 neutral	gibbons and <i>Ateles</i>
	2 dorsally and caudally inclined	great apes, <i>Morotopithecus</i>

Appendix B.

Character state coding for Begun et al. (1997), Moyà-Solà & Köhler (1995), Cameron (1997), and postcranial characters

Dataset	Character	<i>Morotopithecus</i>	<i>Pan</i>	<i>Gorilla</i>	<i>Pongo</i>	<i>Hylobates</i>	<i>Proconsul</i>
Begun et al. (1997)	[1] glenoid shape	1	1	1	1	1	?
	[75] vertebral body height	2	2	2	2	1	0
	[76] accessory processes	2	2	2	2	1	1
	[77] transverse processes	2	2	2	2	1	0
	[85] trochanteric fossa	0	2	2	2	1	0
	[86] femoral head	1	2	2	2	2	1
	[87] femoral neck tubercle	0	1	1	1	0	0
	[88] femoral condyle depth	1	1	1	1	1	1
	[89] femoral condyle shape	2	2	2	2	0	1
	[122] incisors length	0	0	0	0	0	0
	[123] I2 (u) cingulum	0	1	1	1	0	0
	[124] relative male canine size	0	1	1	1	0	0
	[125] male canines	0	1	1	1	1	0
	[126] canine cingula	1	1	1	1	0	0
	[127] P3(u) cusp heteromorphy	1	1	1	1	0	0
	[128] P3(u) paracones	1	1	1	1	0	0
	[134] M2-3(u) metacones	0	1	1	1	0	0
	[137] anterior/posterior dentition	0	0	0	0	0	0
	[138] palatine process	1	1	1	1	0	0
	[139] alveolar premaxilla	0	1	1	0	0	0
	[140] incisive fossa position	0	2	1	1	0	0
	[141] maxillary sinus size	2	2	2	2	0	0
	[142] maxillary sinus floor	0	1	1	1	0	0
	[143] nasal aperture base	1	1	1	0	0	0
	[144] maxillary depth	1	1	1	1	0	0
	[148] nasal bones at nasion	1	1	1	1	0	0
	[156] facial profile	0	0	0	1	0	0
	[176] maxillary sinus/canine position	0	1	1	1	0	0
	[177] maxillary nasal process	0	1	1	1	0	0
	[178] orbital/nasal distance	2	1	0	1	1	0

Dataset	Character	<i>Morotopithecus</i>	<i>Pan</i>	<i>Gorilla</i>	<i>Pongo</i>	<i>Hylobates</i>	<i>Proconsul</i>
Begun et al. (1997)	[180] interorbital distance	0	0	0	1	0	0
	[185] nasal aperture breadth	1	0	1	1	0	0
	[186] nasal aperture/orbit position	2	2	0	2	2	0
	[187] nasal aperture/alveolar	0	1	1	1	0	0
	[190] nasal bone length	2	0	1	1	0	0
	[195] canine fossa	0	0	0	1	1	0
	[196] C(l) root angulation	0	0	0	1	0	0
	[197] C(l) root rotation	0	0	0	0	0	0
	[198] maxillary alveolar process	0	2	2	1	0	0
	[201] greater palatine position	0	1	1	1	1	0
	[203] horizontal palatine	1	1	1	1	0	0
	[206] pyramidal process position	0	1	1	1	0	0
	[207] pterygoid process	1	1	1	0	0	0
	[208] alveolar process depth	0	1	1	1	0	0
	[209] zygomatico-alveolar crest	1	1	1	0	0	0
	[210] zygomatic root height	0	1	1	1	0	0
	[211] incisive fossa	0	2	2	1	0	0
	[212] subnasal floor	0	1	1	2	0	0
	[213] nasal clivus	0	0	1	1	0	0
	[214] naso-alveolar clivus length	0	2	1	2	0	0
	[215] naso-alveolar clivus orientation	0	0	0	1	0	0
	[216] incisive canal caliber	0	3	2	4	0	0
	[217] mandibular canine roots	0	0	0	1	0	0
	[221] lower molar cingula	0	1	1	1	1	0
	[222] lower M1/M2 size ratio	0	1	1	1	0	0
	[223] lower M3/M2 size ratio	1	0	0	0	0	0
	[225] I2(u) morphology	0	1	0	0	0	0
	[226] upper canine height	0	0	0	0	0	0
	[227] upper canine cervical flare	0	0	0	0	0	0
	[228] P4(u) shape	0	1	1	1	0	0
	[229] P3(u) shape	0	0	0	0	0	0
	[230] premolar buccal flare	1	0	0	0	0	0
	[231] P4(u) lingual flare	1	1	0	0	0	0
[232] M1(u) shape	1	1	1	1	0	0	
[233] M2(u) shape	1	1	1	1	0	0	
[234] upper molar cingula	0	1	1	1	1	0	
[235] M1/M2(u) size ratio	1	1	1	1	1	0	
[236] upper molar crowns	0	1	1	1	0	0	
[237] upper molar sides	0	1	1	1	0	0	
[238] molar enamel	0	0	0	1	0	0	
[239] M3(u) size	0	1	0	1	1	0	
Moyà-Solà & Köhler (1995)	MSK 1	0	1	0	1	0	0
	MSK 2	0	1	1	2	0	0
	MSK 8	0	0	0	1	0	0
	MSK 11	1	1	1	1	0	0
	MSK 12	0	1	1	1	0	0
	MSK 16	0	0	0	1	0	0
	MSK 17	1	1	1	1	0	0
	MSK 18	0	0	0	0	0	0

Dataset	Character	<i>Morotopithecus</i>	<i>Pan</i>	<i>Gorilla</i>	<i>Pongo</i>	<i>Hylobates</i>	<i>Proconsul</i>
Moyà-Solà & Köhler (1995)	MSK 19	0	1	1	1	0	0
	MSK 20	0	1	0	1	0	0
Cameron (1997)	CAM 7	0	0	0	2	?	?
	CAM 14	1	0	1	0	?	?
	CAM 15	1	1	1	1	?	?
	CAM 19	2&3	3	3	1	?	?
	CAM 20	0	0	0	1	?	?
	CAM 21	0	2	2	3	?	?
	CAM 22	1	2	2	1	?	?
	CAM 24	0	2	2	2	?	?
	CAM 27	0	1	1	1	?	?
	CAM 28	0	0	0	0	?	?
	CAM 29	0	0	0	1	?	?
	CAM 30	1	0	0	2	?	?
	CAM 31	0	2	2	2	?	?
	CAM 32	0	0	0	0	?	?
	CAM 33	0	1	0	1	?	?
	CAM 34	2	0	0	1	?	?
	CAM 35	1	1	1	1	?	?
	CAM 36	1	1	1	1	?	?
	CAM 37	0	1	1	1	?	?
	CAM 38	1	1	1	2	?	?
CAM 39	1	0	1	0	?	?	
Young & MacLatchy	glenoid curvature	1	1	1	1	1	?
	fem head/mid shaft	0	1	1	1	1	0
	hypotrochanteric fossa	0	1	1	1	0	?
	linea aspera	0	1	1	1	0	?
	intercondylar notch	1	1	1	1	0	0
	popliteal groove	1	1	1	1	0	0
	gluteal ridge	1	1	1	1	0	?
	distal shaft shape	1	1	1	1	0	0
	ventral keeling	1	1	1	1	1	0
	lumbar centrum/spooling	1	1	1	1	1	0
lumbar centrum/hollowing	1	1	1	1	1	0	
spinous inclination	1	1	1	1	1	0	
transverse inclination	2	2	2	2	1	0	

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