Primate evolution – in and out of Africa

Caro-Beth Stewart* and Todd R. Disotell†

A synthetic analysis of molecular, fossil and biogeographical data gives a remarkably consistent scenario for the evolution of the catarrhine primates – the hominoids and Old World monkeys. This analysis supports the African location of the common ancestor of the Old World monkeys, and suggests that the Asian colobine monkeys and macaques dispersed out of Africa into Eurasia within the past ten million years. More interestingly and controversially, this analysis further suggests that the lineage leading to the living hominoids dispersed out of Africa about twenty million years ago, and that the common ancestor of the living African apes, including humans, migrated back into Africa from Eurasia within about the past ten million years.

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

Current Biology 1998, 8:R582–R588
http://biomednet.com/elecref/09609822008R0582

Introduction

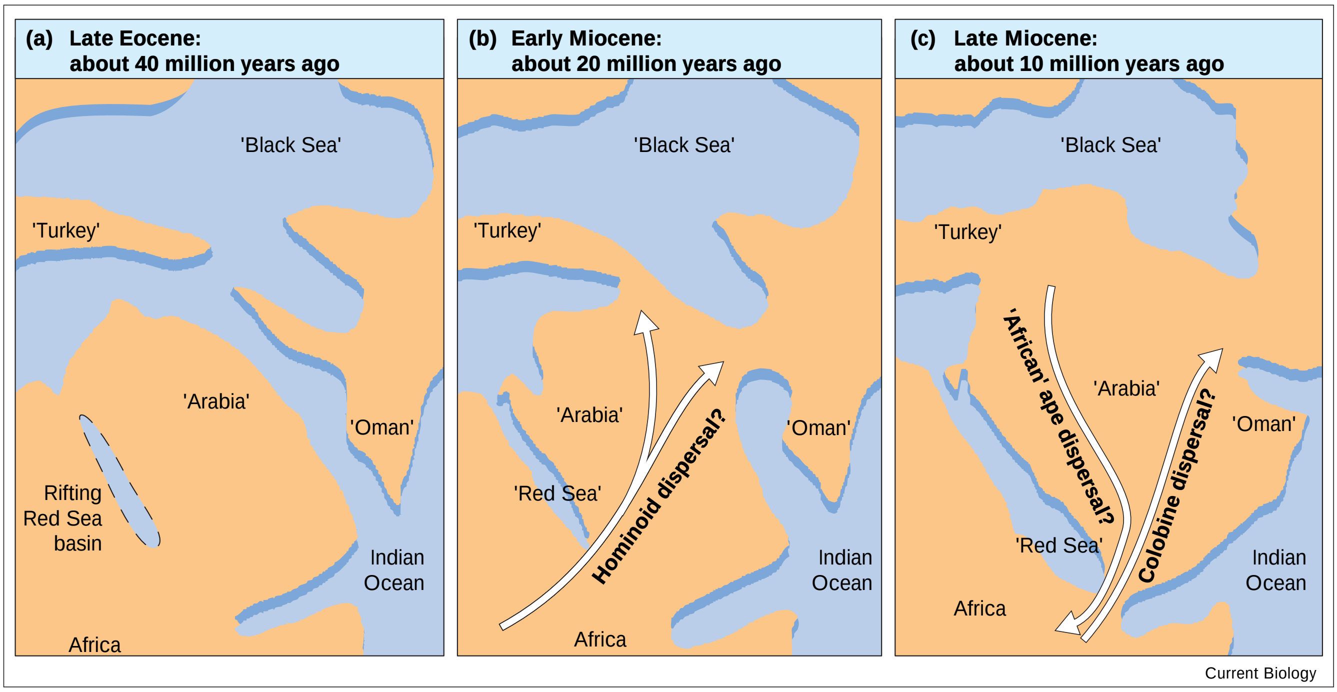
The hominoids — apes and humans — and Old World monkeys are collectively named the catarrhine primates. Today, with the exception of humans, the catarrhines are native to Africa and southeastern Asia, but the fossil record indicates that apes and monkeys were also present in Europe and western Asia during the Miocene, from about 5 to 17 million years ago [1,2]. The African and Eurasian land masses have often been separated by water, which imposes a barrier to dispersal of land mammals. Furthermore, northern Africa and southwestern Asia have sometimes had, as they have now, a desert-like environment that is unsuitable for forest-dwelling species. The exact times, locations and environments of the various land bridges between Africa and Eurasia are still under debate (see Figure 1), but it is clear that the catarrhines must have moved between the two land masses several times during evolutionary history to account for both their genetic relationships and geographical distributions. Despite many years of study by scientists from diverse disciplines, the geographical origins, dispersal patterns and evolutionary histories of the catarrhine primates remain controversial [1–4].

As discussed here, however, we find that recent parsimony analyses of key catarrhine fossils, numerous molecular phylogenetic studies and the geographical distributions of the species can be integrated to give a consistent scenario for the evolutionary history of this group. The well-dated phylogeny that emerges provides a powerful framework for the study of the rate and mode of molecular evolution in the primates (see [5], for example). Such a phylogeny is necessary for a correct evolutionary interpretation of the vast amounts of sequence data that are being generated by the human genome project, for only in this context can we identify those genetic changes that are uniquely human.

Phylogenies and fossils

The genetic relationships among the living hominoids have been the subject of numerous molecular studies over the past 30 years, and the branching order of the genera is now known with statistical certainty (see [6] and references therein). Recent DNA sequencing studies (see [5,7–10], for example) have focused upon resolving the genetic relationships among the major lineages of Old World monkeys. However, a complete evolutionary tree, or phylogeny, includes both the branching order and times of divergence of the species. Estimation of divergence dates within molecular phylogenies requires external calibration of the rate of molecular evolution, typically through interpretation of a few key fossils from the group of interest. From the early catarrhine fossil record (see

Figure 1



Potential contacts between Africa and Eurasia during the past 40 million years, based upon geological and faunal evidence (after [28,29]). **(a)** Late Eocene, approximately 40 million years ago. The Tethys seaway prevents migration between Africa and Eurasia. Uplifting in the western region of the Arabian peninsula coincides with the rifting of the future Red Sea. **(b)** Early Miocene, approximately 20 million years ago. The Red Sea begins to form, while potential land bridges exist between Africa and Eurasia. **(c)** Late Miocene, approximately 10 million years ago. The Red Sea continues to grow, and potential connections between Africa and Eurasia exist along the Indian Ocean margin.

below), the date of divergence of the Old World monkey and the hominoid lineages has often been estimated to be about 25 to 30 million years ago [11,12].

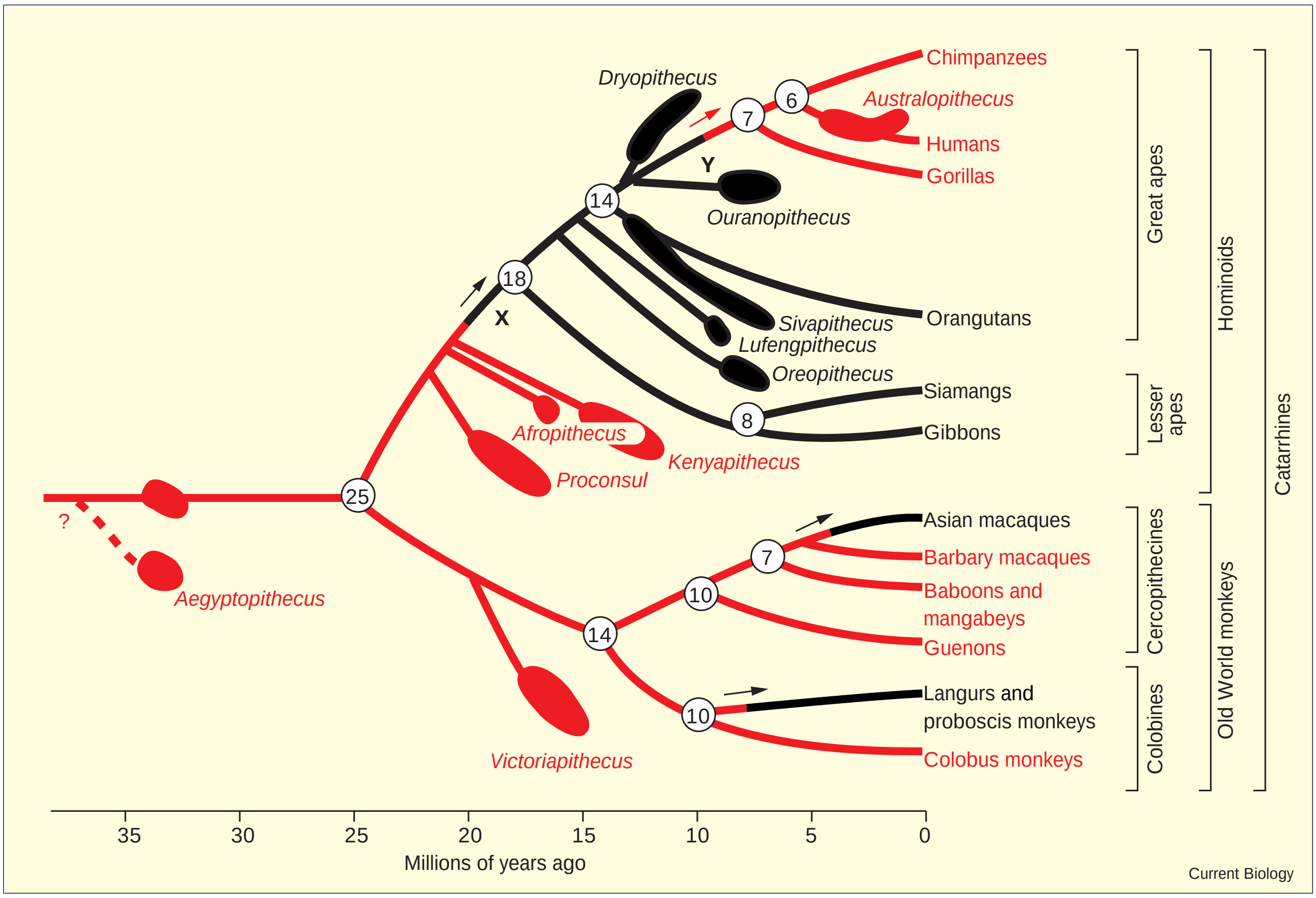
In the past, the presumed phylogenetic relationships of fossil primates have been based primarily on the informed opinions of paleoanthropologists; even the most thorough studies typically applied cladistic analysis of selected morphological characters by hand, without computer-assisted searches for most-parsimonious trees — those trees that require the fewest evolutionary events to explain the data — or quantitative comparison of competing hypotheses [13]. Some paleoanthropologists have begun to present their data matrices, to explicitly state their assumptions and to adopt computer-assisted phylogenetic analysis [4,11,13–15], as routinely done by other evolutionary biologists [16]. Such explicit presentation is needed, as the scoring of morphological characters is often quite subjective, and assumptions can influence the outcome. Furthermore, as fossils are fragmentary, their placement in trees is based on comparatively few morphological characters.

Several recent papers [4,11,14,15] present the most explicit and rigorous analyses to date of the phylogenetic positions of extinct catarrhine species. Most notably, Begun *et al.* [4] have collaborated in tallying 240 morphological characters (both cranial and post-cranial) from the living hominoids, and then scored those characters present in the nine most complete hominoid fossil species available. (Approximately 20 other genera of Miocene fossil hominoids have been described [1], but the highly fragmentary nature of most of these fossils may preclude their use in meaningful phylogenetic analyses [2].) Begun *et al.* [4] then performed computer-aided parsimony analysis [17] on this large dataset to find most-parsimonious trees. Such computer-based analysis allows complete and objective evaluation of the data with respect to the numerous possible relationships of the living and fossil species, which cannot be done by hand.

A synthesis

We have synthesized these recent parsimony analyses of catarrhine fossils [4,11,14,15] with the molecular phylogenies of the living species [5–11,18], and find that the estimated dates of divergence are internally consistent (Figure 2). That is, using one fossil divergence date to calibrate a molecular clock yields divergence estimates compatible with other dates derived from the fossil record.

Figure 2



A synthetic hypothesis of catarrhine primate evolution. The branching order shown for the living species is well-supported by numerous molecular phylogenetic studies (for example [6–12,18,24,25]). We present the dates of divergence calculated by Goodman and colleagues [11], on the understanding that these are still rough estimates and more precise measurements are needed, especially for the Old World monkeys. The fossil species (genus names in italics) were placed on this tree by parsimony analyses of relatively large morphological datasets [4,11,14,15]. Known dates for fossils [1,2,21] are indicated by the thicker lines; these lines are attached to the tree as determined by the parsimony analyses, although the dates of the attachment points are our best guesses. Species found in Africa are in red and species found in Eurasia are in black. The continental locations of the ancestral lineages were inferred by parsimony using the computer program MacClade [30]. The intercontinental dispersal events required, at a minimum, to explain the distribution of the living and fossil species are indicated by the arrows.

We then mapped the geographical locations of the living and fossil species onto this evolutionary tree in the most-parsimonious way, allowing us to infer the geographical locations of the ancestral lineages, and therefore the minimum number of catarrhine dispersal events between the African and Eurasian land masses. (We exclude consideration of post-*Australopithecus* dispersals of the genus *Homo* out of Africa.) We shall briefly discuss this synthetic hypothesis and some of its implications for Old World monkey and ape evolution. We must note that the migration scenario for the hominoids that we present does not represent the consensus opinion of primatologists at this time, although some authors [3,4,19,20] have seriously considered similar scenarios.

Early catarrhines

The oldest fossil on the tree in Figure 2 is *Aegyptopithecus*, which is most-parsimoniously placed on the ancestral catarrhine lineage [11,15]. This fossil genus is African, and is found from about 33 to 34 million years ago. As *Aegyptopithecus* looks like an ancestral catarrhine, 34 million years ago has often been assumed to be the earliest possible divergence date for the lineages leading to the Old World monkeys and hominoids. But this would be true only if *Aegyptopithecus* were directly on the stem lineage leading to the living catarrhines. If, instead, *Aegyptopithecus* were a sister group to the real stem lineage, then it would attach to the lineage earlier than 34 million years ago and the divergence date of the Old

World monkey and hominoid lineages could be earlier. These two possibilities are illustrated in Figure 2 for *Aegyptopithecus*. This difficulty, however, applies to the use of any fossil for establishing the earliest possible divergence date of two lineages.

In contrast, establishing the latest date that two lineages could have diverged is theoretically straightforward: the age of a fossil that belongs on either descendant lineage sets the most recent date that the two lineages could have diverged. As an example, parsimony analysis [11] of fragmentary remains from the extinct east African monkey *Victoriapithecus* places this genus on the Old World monkey lineage after its divergence from the hominoid lineage, but before the divergence of the two major clades of extant Old World monkey species, the colobines and the cercopithecines (see Figure 2). This relationship was also proposed in the recent description of a beautifully-preserved cranium from *Victoriapithecus* [21]. Evidence exists for *Victoriapithecus* occurring from about 15 to 17 million years ago, but Old World monkey teeth, which have distinctive bilophodont molars, have been found that are about 19 million years old. Similarly, three African fossil genera —*Proconsul*, *Afropithecus* and *Kenyapithecus* — are placed on the early hominoid lineage by parsimony analysis [4,11]. *Proconsul* remains are found in deposits that are 17 to 20 million years old, with some possibly both younger and older. Taken together, the phylogenetic placements and dates of these fossils would mean that the Old World monkey and hominoid lineages must have diverged before about 20 million years ago.

The often-assumed catarrhine divergence date of 25 to 30 million years ago thus appears reasonable, although logically this date could be earlier or slightly later. Moreover, this time range is consistent with estimates derived from multiple genetic datasets calibrated by other catarrhine fossils. For example, using as calibration points the fossil-based dates of either the *Sivapithecus*–orangutan divergence (about 13 to 14 million years ago) or the cercopithecine–colobine divergence (about 14 to 15 million years ago) discussed below, analysis of multiple genetic datasets gives estimates ranging from 24 to 28 million years ago for the Old World monkey–hominoid split ([11,12] and our unpublished analyses). Additional fossils closer to this key divergence would help pin down this date; parsimony analysis of catarrhine biogeography (Figure 1) supports the view that such fossils will be found in Africa.

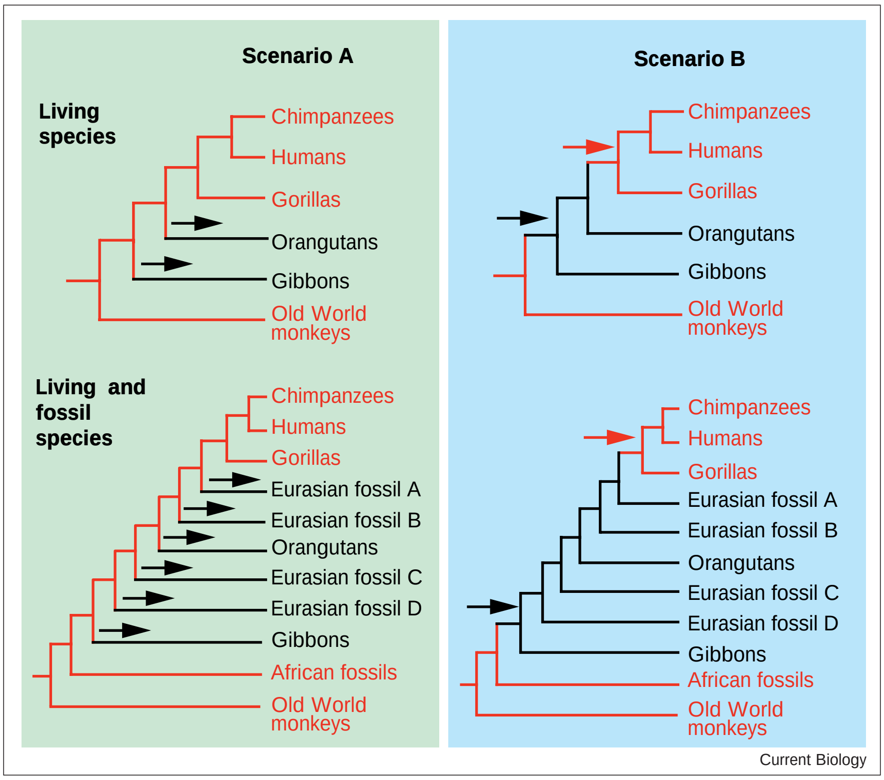
Old World monkeys

From the limited molecular data published for both the colobines and cercopithecines, their divergence date has been estimated to be about 14 million years ago [11]. This estimation is consistent with recent analysis of the *Victoriapithecus* materials [21] suggesting that the colobine–cercopithecine divergence was less than 15 million years ago. But as *Victoriapithecus* was probably a sister group to the living Old World monkeys [21], this date could be earlier. Determining the latest date for this divergence is also difficult, as virtually no Old World monkey fossils (or, indeed, appropriate African fossil beds) are known for the period between 10 and 15 million years ago. Nevertheless, the divergence of the colobines and cercopithecines must have occurred before 10 million years ago, as fossils of colobines (which have sharper bilophodont teeth than other Old World monkeys) have been found in Africa that are about this old [1,22].

Recent molecular studies [5,7,10] have shown that, contrary to some morphological interpretations [23], the Bornean proboscis monkeys branch with the other Asian colobines, and together form a clade with respect to the African colobus monkeys (Figure 2). The molecularly-estimated divergence date of the Asian and African colobine clades is about 10 million years ago [11]. The most-parsimonious explanation for colobine origins is that they first evolved in Africa, and then dispersed into Asia ([10]; Figures 1 and 2) less than 10 million years ago. Consistent with this inference, the fossil colobine species *Mesopithecus* appeared in Europe and western Asia by at least 8.5 million years ago (and perhaps as early as 10 million years ago) [1,22], and colobine fossils become relatively abundant in southern Asia by 7 million years ago [22]. Today, approximately 24 species of colobine monkeys are found in southern Asia.

There are several major lineages of cercopithecines, some of unresolved relationship [8,12]. The earliest divergence is probably between a clade composed of the cercopithecines (such as guenons, talapoins and green monkeys) and one composed of the papionins (such as macaques, baboons and mangabeys) [8,12]. This divergence has been estimated from molecular data to be about 10 million years ago [11]. Most living cercopithecine species, including the Barbary macaque, live only in Africa, although about 15 other species of macaques occur in southern and eastern Asia. Recent molecular studies [9,18] have confirmed that the Asian macaques form a clade with respect to the Barbary macaques (see Figure 2), as proposed by many morphologists. As with the colobines, the biogeographical analysis shown in Figure 2 suggests that the cercopithecines first evolved in Africa, and that the Asian macaque ancestral lineage dispersed out of Africa within the past few million years [18]. Again, the fossil record appears to be consistent with this logical inference; the earliest cercopithecine fossils known in the Eurasian fossil record are macaque-like and appear in Europe at about 5.5 million years ago (E. Delson, personal communication). Around this time, the Mediterranean Sea had dried up, allowing free passage of many land species.

Figure 3



Two dispersal scenarios for the hominoids, both assuming an African origin for the catarrhines. As in Figure 2, species found in Africa are in red and species found in Eurasia are in black, and arrows indicate the intercontinental dispersal events required to explain the distribution of the living and fossil species. Scenario A: separate dispersal events from Africa to Eurasia for each of the Eurasian hominoid clades. Scenario B: the common ancestor of all living apes dispersed out of Africa, and later the common ancestor of the modern African apes (gorillas, chimpanzees and humans) dispersed back into Africa. For just the living species (top trees), these two scenarios are equally parsimonious, in that each requires two dispersal events (arrows). When the fossil lineages shown in Figure 2 are included, scenario B is favored, as scenario A now requires a minimum of six independent dispersal events, whereas scenario B still requires only two (bottom trees). Note that the exact branching order of the Eurasian fossil species does not matter for this argument, so long as the fossils do not all branch with the gibbon or orangutan clades; we emphasize this by not naming the fossils in this figure.

Hominoids

These dispersal scenarios for Old World monkeys would not appear to be highly controversial, as most primatologists seem to accept the African origin of the Old World monkeys. The dispersal scenario that our synthetic analysis supports for the hominoids has, however, aroused vehement discourse, both in print and in dialogue, so we shall clearly outline our assumptions and reasoning. First, we assume that dispersals to and from Africa are equally likely events. Second, we take as a given the branching order of the living hominoids determined by molecular studies (Figure 2) [6]. Third, we assume an African origin for the ancestor of the living catarrhines, as suggested by the biogeographical analysis in Figure 2.

Given these assumptions, if one considers only the phylogeny and distribution of the living catarrhines, two scenarios are equally parsimonious (Figure 3, top trees), in that they each require a minimum of two dispersal events. In scenario A, the lineage leading to the ‘lesser’ apes (the gibbons and siamangs) dispersed out of Africa to Eurasia, leaving representatives of the lineage leading to the ‘great’ apes (orangutans, African apes and humans) in Africa. Subsequently, the lineage leading to modern orangutans, which are currently restricted to Borneo and Sumatra, left Africa, while the African ape ancestor remained behind. In scenario B, the common ancestor of all living apes dispersed out of Africa, and then speciated into the lesser and great ape lineages in Eurasia. Subsequently, one of the great ape species dispersed back into Africa; this lineage eventually speciated into gorillas, chimpanzees and humans.

Scenario B was advocated over 20 years ago [20] on the basis of the branching order of the living hominoid species. From an analysis of just the living species, however, the alternative scenario of two independent migrations into Asia cannot be ruled out by parsimonious reasoning (Figure 3, top trees). It is only when the fossil species are placed in the most-parsimonious fashion on the known hominoid phylogeny that dispersal scenario B is clearly favored over scenario A (Figure 3, bottom trees). Scenario A now requires at least *six* independent dispersal events of hominoids from Africa into Eurasia — one for each of the living and fossil Asian hominoid lineages that attach to the hypothetical African ancestral stem of the tree (Figure 3, bottom left tree). Note that Scenario A would require that a land bridge, with habitat suitable for primates, existed between Africa and Eurasia more-or-less continuously from about 10 to 20 million years ago. Furthermore, the hypothetical African hominoid stem lineage appears to have left no trace in the fossil record, in that none of the African fossils is placed by parsimony in the Eurasian portion of the tree (that is, between the points labeled X and Y in Figure 2).

In contrast, Scenario B still requires only the *two* hominoid migration events shown in Figures 2 and 3 (bottom right tree). Scenario B is thus favored by parsimony. In scenario B, about 20 million years ago an early hominoid species dispersed out of Africa into Eurasia, leaving species such as *Kenyapithecus* in Africa. This Eurasian hominoid lineage speciated into the lesser and great ape lineages about 18 million years ago.

Consistent with widely-held belief about the phylogenetic affinity of *Sivapithecus* [1,4], parsimony analysis places this fossil on the orangutan lineage [4,11,14]. *Sivapithecus* was found in southern Asia from approximately 7 to 13 million years ago [1], so the lineage leading to orangutans must have diverged from the lineage leading to the African apes before this time. Begun and colleagues [4,14] most-parsimoniously place the hominoid fossils *Dryopithecus* and *Ouranopithecus* (also named *Graecopithecus*) on the lineage leading to the African apes (Figure 2). *Dryopithecus* was found in central and western Europe at about 8.5 to 13 million years ago, and *Ouranopithecus* and its close relatives were found in Greece and Turkey from about 7.5 to 9.5 million years ago [16]. These fossils provide independent markers for the divergence of the two major lineages of great apes, again which logically must have occurred before 13 million years ago, if the placement of these fossils is correct. This fossil-derived date is consistent with the molecularly-estimated divergence date of 14 million years ago, which was calculated using large molecular datasets and assuming 25 million years ago as the date of divergence of the Old World monkeys and hominoids [11].

If correct, the synthetic phylogeny shown in Figure 2 places certain constraints on our views of primate evolution, and not just about fossils. For example, from analysis of limited molecular sequence data, some authors [19,24] have estimated that the divergence between the gibbons and great apes occurred about 12 to 13 million years ago. In stark contrast, from mitochondrial DNA sequences, others [25] have claimed that this divergence date is approximately 36 million years ago. This early date, while hard to rule out logically for the reasons explained for *Aegyptopithecus*, is not consistent with the primate fossil record, which contains no evidence of apes before about 20 million years ago. The more recent dates are incompatible with the *Dryopithecus* and *Sivapithecus* fossils, which set the divergence of the orangutan and African ape lineages at earlier than 13 million years ago. The phylogenetic placement of these ape fossils also rules out a recent estimate of the orangutan divergence date at 8.2 million years ago, which was calculated using a few protein-coding sequences [26]. Thus, the fossil record would appear to disfavor all of these extreme molecular estimates.

We find that the ages and geographical locations of *Dryopithecus* and *Ouranopithecus* are both consistent with scenario B. It has long been noted that no diagnosable hominoid fossils have been found in Africa that date between about 12 million years ago (perhaps the last appearance of *Kenyapithecus*) and 9.5 million years ago (the age of *Samburupithecus*, believed to be immediately ancestral to the African apes [27], although this fossil has yet to be analyzed by parsimony). We suggest that this gap in the African hominoid fossil record may represent historical reality. The early African hominoids, such as *Proconsul*, *Afropithecus* and *Kenyapithecus*, probably went extinct, leaving no modern descendants in Africa. The ancestry of the modern African ape lineage instead traces its roots through Eurasia until about 10 million years ago, when a great ape — perhaps similar to *Ouranopithecus* or *Samburupithecus* — most likely made its way back into sub-Saharan Africa (Figure 1c).

We note that this time corresponds to when the three-toed horses and murid rodents first appeared in Africa [3], and it is approximately the time we suggest that the colobine monkeys dispersed out of Africa into Eurasia. These primate dispersal events suggest that a suitable (probably forested) connection between Africa and Eurasia must have existed at this time, perhaps in the southern portion of the Arabian peninsula (Figure 1c). If these proposed primate dispersal pathways through what is now the Arabian peninsula are correct, this suggests that key hominoid and Old World monkey fossils should be found in western Asia and the Arabian peninsula. Unfortunately, this region appears to have had less paleoanthropological study than other, more geopolitically-accessible, regions of the world.

Concluding remarks

Notice that dispersal scenario B is quite robust about the exact phylogenetic positions of the Eurasian hominoid fossils, all of which seem to be highly controversial among paleoanthropologists (see for example [1,2,4]). Various authors have, for example, argued that *Dryopithecus* branches off before the divergence of the orangutans from the African apes, or even before the divergence of the lesser and great apes. Such rearrangements within the Eurasian portion of the tree — between points X and Y in Figure 2 — make no difference as to the likely number of African–Eurasian dispersal events under the parsimony argument (Figure 3, bottom trees). The same is true for rearrangements of the fossil species within the African portions of the tree (outside of points X and Y in Figure 2).

We know of no fossils with clearly diagnosable traits that are in conflict with dispersal scenario B. This hypothesis could be falsified, however, if in future phylogenetic analyses enough African fossils are placed within the Eurasian ape portion of the tree (that is, between points X and Y in Figure 2) to make an African origin of the modern apes (scenario A) the most-parsimonious explanation. We hope that paleoanthropologists will directly test this hypothesis using rigorous methods of phylogenetic analysis, including computer-assisted parsimony or likelihood methods [16,17]. Such analyses will allow explicit phylogenetic hypothesis testing in paleoanthropology, which is now standard practice in molecular evolutionary studies [16].

Acknowledgements

We thank many of our paleontological friends and colleagues – few of whom agree with our conclusions – for offering their honest and strong opinions about this manuscript. We also thank Jonathan Kingdon for encouragement and for helpful discussions about primate biogeography. Supported by NSF grants SBR-9506892 (T.R.D.) and DEB-9453469 (C-B.S.), and NIH grant R01-GM47474 (C-B.S).

References

1. Andrews P, Harrison T, Delson E, Bernor RL, Martin L: Distribution and biochronology of European and Southwest Asian Miocene Catarrhines. In *The Evolution of Western Eurasian Neogene Mammal Faunas.* Edited by Bernor RL, Fahlbusch V, Mittmann H-W. New York: Columbia University Press; 1996:168-207.
2. Pilbeam D: Genetic and morphological records of the Hominoidea and hominid origins: a synthesis. *Mol Phylogenet Evol* 1996, **5**:155-168.
3. Ciochon RL, Etler DA: Reinterpreting past primate diversity. In *Integrative Paths to the Past; Paleoanthropological Advances in Honor of F. Clark Howell.* Edited by Corruccini RS, Ciochon RL. Englewood Cliffs, NJ: Prentice Hall; 1994:37-67.
4. Begun DR, Ward CV, Rose MD: Events in hominoid evolution. In *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations.* Edited by Begun DR, Ward CV, Rose MD. New York: Plenum; 1997:389-415.
5. Messier W, Stewart C-B: Episodic adaptive evolution of primate lysozymes. *Nature* 1997, **385**:151-154.
6. Ruvolo M: Molecular phylogeny of the hominoids: inferences from multiple independent DNA sequence data sets. *Mol Biol Evol* 1997, **14**:248-265.
7. Collura RV, Auerbach MR, Stewart C-B: A quick, direct method that can differentiate expressed mitochondrial genes from their nuclear pseudogenes. *Curr Biol* 1996, **6**:1337-1339.
8. Disotell TR: The phylogeny of Old World monkeys. *Evolutionary Anthropology* 1996, **5**:18-24.
9. Hayasaka K, Fujii K, Horai S: Molecular phylogeny of macaques: implications of nucleotide sequences from an 896-base pair region of mitochondrial DNA. *Mol Biol Evol* 1996, **13**:1044-1053.
10. Zhang Y-P, Ryder OA: Mitochondrial cytochrome ***b*** gene sequences of Old World monkeys: with special reference on evolution of Asian colobines. *Primates* 1998, **39**:39-49.
11. Goodman M, Porter CA, Czelusniak J, Page SL, Schneider H, Shoshani J, Gunnell G, Groves CP: Toward a phylogenetic classification of primates based on DNA evidence complemented by fossil evidence. *Mol Phylogenet Evol* 1998, **9**: 585-598.
12. Purvis A: A composite estimate of primate phylogeny. *Philos Trans R Soc London [Biol]* 1995, **348**:405-421.
13. Conroy GC: Otavipithecus: or how to build a better hominid – not. *J Hum Evol* 1994, **27**:373-383.
14. Begun DR, Kordos L: Phyletic affinities and functional convergence in ***Dryopithecus*** and other Miocene and living hominids. In *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptation.* Edited by Begun DR, Ward CV, Rose MD. New York: Plenum; 1997:291-316.
15. Kay RF, Ross C, Williams BA: Anthropoid origins. *Science* 1997, **275**:797-804.
16. Hillis DM, Moritz C, Mable BK (eds): *Molecular Systematics.* 2nd edn Sunderland, MA: Sinauer; 1996.
17. Swofford DL: *PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1.* Champaign, IL: Illinois Natural History Survey; 1993.
18. Morales JC, Melnick DJ: Phylogenetic relationships of the macaques (Cercopithecidae: ***Macaca***), as revealed by high resolution restriction site mapping of mitochondrial ribosomal genes. *J Hum Evol* 1998, **34**:1-23.
19. Easteal S, Herbert G: Molecular evidence from the nuclear genome for the time frame of human evolution. *J Mol Evol* 1997, **44** (Suppl 1):S121-S132.
20. Sarich VM, Cronin JE: Molecular systematics of the primates. In *Molecular Anthropology.* Edited by Goodman M, Tashian RE, Tashian JH. New York: Plenum Press; 1976:141-170.
21. Benefit BR, McCrossin ML: Earliest known Old World monkey skull. *Nature* 1997, **388**:368-371.
22. Delson E: Evolutionary history of the colobine monkeys in paleoenvironmental perspective. In *Colobine Monkeys: Their Ecology, Behaviour and Evolution.* Edited by Davies AG, Oates JF. Cambridge: Cambridge University Press; 1994:11-43.
23. Groves CP: *A Theory of Human and Primate Evolution.* Oxford: Clarendon Press; 1989.
24. Hasegawa M, Kishino H, Yano T-A: Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. *J Mol Evol* 1985, **22**:160-174.
25. Arnason U, Gullberg A, Janke A, Xu X: Pattern and timing of evolutionary divergences among hominoids based on analyses of complete mtDNAs. *J Mol Evol* 1996, **43**:650-661.
26. Kumar S, Hedges SB: A molecular timescale for vertebrate evolution. *Nature* 1998, **392**:917-920.
27. Ishida H, Pickford M: A new Late Miocene hominoid from Kenya: ***Samburupithecus koptalami*** gen. et sp. nov. *Earth & Planetary Sciences* 1997, **325**:823-829.
28. Whybrow PJ: Geological and faunal evidence for mammal 'migrations' between Asia and Africa during the Miocene. *Cour Forsch Inst Senckenberg* 1984, **69**:189-198.
29. Whybrow PJ: Land movements and species dispersal. In *The Cambridge Encyclopedia of Human Evolution.* Edited by Jones S, Martin RE, Pilbeam D. Cambridge: Cambridge University Press; 1992:169-173.
30. Maddison WP, Maddison DR: *MacClade: Analysis of Phylogeny and Character Evolution Version 3.04.* 1994, Sunderland, MA: Sinauer.