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## Human Paleontology and Prehistory (Paleoanthropology)

# Hominoid evolution: synthesizing disparate data

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### Abstract

Genetic studies have demonstrated that humans and chimpanzees are sister taxa, with gorillas, orangutans and gibbons successively more distant. Hominoid similarities suggest that the crown ape ancestor was a suspensory, frugivorous, tropical forest ape. The common ancestor of *Pan* and *Gorilla* would likely have been *Pan*-like. It is therefore likely that the common ancestor of chimpanzees and humans was also *Pan*-like, and lived in Late Miocene Africa. But it is possible that most if not all Miocene apes are unrelated to crown hominoids. More fossils are urgently needed from within the probable Later Neogene geographical range of the living ape clades. Recent discoveries of very early hominids from Chad raise interesting questions about this hypothesis. **To cite this article: D. Pilbeam, N. Young, C. R. Palevol 3 (2004).**

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### Résumé

**L'évolution des hominoïdés : synthèse de données divergentes.** Plusieurs analyses génétiques démontrent que l'homme et les chimpanzés forment un groupe-frère, avec les gorilles, l'orang-outan et les gibbons phylogénétiquement plus éloignés. Les ressemblances anatomiques au sein d'Hominoidea suggèrent que leur ancêtre commun était un grand singe frugivore, adapté à la suspension par les membres supérieurs, vivant en milieu tropical. De plus, l'ancêtre commun de *Pan* et *Gorilla* ressemblait probablement à *Pan*. Il en découle que l'ancêtre commun des chimpanzés et de l'homme était aussi du type *Pan*, vivant en Afrique au Miocène récent. Toutefois, il est aussi possible que peu, si ce n'est aucun des grands singes du Miocène ne soient directement apparentés aux hominoïdés. Il y a un grand besoin de nouveaux fossiles provenant de la distribution géographique probable des clades de grands singes actuels au Néogène plus récent. Plusieurs découvertes récentes de restes des plus anciens hominidés soulèvent d'intéressantes questions à ce sujet. **Pour citer cet article : D. Pilbeam, N. Young, C. R. Palevol 3 (2004).**

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### Version française abrégée

Au début des années soixante, des données génétiques démontrèrent que les hominidés formaient une tritomie non résolue, regroupant les gorilles et les chimpanzés, à l'exclusion des grands singes d'Asie. Plusieurs études tentèrent de reconstruire les liens phylogénétiques des hominoïdés en utilisant des caractères anatomiques. Quatre études dans les années quatre-vingts arrivèrent à des conclusions différentes au sujet des relations de parenté entre les grands singes (l'orang-outan, le gorille, les chimpanzés et l'homme), indiquant le manque de fiabilité de ce type de caractères. De plus récentes études génétiques montrent sans équivoque que les chimpanzés et l'homme forment un clade monophylétique, alors que les gorilles sont plus éloignés. Certaines, mais de loin pas toutes les analyses anatomiques soutiennent ces liens phylogénétiques. Les données moléculaires sont suffisamment denses et solides pour établir un arbre phylogénétique dans lequel la longueur des branches est plus ou moins proportionnelle au temps. Suivant la date de calibration utilisée, un âge maximal absolu peut être estimé pour chaque nœud de l'arbre. Les ressemblances au sein d'Hominoidea sont prononcées et suggèrent que l'ancêtre commun de ce groupe aurait pu être un grand singe frugivore adapté à la suspension par les membres supérieurs, vivant en milieu tropical. Différentes analyses des relations de parenté des grands singes du Miocène, obligatoirement basées sur des données anatomiques fossiles, donnent des résultats contradictoires, indiquant que la fiabilité de ces données n'est pas meilleure dans un contexte fossile, qu'elle ne l'est pour les espèces vivantes. Il est possible que la plupart, si ce n'est la totalité des grands singes du Miocène, n'aient aucune relation de parenté avec les hominoïdés. Ceci est d'autant plus pertinent que la distribution de ces fossiles est presque entièrement en dehors du domaine géographique des grands singes actuels, et probablement aussi à l'extérieur du domaine des ancêtres de ces derniers au Miocène moyen et récent. Il y a ainsi un grand besoin de nouveaux fossiles provenant de la distribution géographique probable des clades de grands singes actuels au Néogène plus récent. Étant donné le haut degré de similitude allométrique entre les espèces de *Pan* et de *Gorilla*, il est probable que leur ancêtre commun ressemblait à un chimpanzé (en effet, des années soixante aux années quatre-vingts,

plusieurs auteurs proposèrent que les chimpanzés et les gorilles étaient congénériques). De ce fait, il est probable que l'ancêtre commun des chimpanzés et de l'homme était anatomiquement aussi du type *Pan*, vivant en Afrique à la fin du Miocène. Plusieurs découvertes récentes de restes des plus anciens hominidés soulèvent d'intéressantes questions à ce sujet.

### 1. Introduction

In this paper we focus mainly on the phylogenetic relationships of Miocene and living hominoids, the timing of the major splitting events in ape evolution, inferences about the various hominoid morphotypes, and what can be deduced thereby concerning evolutionary patterns among the hominoids.

We begin by discussing what is currently known of living hominoid relationships based on genetic data and what can be inferred about their divergence times using these genetic data, and follow this by reviewing some of the attempts to determine relationships using phenotypic data and note that results vary depending on who does the analysis. Most analyses are not congruent with the phylogeny inferred from very abundant genetic data. In particular, hard tissue characters of the kind available to paleontologists perform for the most part poorly. As we discuss, there is little better agreement among paleontologists working with Miocene apes. These differences of interpretation arise because there is no agreement on how to describe any particular piece of phenotype as characters. Unlike the situation with genetic data there are few if any objective rules for subdividing anatomical complexes into characters, so different workers will get different results. Sorting out relationships among the fossil apes will require both more careful attention to how characters are selected and more fossil material, particularly from areas in which living apes are currently found. Even this may not be enough.

Because many of the relationships among Miocene apes are currently indeterminate in our view, and because most Miocene apes are different in many features from the living apes, we cannot yet have an adequate understanding of patterns of change in relation to environmental change. But environmental change during the Neogene has clearly been important in shaping both the distribution and the adaptations of the apes.

## 2. Living apes: key adaptations

Living apes are unusual animals in that the four genera, *Hylobates*, *Pongo*, *Gorilla*, and *Pan*, are confined to equatorial tropical rain forest and a close relationship to this forest type is reflected in many aspects of behavior and morphology [26]. All apes are frugivores, but most importantly they are animals that seek specifically ripe fruit [22,50,54,90]. Even gorillas will prefer ripe fruit when it is available [92]. The apes survive periods when this ‘preferred food’ (ripe fruit) is scarce by eating a range of lower-quality ‘fallback foods’; in the case of the African apes, frequently piths [22,92]. The distribution of living apes is therefore closely associated with forest type, and particularly by the availability of enough ripe fruit throughout a significant part of the year, along with appropriate fallback foods.

Forest structure is also implicated in the unusual positional behavior and postcranial anatomy of apes [76]. All four genera show widespread adaptations to a current or previous positional repertoire in which suspension, arm-swinging, and vertical climbing are very important. Many features of the torso (such as a broad and shallow thorax, short lumbar region, broad pelvic region) and appendicular skeleton (long and limber forelimbs, long hands, elongated and mobile dorsally placed scapulae) are adaptations associated with these behaviors.

Hominins are first detected in the African fossil record in the Latest Miocene [13]. Given what we know from comparative genetics (discussed further below), this would suggest that, if hominins are present in Africa by this time, apes ancestral and probably similar to chimpanzees and probably gorillas too were also present in equatorial African forests during the Latest Miocene and Early Pliocene. The hypothetical distribution of rain forest during this interval (Fig. 1) would have been more extensive latitudinally beyond that of today’s forest but perhaps not significantly more longitudinally [67], and we hypothesize that crown ape lineages would have been coextensive with these forests.

## 3. Living hominoid relationships from genetic characters

Although there has been much debate about the evolutionary relationships of the apes and humans at



Fig. 1. Hypothetical Late Miocene distribution of tropical forest and crown apes (dark grey).

Fig. 1. Distribution hypothétique des grands singes apicaux et de la forêt tropicale au Miocène récent (gris foncé).

least since Thomas Henry Huxley’s 1863 essay [47], we – along with effectively all molecular systematists – regard this issue as now settled. The data overwhelmingly support a tree in which the two chimpanzee species and humans are sisters, with gorillas, orangutans, and gibbons successively more distant (Fig. 2).

One important approach uses DNA-DNA hybridization [14], a technique comparing all single copy nuclear DNA among pairs of species. The technique examines both coding (genes) and non-coding regions, and derives an aggregate measure of genomic similarity, which averages out differences in evolutionary rates across the entire genome. Caccone and Powell [14] clearly show that humans and chimps are closest. Morris Goodman’s group first showed that humans and chimpanzees were probably sister taxa using nuclear

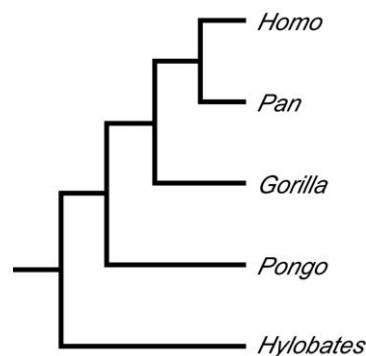


Fig. 2. Genetically determined relationships among living hominoids.

Fig. 2. Relations de parenté au sein des hominoïdés actuels basées sur des données génétiques et moléculaires.

DNA sequence data from the globin-complex (e.g., Bailey et al. [5]). Horai et al. [46] drew a similar conclusion based on mtDNA sequence data.

In what has become a definitive study, Ruvolo [70] analyzed a large number of independently inherited genes (independent in the sense that they do not segregate together), most of them on different chromosomes. Because these genes are inherited independently of each other they are independent estimates of the true phylogeny (Fig. 3). For each gene a gene tree can be calculated, and the consensus of all gene trees estimates the species tree. In the case of the hominoids, the data overwhelmingly support a tree in which chimpanzees and humans are sisters, with gorillas, orangutans, and gibbons successively more distant (Fig. 2). This analysis has been expanded by Satta et al. [74] with additional genes, although the analysis did not take into account criteria of independence. Oversimplifying by assuming that genes on the same chromosome are linked regardless of genomic distance yields the same result as Ruvolo [70]. Finally, Chen and Li [21] examined 53 randomly selected autosomal intergenic nonrepetitive (noncoding) DNA sequences, sampling across the genome, and demonstrated once again the close relationship of humans and chimpanzees, with gorillas more distant.

CLADE	Supporting Genetic Datasets
<i>Homo-Pan</i>	mtDNA
	Glycophorin A
	c-myc
	Carbonic anhydrase 1 (CA1)
	Immunoglobulin Cε3 pseudogene
	α1,3 galactosyl-transferase
	δ-β-globin intergenic region, γ globin, ψ-η globin
	B cell growth factor
	HOX2B
	Glucose-6-phosphate dehydrogenase (G6PD)
Y-specific regions of ABY; ZFY; SRY	
<i>Pan-Gorilla</i>	Involucrin
	Protamine
<i>Homo-Gorilla</i>	Immunoglobulin Cα1

Fig. 3. Genetic data sets used by Ruvolo [70] in analyzing chimpanzee–human relationships. Protamine later shown [55] to be uninformative.

Fig. 3. Ensemble de données génétiques utilisées par Ruvolo [70] pour établir les liens de parentés d'Hominoidea. La protamine s'avèrera ultérieurement inutile à cette fin [55].

Inasmuch as any issue in such a contentious area as paleoprimatology can be considered settled, this is settled.

#### 4. Genetics and the timing of the hominoid radiation

The use of genetic comparisons between species has become commonplace in estimating both phylogenetic relationships and divergence times in combination with information from the fossil and geological records. We believe that, despite this general familiarity, it is still worth drawing attention to the assumptions and procedures that lie behind such inferences, to the existence of several different steps in the process, and to inherent problems.

Several different analytical approaches are available for estimating phylogenetic relationships from genetic data: cladistic, probabilistic, and phenetic. Several different kinds of data are available for inter-species comparisons: amino acid sequences [36], nucleotide sequences both nuclear and mitochondrial, and DNA–DNA hybridization measures of “total” single copy nuclear DNA. In the case of densely sampled groups such as (fortunately for us) the Hominoidea, enough data exist to be sure about evolutionary relationships.

The “clock-like” nature of genetic change matters less for inferring relationships, but becomes critical if proportional or “relative” trees are to be usefully transmuted into “absolute” trees from which divergence dates are estimated. The degree of clock-like behavior of any genetic system can be determined using the “rate-test” [72], a measure of the difference in amount(s) of genetic difference between an outgroup species and respectively two (or more) ingroup species. If the amount of genetic difference in such comparisons is subequal (more-or-less equal, or sufficiently so for the task in hand) it can be deduced that the rates of genetic evolution along the different lineages have also been subequal. It is also possible to detect situations in which one or more of a group of monophyletic species has evolved at a faster or slower rate than the rest. It is worth re-emphasizing that the rate test is entirely independent of any assumptions about actual evolutionary rates.

In building such trees, as with estimating relationships, more is better. The more genetic information is

available, the more likely it is that the number of tree segments (branches) will be proportional to time. For example, DNA-DNA hybridization is a technique which compares all single copy nuclear DNA among pairs of species, examining both coding (genes) and the much more extensive non-coding regions, and deriving an aggregate measure of genomic similarity which will average out differences in evolutionary rates both within and between genomes. For closely related species this is perhaps the best technique for producing relative trees.

Some single genes, or combinations of genes, are also useful. Because nucleotide changes can accumulate over time in such a way as to 'hide' them (through back mutations or convergence), mathematical techniques are used to "correct" for these missed changes: it is then the total number of inferred accumulated nucleotide changes which are linearly proportional to time, rather than the actual number of observed differences. We should remind ourselves that genes need to be chosen with care. Rapidly evolving genes are essential for estimating branching sequences and ages of recently evolved species, but lose their resolving power with increasingly older divergences. Slowly evolving genes are important for addressing older divergences, but lose resolving power when much younger divergence points are being estimated. With the possible exception of DNA-DNA hybridization, no single gene will perform adequately over broad ranges of time. Care is needed in selecting genes for this reason.

Calibrating relative trees using fossil or geological data also needs to proceed with care. The fossil record will always allow us to infer a minimum age for the divergence of two sister lineages, providing that at least one of the lineages can be recognized on the basis of (probable) derived characters. It is of course more difficult to estimate when a split had definitely *not* occurred. This requires a very densely sampled fossil record, dense enough to demonstrate with strong probability that absence of evidence is evidence of absence. The solution is to calibrate a well-founded relative tree at as many branch points as possible, inevitably using mostly minimum divergence estimates, and then judge the plausibility of this hypothesis against alternatives, based on all available evidence.

Our emphasis here is on the Hominoidea. We know branching sequence; how might we estimate divergence dates? Cercopithecoids and hominoids are sister

taxa, evolving in the Later Cenozoic of Africa. Cercopithecoids have clearly derived bilophodont cheek teeth, which are readily recognizable in the fossil record. The oldest eastern African localities with cercopithecoids are around 19 Ma [57]. Hominoids can be recognized with only marginally less confidence around 21 Ma [32]. So, we can conclude that the divergence of hominoids and cercopithecoids had happened certainly 19 Ma and very probably 21 Ma. It is more difficult to estimate when a cercopithecoid-hominoid split had definitely *not* occurred. The abundant anthropoid fauna represented in the younger Oligocene Fayum sediments in Egypt, dated around 33 Ma, probably samples a period prior to the divergence of these two groups [69]. Unfortunately, the African fossil record between 33 and about 21 Ma is extremely poor, and selecting a plausible fossil-based cercopithecoid-hominoid divergence between these extremes is therefore difficult.

Estimating the age of the cercopithecoid-hominoid split, and those of the various hominoid lineages, can be approached in two ways: by extrapolating from the youngest divergence, *Pan-Homo*; and by interpolating from much older divergences associated with the radiation of placental mammalian orders. Starting with extrapolation, the oldest hominin is *Sahelanthropus tchadensis*, with a plausible faunal age of older than 6 Ma and perhaps as old as 7 Ma [13]. As a current best estimate we choose 6.5 Ma, which dates minimally the *Pan-Homo* divergence, and this can then be used to estimate the other hominoid divergences by extrapolating. Fig. 4 lists ranges of estimated dates for each hominoid divergence; these vary because relative branch proportions vary depending upon the genetic system being used. The dates for the cercopithecoid-hominoid split range from 27 to 29 Ma.

As we noted earlier, a complementary approach to estimating the hominoid-cercopithecoid split is by interpolation from an older calibration point. For this we need a placental mammal tree that is well supported, both for ordinal relationships and basal divergence dates. Considerable progress has been made, but there are still some interesting problems. Challenges reflect difficulties in determining and dealing with varying rates of genetic change between and within major lineages, and with finding adequate calibration points.

There is general agreement among paleontologists that the radiation of eutherian orders began in the

MA	DNA-Hybridization <sup>1</sup>	DNA-Hybridization <sup>2</sup>	Globins <sup>3</sup>	Proteins <sup>4</sup>	Proteins <sup>5</sup>
6	*Chimpanzee	*Chimpanzee	*Chimpanzee	*Chimpanzee	*Chimpanzee
8			Gorilla	Gorilla	Gorilla
10	Gorilla	Gorilla		Orangutan	
12					
14	Orangutan	Orangutan	Orangutan		Orangutan
16					
18				Gibbon	
20	Gibbon	Gibbon	Gibbon		Gibbon
22					
24					
26					
28			OWM	OWM	OWM
30	OWM	OWM			

Fig. 4. Estimated divergence times for living hominoids based on relative ages using different genetic systems and calibrated using a date of 6.5 Ma for the hominin–Pan divergence. <sup>1</sup>Caccone and Powell [14], <sup>2</sup>Sibley et al. [80], <sup>3</sup>Goodman et al. [37], <sup>4</sup>Kumar and Hedges [52], <sup>5</sup>Stauffer et al. [83].

Fig. 4. Temps de divergence extrapolés estimés pour les grands singes actuels, basés sur des âges relatifs obtenus par diverses analyses génétiques et calibrés à 6,5 Ma pour la divergence entre les hominins et *Pan*. <sup>1</sup>Caccone and Powell [14], <sup>2</sup>Sibley et al. [80], <sup>3</sup>Goodman et al. [37], <sup>4</sup>Kumar and Hedges [52], <sup>5</sup>Stauffer et al. [83].

Cretaceous, although less agreement as to whether this was later (around 70 Ma) or earlier (100 to 110 Ma). A recent and in our opinion plausible analysis [82] uses segments of 19 nuclear and 3 mitochondrial genes, 9 fossil based calibration points, and a Bayesian analytical approach to estimate a eutherian mammal tree which has its basal root set at 105 Ma. The eutherian orders diverge in the last 40 Ma of the Cretaceous, but only begin their crown radiations just before or just after the Cretaceous/Cenozoic boundary.

An important area of disagreement concerning ordinal relationships of placental mammals lies with the

Rodentia. Springer et al. [82] locate a monophyletic Rodentia as an order in the super-order Euarchontoglires, with rodent crown group radiation beginning 74 Ma. Rodent monophyly is supported by other recent genetic studies [1,56,66]. Both Lin et al. [56] and Poux et al. [66] also find support for Euarchontoglires, although Adkins et al. [1] do not. Adkins et al. estimate the rodent crown group radiation beginning 75 Ma, in close agreement with Springer et al. [82].

These results disagree with those of Kumar and Hedges [52] and Hedges and Kumar [45], whose studies use amino acid sequences of a large number of

nuclear genes to build a tree, calibrated initially at 310 Ma (estimated age of bird-mammal divergence). Another [34,59] adopts a similar approach. In these analyses, the rodents are both paraphyletic and diverge very early (*ca.* 110 Ma). However, most other interordinal age estimates are reasonably concordant with those of Springer et al. [82]. The rodent discrepancy can perhaps best be explained by a higher rate of nucleotide evolution in the rodents [1,91].

We are interested in interpolating estimates for the hominoid-cercopithecoid divergence, along with intra-hominoid splits. Kumar and Hedges [52] and (updated) Hedges and Kumar [45] interpolated estimates for the various hominoids: cercopithecoid/hominoid 23.3 Ma, human/chimp 5.4 Ma, /gorilla 6.4 Ma, /orang 11.3 Ma, /gibbons 14.9 Ma. The intra-hominoid estimates were based on a calibration point of rodents/other mammals of 110 Ma [44]. As noted above, this is likely to be a (considerable) overestimate, the date we prefer being 87 Ma for Rodentia/Primates [82]. Recalibrated hominoid dates are then clearly too young, with new dates for both human/chimp (4.3 Ma) and human/gorilla (5.1 Ma) being younger than documented fossil hominins. The cercopithecoid/hominoid divergence of 23.3 Ma estimated by Kumar and Hedges [52] and Hedges and Kumar [45] is based on a mix of 310 Ma and 110 Ma calibration points [44], and is again therefore likely to be an overestimate once the 110 Ma-based dates (rodent divergence) are recalibrated.

Stauffer et al. [83] begin their estimation of hominoid divergence dates by assuming that 23 is good date, in part because it coincides, approximately, with the Oligocene-Miocene boundary. Several points can be made here. There is no African fossil record spanning the relevant interval so we have no way of knowing whether or not there was a peak of speciation events at this time. In addition, the Kumar and Hedges' [52] and Hedges and Kumar's [45] analyses show no other major divergence events coincident with other epoch boundaries.

Springer et al. [82] estimate a date for the crown primate radiation of 77 Ma. This is close to the paleontologically based estimate of Tavaré et al. [85] of 82 Ma. Figure 5 shows interpolated estimates using several data sets: the hominoid-cercopithecoid divergence dates range from 23 Ma to 31 Ma. Our preference is for the DNA–DNA hybridization dataset [2]; calibrating the strepsirhine/haplorhine split at 77 Ma,

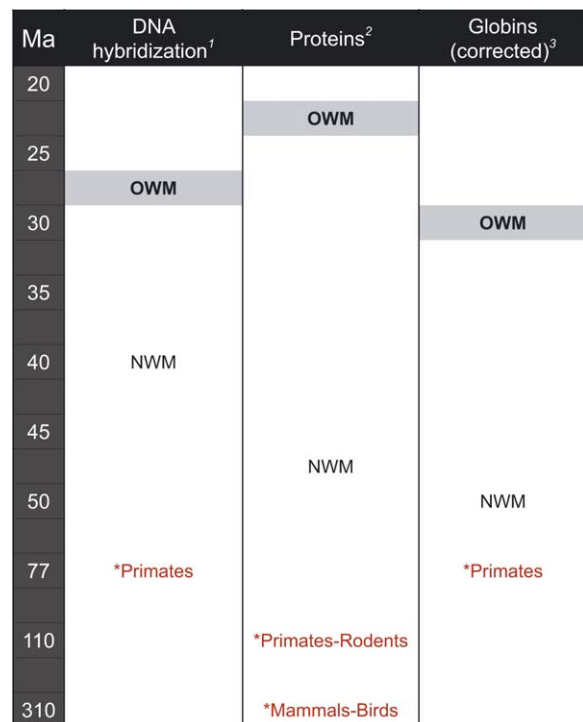


Fig. 5. Estimated divergence times for various primate groups based on relative ages using different genetic systems, with calibration points indicated. <sup>1</sup>Ahlquist [2], <sup>2</sup>Kumar and Hedges [52], <sup>3</sup>Goodman et al. [37].

Fig. 5. Temps de divergence interpolés estimés pour les grands singes actuels basés sur des âges relatifs obtenus par diverses analyses génétiques. Les points de calibration sont indiqués par des astérisques. <sup>1</sup>Ahlquist [2], <sup>2</sup>Kumar and Hedges [52], <sup>3</sup>Goodman et al. [37].

the interpolated New World/Old World anthropoid split is 40 Ma and the hominoid-cercopithecoid split is 28 Ma, concordant with extrapolated estimates summarized above (Fig. 4).

## 5. Living hominoid relationships from phenotypic characters

Since the 1950s almost all-possible combinations of relationships based on phenotypic characters have been suggested. Schultz's [75] proposal for a monophyletic Pongidae represents the early 20th century consensus. Simpson's tree [81] moved hominins to become sisters to the African apes (Simpson advocated a single genus *Pan* for both chimps and gorillas, common during this period). Simpson was influenced by

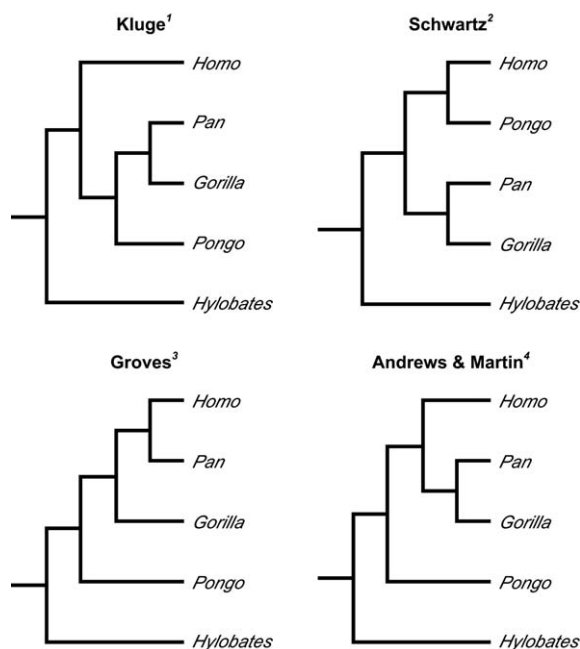


Fig. 6. Phylogenetic relationships of hominoids as proposed during the 1980s. <sup>1</sup>Kluge [49], <sup>2</sup>Andrews and Martin [4], <sup>3</sup>Schwartz [77], <sup>4</sup>Groves [39].

Fig. 6. Relations phylogénétiques entre les hominoïdés, telles que proposées dans les années quatre-vingts. <sup>1</sup>Kluge [49], <sup>2</sup>Andrews and Martin [4], <sup>3</sup>Schwartz [77], <sup>4</sup>Groves [39].

Morris Goodman's early genetic work [35] showing humans close to African apes, and this is clearly reflected in his tree. However, Goodman had detected equidistant genetic relationships among *Pan*, *Gorilla*, and *Homo*, while Simpson and other morphologists who followed his results always placed *Pan* and *Gorilla* much closer to each other.

By the 1980's this was perhaps the preferred pattern among primatologists. This decade saw a burst of creative analyses: Kluge [49] rediscovered a monophyletic Pongidae; Schwartz [77] proposed that humans and orangutans were sisters; Andrews and Martin [4] preferred characters that showed chimps and gorillas to be closest; while Groves [39] proposed tentatively that humans and chimps were closest relatives (Fig. 6). As we know now, Groves was correct, although at that time the genetic data were still far from definitive in showing a chimp-human link. But even though genetic data did become more clearly supportive of that rather surprising relationship during the 1990's, disagreements continued among morphologists, and between morphologists and geneticists (Fig. 7).

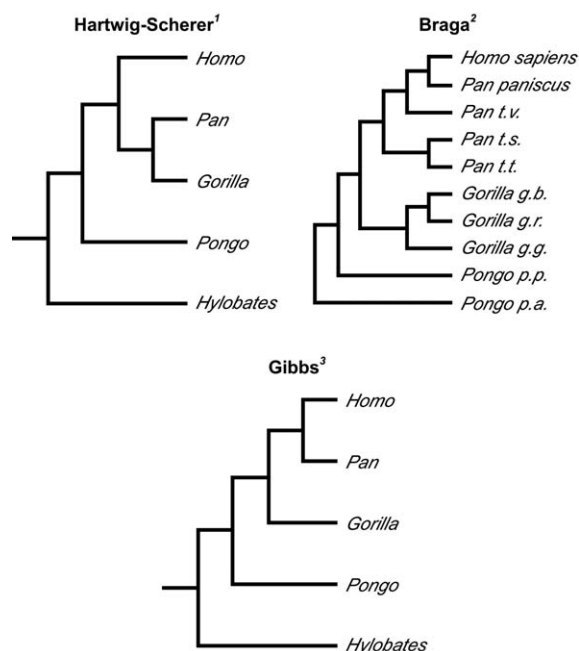


Fig. 7. Phylogenetic relationships of hominoids as proposed during the 1990s. <sup>1</sup>Hartwig-Scherer [43], <sup>2</sup>Braga [12], <sup>3</sup>Gibbs et al. [33].

Fig. 7. Relations phylogénétiques entre les hominoïdés, telles que proposées dans les années quatre-vingt-dix. <sup>1</sup>Hartwig-Scherer [43], <sup>2</sup>Braga [12], <sup>3</sup>Gibbs et al. [33].

Thus Hartwig-Scherer [43] argued for a *Pan-Gorilla* link using elegant allometric studies of apes to show that many chimp-gorilla similarities in growth patterns are likely to be homologous, but without recognizing the possibility that they could be symplesiomorphies (which most probably are). Braga [12] looked at hominoid non-metric cranial traits, and included ape subspecies also covered in a number of genetic studies [30,71]. Although his preferred tree linked humans and bonobos, in other details it resembled genetic trees. In several papers, Begun (e.g., [8]) used hard tissue characters to analyze relationships among living and fossil hominoids, and was able to (just) recover a tree joining hominins (represented by *Australopithecus*) and *Pan*. However, this study, and others, raises the serious question of character definition, choice, and selectivity. Finally, Gibbs et al. [33] used soft tissue characters (muscles, nerves, blood vessels) and recovered a tree identical to the genetic tree, with humans and chimps closest.

So, unlike the situation with genetic data where different workers can come to similar conclusions concerning the nature of independence and objectivity,



CLADE	Shared Similarities
<i>Homo-Pan</i>	I <sup>2</sup> similar in size and shape to I <sup>1</sup>
	Basal keel of lower canine absent
	Ankle epiphyses fuse at same time as hip and elbow
	Pendulous scrotum
<i>Pan-Gorilla</i>	Dorsal extension of articular surface of metacarpals
	Thumb short relative to body weight
	Flexor digitorum superficialis strongly developed
	Proportion Pattern 1 Enamel
<i>Homo-Gorilla</i>	Brachial index <80
	Power arm of foot >35% of lever
	Valvulae conniventes well developed in adult
	Ovaries >40mm long
<i>Pongo-Homo</i>	Metaconid of P <sub>3</sub> enlarged
	Upper ear height 40% of ear length
	Gall bladder with very slight or no bend
	Retardation of shoulder and wrist ossification
<i>Pan-Gorilla-Pongo</i>	Eccrine glands abundant over body
	Small single larynx tuberculum cuneiforme
	Six sacral vertebrae
	Short ethmoid-lachrymal contact (40-90%)

Fig. 8. Phenotypic similarities supporting different hominoid sister relationships (from Groves and Paterson [40]).

Fig. 8. Ressemblances phénotypiques soutenant différentes phylogénies au sein d'Hominoidea [40].

with morphological data different workers can arrive at radically different phylogenetic results, largely because of lack of rules governing character description and selection. It is not a case of 'molecules' versus 'morphology', because there are morphological analyses that concur with the molecular, but rather a problem of differing results from different morphological studies and the absence of biologically plausible criteria for choosing the 'correct' characters and therefore the 'correct' morphological tree. It is worth noting that differences between genetic and phenotypic trees have also been found in other primate groups. For example, among papionins, baboons and mandrills are not sister taxa, despite their morphological similarities [25]. And spider monkeys and woolly spider monkeys are probably not sisters, again despite many morphological similarities [27].

Returning to the hominoids, in summary we can see a clear difference between the genetic data sets and the phenotypic data sets. As the genetic data accumulated, it became increasingly clear that just one tree (Fig. 3) was abundantly supported [70]. This did not occur with phenotypic characters. Chimp-human morphological similarities are obviously present (Fig. 8), but so too are similarities supporting just about every other possible combination of hominoids [40]. The problems are first, there are no clear and objective rules for selecting characters; the same anatomical region can be de-

scribed differently by two morphologists. And second, there are no rules for deciding whose characters are better [19,20,64,73]. Finally, we suspect that some notion of the "correct" phylogeny unconsciously may guide the selection of morphological characters.

We find the Gibbs et al. [33] hominoid soft tissue data set particularly interesting here because it is congruent with the genetic tree, and supports a human-chimpanzee sister relationship. Characters were collected from a literature accumulated mostly during a pre-Hennigian era, and by scholars who were not primarily concerned with phylogenetic analysis. Characters tend to be discrete, easy to describe and count, and largely unaffected by epigenetic interactions. Unfortunately, they are the kinds of characters we do not have for fossils!

## 6. Hominoid morphotypes: until the Miocene ape fossil record began to improve...

Until the description of *Proconsul* postcrania in the 1960's it was assumed by many that the common ancestor of living apes was postcranially ape-like rather than monkey-like. 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 [48,75,76,86]. With the discovery of the obviously non ape-like *Proconsul* the idea that at least some hominoid postcranial features had evolved in parallel became more common. However, it was still widely believed that the common ancestor of chimps and gorillas was chimp-sized and chimp-like because many (although by no means all) cranial and postcranial features scale allometrically in *Pan* and *Gorilla* [43,79]. So close was the gorilla-chimp relationship believed to be that they were widely treated as congeneric (e.g., Simpson [81], Tuttle [86], Groves [38]). That the common ancestor of chimps and gorillas was chimp-sized and chimp-like was almost universally accepted until very recently when the closer relationship of humans and chimps was established. Similarly, postcranial similarities of the African apes and the orangutan were generally treated as homologies [39,76].

But as the Miocene ape record has accumulated over the past two decades, paleontologists have noted

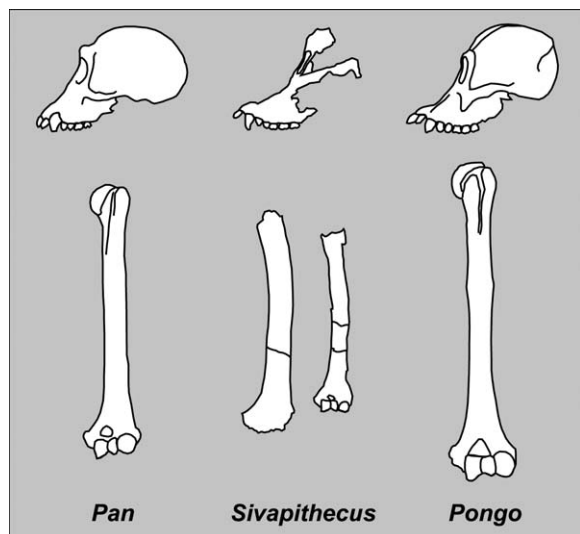


Fig. 9. Cranium and humerus of *Pan* (left), *Sivapithecus* (center), and *Pongo* (right). *Sivapithecus* and *Pongo* are similar facially, while *Sivapithecus* differs from all living apes in humeral shaft morphology.

Fig. 9. Crâne et humérus de *Pan* (à gauche), *Sivapithecus* (au centre) et *Pongo* (à droite). L'anatomie faciale de *Sivapithecus* et *Pongo* est similaire, tandis que *Sivapithecus* est différent de tous les grands singes actuels dans l'anatomie de la colonne humérale.

the generally nonape-like postcrania of most of these fossil taxa. Based on cranial or dental features, they have concluded that many of these apes are crown hominoids, and therefore that some to many suspensory postcranial adaptations of living apes have evolved in parallel (e.g., Begun et al., [11]). A major reason for this conclusion is the recognition that the Asian Miocene ape *Sivapithecus* resembles the orangutan specifically in facial-palatal characters while differing markedly from all living apes, and especially the large apes, in a number of postcranial features (discussed further below) (Fig. 9).

Evidence from the comparative analysis of living mammals including primates has been used to support the plausibility of parallelism. First, not all ape postcranial similarities are unique to this group, as some of these features have either evolved in hanging mammals (e.g., sloths) or suspensory primates such as the spider monkey, *Ateles* [18,28]. This suggests these traits are highly associated with function and are likely to evolve in parallel given similar selection pressures, particularly in animals that share a very similar morphological/genetic starting point. Second, a recent study has showed that living ape postcrania are much more

variable than had been previously recognized and are markedly similar in only those features found in Miocene apes [53]. This observation has been used to argue for multiple independent pathways for the evolution of suspensory characters from a quadrupedal ape ancestor.

However, reanalysis of many of the trunk and limb traits [53] which link the living apes along with new fossil evidence from the Early Miocene indicates the above arguments for parallelism may need to be refocused. Young [93,94] demonstrated that both hominoid overlap with *Ateles* and within hominoid variability can be largely ascribed to *Hylobates*. A likely functional explanation for this result is that the locomotion of both *Ateles* and *Hylobates* includes a high percentage of brachiation (20 and 40%, respectively) [16, 29,31] and these behaviors play a proportionally large selective role on anatomy. On the other hand, great apes are much more similar to each other and distinct from other primates, despite locomotor differences. This contrast suggests that including *Hylobates* specializations may lead to a skewed reconstruction of the ancestral morphotype, both in terms of anatomy and behavior.

An alternative to the assumption that all living hominoids inform equally about the ancestral morphotype is to instead interpret *Hylobates*' morphology as specialized/divergent and secondarily-derived from a more great ape-like ancestor. The Early Miocene ape *Morotopithecus* makes its first appearance before or contemporaneous with the inferred *Hylobates* divergence date (Fig. 4), yet shares a number of postcranial similarities with great apes to the exclusion of *Hylobates* [95]. Although, not the only possible interpretation, this result is congruent with a model in which the earliest apes shared a body plan more in common with great apes than with gibbons. Apes lacking these postcranial features, such as *Proconsul* and *Sivapithecus*, would be unrelated to the crown radiation. A more appropriate locus for testing parallelism would then be the characters where the great apes resemble each other and some fossil apes, but differ from all others.

These inferences clearly imply that the focus of future tests of parallelism should be on the documentation and exploration of great ape postcranial variability and selection pressures. Here there are many unanswered questions. For example, unlike the case for *Hylobates* and *Ateles*, it is less clear what behaviors

unify great apes and link them to some fossil apes (e.g., selection for vertical climbing? hang-feeding? slower, more cautious generalized climbing?), and, consequently, what could be the common selection factor that led to parallelism. Indeed, the postcranial parallelism model must explain how, if the most common locomotor behaviors of living great apes range from predominantly terrestrial and quadrupedal knuckle-walking (e.g., gorillas) to virtually exclusive arboreality and quadrumanism (e.g., orangutans), these species could still look so similar. In other words, if current similarities are the result of functional convergence rather than common ancestry, it is somewhat perplexing that these species have evolved to be so similar given their divergent current locomotor behaviors.

But it is also important to remember that although great apes share a number of similarities, they also differ in many interesting and largely unexplored ways that have the potential to help illuminate this problem. For example, in an analysis of similarity in the primate scapula, Young [93] demonstrated that there are notable morphological differences between African apes and the orangutan. These include the size and shape of the supraspinous fossa, the angle, orientation and length of the scapular spine, and the size of the teres major fossa. However, it is not clear at this time what the functional meaning of these differences may be or, critically, whether they correspond to unique locomotor differences or are different ways of solving similar functions. Questions such as these will need to be better addressed in order to decide between the alternative models.

In sum, the substantial similarities of the living apes, and particularly the great apes, suggest that the ancestral hominoid morphotype was more like a large ape (e.g., *Morotopithecus* or *Dryopithecus*) than *Hylobates*. A possible interpretation is that *Hylobates*' small size and postcranial specializations are secondarily derived specializations for brachiation. Alternatively, the postcranial parallelism model posits the ancestral morphotype was an above-branch, quadrupedal arboreal, and fossil and living ape suspensory similarities are the result of multiple episodes of parallelism (as many as five independent events). To decide between these alternatives will require a more detailed understanding of living great ape postcranial variability, how it is linked to common functions or behaviors, and a more complete record of the postcranial evolution of fossil apes.

## 7. Miocene ape relationships and distributions

As we have noted, the Miocene apes are for the most part quite different from the living apes cranially, dentally, and postcranially, and this presents a challenge to understanding hominoid evolutionary history because it makes both phylogenetic and behavioral reconstruction difficult [62,63,64]. For example, one of the two best known Miocene ape genera (in terms of skeletal parts sampled) is *Proconsul* from the Early Miocene of east Africa, which differs from all living apes in many skeletal features [89]. Its phylogenetic position is still unclear, although there is general agreement about its fundamentally nonape-like nature. Another well-sampled genus is *Oreopithecus* from the Late Miocene of Italy [41,51]. Some postcranial features recall extant arboreal apes, others bipedal hominins, while cranially and dentally the genus is uniquely different from all living hominoids. Most other Miocene ape genera are less to much less well sampled, making phylogenetic and paleobiological interpretation problematic.

The Miocene ape record has improved considerably over the past two decades, but most taxa are still known primarily from teeth, jaws, some facial material, and generally inadequate postcranials [62,63]. There are considerable differences of opinion (Fig. 10) over the phylogenetic relationships of Miocene apes and their positioning relative to crown hominoids (e.g., Begun et al. [11], Moyà-Solà and Köhler [58], Harrison and Rook [42], Cameron [15], Schwartz [78]). *Sivapithecus* is an exception to this; there is general agreement that it is sister to the orangutan, *Pongo*. This is because of significant facial-palatal resemblances in the two genera. Yet there are significant dental and postcranial differences between *Sivapithecus* and all large hominoids [23,62,87].

This is a good example of an important problem – that of character conflict between cranial-facial and dental-postcranial features (Fig. 9). Depending on how many characters are defined for a particular body region, or how much weight is given to particular characters, the phylogenetic position of *Sivapithecus* or any other taxon can change. *Sivapithecus* might be sister to *Pongo*; this would mean either that crown ape postcranial similarities evolved in parallel, or that *Sivapithecus* postcranials are derived relative to the crown ape pattern. Alternatively, *Sivapithecus* might be unrelated to any crown hominoid.

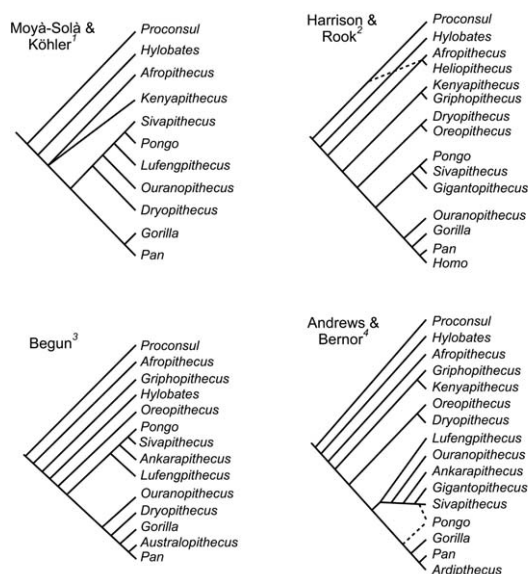


Fig. 10. Proposed phylogenetic relationships of Miocene and crown hominoids. <sup>1</sup>Moyà-Solà and Köhler [58], <sup>2</sup>Harrison and Rook [42], <sup>3</sup>Begun [9], <sup>4</sup>Andrews and Bernor [3].

Fig. 10. Relations phylogénétiques proposées pour les grands singes miocènes et actuels. <sup>1</sup>Moyà-Solà and Köhler [58], <sup>2</sup>Harrison and Rook [42], <sup>3</sup>Begun [9], <sup>4</sup>Andrews and Bernor [3].

In addition to inadequate sampling of body parts, there is a second significant problem to which we have already alluded – that of character definition. The same piece of anatomy can be described differently when rendered into characters [17,19,20,73]. For example, Begun et al. [11] and Moyà-Solà and Köhler [58] describe the nasoalveolar region with both different character descriptions and numbers of characters (Fig. 11), and the phylogenetic trees supported by these characters are different. Begun et al.’s characters support a *Sivapithecus-Pongo* clade with *Dryopithecus* linked to African apes and humans, whereas Moyà-Solà and Köhler’s single character supports a *Pongo* clade including *Sivapithecus*, *Lufengpithecus* and *Dryopithecus*. This disagreement can occur because there are no rules governing the language of anatomical description [65]. The precise nature of the character, or how many characters are used to describe an anatomical region, are not subject to any rules governing selection and description. This was one factor contributing to the lack of phylogenetic agreement in the case of living hominoids, although in that case we have genetics to guide us to the correct relationships. But with fossils we are less fortunate.

## 8. Geography of Miocene apes

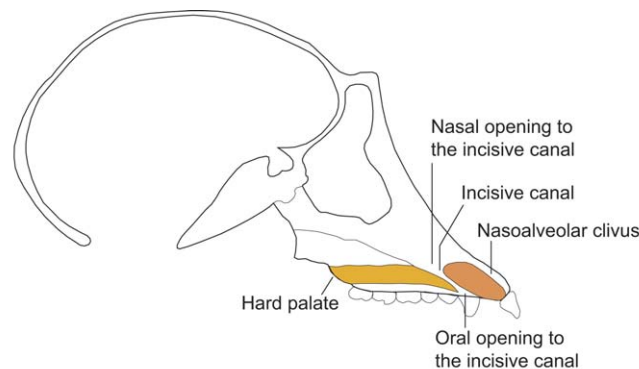
A final problem concerns the geographical distribution of Middle and Late Miocene ape localities. With few exceptions they fall outside the current and probable recent past range of living apes (Fig. 12). We cannot reconstruct habitats for most of these fossil apes with sufficient accuracy to say definitely they could not have supported living apes. But we think it improbable that sufficient ripe fruit would have been available in most of them to make suitable habitats for an orangutan or a chimpanzee.

Faunal evidence from several regions of Europe and Asia suggests that substantial environmental change happened during the Later Miocene. In Pakistan this is clearly documented by a habitat shift on the floodplains around 8 Ma from C3-dominated forests and dense woodlands to C4-dominated open woodlands and grasslands [6]. Among other faunal changes, *Sivapithecus* disappears at this time [7]. Similar events occur throughout Eurasia during the Late Miocene [3].

A recent detailed study by Nelson [60,61] of fauna from the late Miocene of the extensive and highly fossiliferous Siwalik Series of Pakistan shows that *Sivapithecus* and associated fauna inhabited seasonal monsoon forests similar to those found today in southern China. Microwear and stable isotopes of both *Sivapithecus* and many elements of the associated fauna indicate a degree of frugivory equivalent to that found in extant apes. But we still do not understand in sufficient detail the nature of such Miocene ‘forest’ habitats outside the current equatorial forest zones of west and central Africa and southeast Asia. And we have yet to decipher adequately the dental and postcranial anatomy of these Miocene apes. So, we do not understand sufficiently the possible range of their adaptations and are limited therefore in our understanding of the mechanisms underlying the pattern of extinctions and survivals we see with these hominoids.

## 9. Hominoid evolution and geography

We have noted already that the distribution of Miocene apes falls almost entirely outside that of living apes and their Late Neogene ancestors, and that the ape fossil record is virtually non-existent within that area. Did crown hominoids evolve in Africa? This is perhaps



Begun <i>et al.</i> (1997)
incisive fossa position
incisive fossa
subnasal foor
nasal clivus
nasoalveolar clivus length
nasoalveolar clivus orientation
incisive canal caliber

Moyà-Solà & Köhler (1996)
nasoalveolar morphology

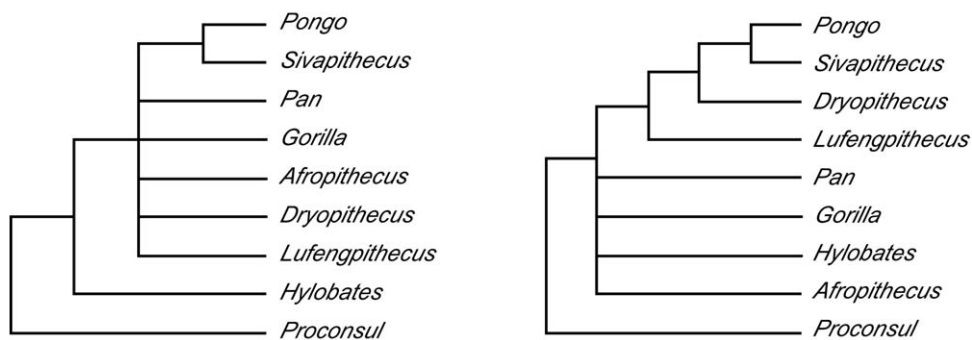


Fig. 11. Alternative phylogenies supported by different descriptions of hominoid nasoalveolar anatomy.  
 Fig. 11. Phylogénies alternatives soutenues par des analyses divergentes de l'anatomie nasoalvéolaire chez les hominoïdés.

the majority opinion [3]. Or did they evolve in Asia; a minority view recently advocated by several colleagues [10,84]? Begun and Güleş [10] and Stewart and Disotell [84], hypothesize crown hominoids radiating from central Eurasian regions including Turkey, outside the equatorial tropics. This hypothesis proceeds from the assumption that absence of evidence (of crown ape ancestors within the distributional geography of their living descendants) is evidence of absence (and therefore that basal crown apes evolved originally outside equatorial Africa (and Asia).

This scenario strikes us as unlikely, given that, for example, we know that Turkish habitats in the Middle Miocene were unlike those in which we find living apes, being more seasonal and open [68]. This would apply even more so to many Late Miocene habitats. We find it an unlikely scenario because, as we noted before, all living apes share the need for a (preferred) diet dominated by abundant ripe fruit, which we regard as a probable crown ape synapomorphy.

An alternative possibility is that the absence of tropical and subtropical equatorial ape fossils, particu-

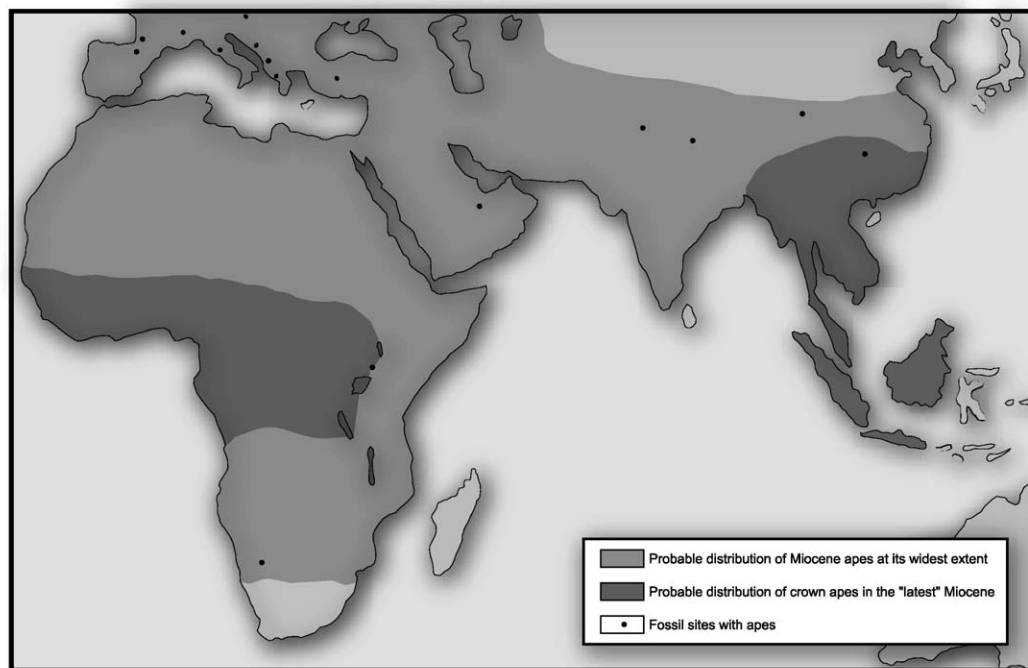


Fig. 12. Distribution of Miocene ape localities (dots) relative to hypothetical Late Miocene distribution of tropical forest (dark grey) and crown ape lineages (darker grey).

Fig. 12. Distribution de localités de grands singes du Miocène (points), relative à la distribution hypothétique de la forêt tropicale (en gris clair) et des lignées de grands singes actuels (en gris foncé) au Miocène récent.

larly those from the Late Miocene and Pliocene, is a taphonomic artifact and that until (or if) they are found it will not be possible to improve our currently inadequate phylogenetic picture of the hominoid radiation(s). A recent careful review by Cote [24] has shown that most Later Miocene fossil localities would not be expected to sample apes because of small sample size, poor preservation, or inappropriate habitat sampling. We incline to the belief that the African and Asian tropics have been home to apes with the feeding adaptations of the living species (that is, to a diet dominated by ripe fruit) at least since the Middle Miocene, while the majority of non-tropical Miocene apes are adaptively somewhat different and phylogenetically distant.

Beyond broad generalizations about extinctions of the Miocene non-equatorial apes, until we know more about their paleobiology and can be more confident in their phylogenetic relationships, we cannot go much further.

## 10. Hominin origins

Finally, we make some comments about the earliest hominins and their origins. Brunet et al. [13] describe the oldest currently known hominin, *Sahelanthropus tchadensis*, from Chad. The age, based mainly on faunal comparisons to east African localities, is as we noted earlier at around 6.5 Ma, and perhaps even older. Based on derived features such as small and apically worn canines, and postcanine teeth and basicranium resembling later hominins, the specimen clearly represents a hominin. Its faunal associations and geological context suggest a lakeside habitat comprising gallery forest, but with more open habitats close by; clearly not an equatorial rain forest [88].

We continue to believe that the common ancestor of chimpanzees and humans lived in the African tropical rainforests during the Late Miocene, and was an arboreal-terrestrial knuckle-walking ripe fruit-eater not unlike *Pan troglodytes*. *Sahelanthropus* shows

that, by at least 6.5 Ma, hominins had shifted their habitats, adopted a new diet (evidenced by cheek tooth differences from *Pan*), undergone some significant shift in social behavior (evidenced by reduced male canines and relatively enormous brow ridges), and perhaps positional behavior as well (the basicranial and other cranial changes are compatible with some kind of bipedal posture and locomotion). Postcranial material is of course essential to confirm or refute this hypothesis. Older hominoids from Chad and other areas of Africa are awaited with great interest.

## References

- [1] R.M. Adkins, E.L. Gelke, D. Rowe, R.L. Honeycutt, Molecular Phylogeny and Divergence Time Estimates for Major Rodent Groups: Evidence from Multiple Genes, *Mol. Biol. Evol.* 18 (2001) 777–791.
- [2] J. Ahlquist, personal communication.
- [3] P. Andrews, R. Bernor, Vicariance biogeography and paleoecology of Eurasian Miocene hominoid primates, in: J. Agusti, L. Rook, P. Andrews (Eds.), *Hominoid evolution and climatic change in Europe*, vol. 1, The evolution of Neogene terrestrial ecosystems in Europe, Cambridge University Press, Cambridge, 1999, pp. 454–487.
- [4] P. Andrews, L. Martin, Cladistic relationships of extant and fossil hominoids, *J. Hum. Evol.* 16 (1987) 101–118.
- [5] W.J. Bailey, D.H.A. Fitch, D.A. Tagle, J. Czelusniak, J.L. Slightom, M. Goodman, Molecular evolution of the  $\psi\eta$ -globin gene locus: gibbon phylogeny and the hominoid slowdown, *Mol. Biol. Evol.* 8 (1991) 155–184.
- [6] J.C. Barry, Faunal turnover and diversity in the terrestrial Neogene of Pakistan, in: E.S. Vrba, G.H. Denton, T.C. Partridge, L.H. Burckle (Eds.), *Paleoclimate and Evolution*, Yale University Press, New Haven, 1995, pp. 114–134.
- [7] J.C. Barry, M.E. Morgan, L.J. Flynn, D. Pilbeam, A.K. Behrensmeyer, S.M. Raza, I.A. Khan, C. Badgley, J. Hicks, J. Kelley, Faunal and Environmental Change in the Late Miocene Siwaliks of Northern Pakistan, *Paleobiol. Mem.* 28 (2002) 1–71.
- [8] D.R. Begun, Phyletic diversity and locomotion in primitive European hominids, *Am. J. Phys. Anthropol.* 87 (1992) 311–339.
- [9] D.R. Begun, European hominoids, in: W. Hartwig (Ed.), *The Primate Fossil Record*, Cambridge University Press, Cambridge, 2002, pp. 339–368.
- [10] D.R. Begun, E. Güleç, Restoration of the Type and Palate of *Ankarapithecus meteai*: Taxonomic and Phylogenetic Implications, *Am. J. Phys. Anthropol.* 105 (1998) 279–314.
- [11] D.R. Begun, C.V. Ward, M.D. Rose, Events in Hominoid Evolution, in: D.R. Begun, C.V. Ward, M.D. Rose (Eds.), *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations*, Plenum Press, New York, 1997, pp. 389–416.
- [12] L. Braga, Définition de certains caractères discrets crâniens chez *Pongo*, *Gorilla* et *Pan*: perspectives taxonomiques et phylogénétiques, PhD thesis, University Bordeaux-I, France, 1995.
- [13] M. Brunet, F. Guy, D. Pilbeam, H.T. Mackaye, A. Likius, D. Ahounta, A. Beauvillain, C. Blondel, H. Bocherens, J.R. Boisserie, L. de Bonis, Y. Coppens, J. Dejax, C. Denys, P. Düringer, V. Eisenmann, G. Fanone, P. Fronty, D. Geraads, T. Lehmann, F. Lihoreau, A. Louchart, A. Mahamat, G. Merceron, G. Mouchelin, O. Otero, P. Campomanes, M. Ponce De Leon, J.C. Rage, M. Sapanet, M. Schuster, J. Sudre, P. Tassy, X. Valentin, P. Vignaud, L. Viriot, A. Zazzo, C. Zollikofer, A new hominid from the Upper Miocene of Chad, Central Africa, *Nature* 418 (2002) 145–151.
- [14] A. Caccone, J.R. Powell, DNA Divergence among Hominoids, *Evolution* 43 (1989) 925–942.
- [15] D.W. Cameron, A revised systematic scheme for the Eurasian Miocene fossil Hominidae, *J. Hum. Evol.* 33 (1997) 449–477.
- [16] J.G.H. Cant, D. Youlatos, M.D. Rose, Locomotor behavior of *Lagothrix lagothrica* and *Ateles belzebuth* in Yasuní National Park, Ecuador: general patterns and nonsuspensory modes, *J. Hum. Evol.* 41 (2001) 141–166.
- [17] M. Cartmill, Assessing tarsier affinities: Is anatomical description phylogenetically neutral? *Geobios* 6 (1982) 279–287.
- [18] M. Cartmill, Climbing, in: M. Hildebrand, D. Bramble, K. Liem, D. Wake (Eds.), *Functional Vertebrate Morphology*, Belknap Press, Cambridge, 1985, pp. 73–88.
- [19] M. Cartmill, A Critique of Homology as a Morphological Concept, *Am. J. Phys. Anthropol.* 94 (1994) 115–123.
- [20] M. Cartmill, Anatomy, antinomies, and the problem of anthropoid origins, in: J.G. Fleagle, R.F. Kay (Eds.), *Anthropoid Origins*, Plenum Press, New York, 1994, pp. 549–566.
- [21] F. Chen, W. Li, Genomic divergences between humans and other hominoids and the effective population size of the common ancestor of humans and chimpanzees, *Am. J. Hum. Genet.* 68 (2001) 444–456.
- [22] N. Conklin-Brittain, R.W. Wrangham, K. Hunt, Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance, II. Macronutrients, *Int. J. Primatol.* 19 (1998) 971–997.
- [23] R.S. Corruccini, H.J. McHenry, Cladometric analysis of Pliocene hominids, *J. Hum. Evol.* 9 (1980) 209–221.
- [24] S. Cote, Origins of the African hominoids: an assessment of the paleobiogeographical evidence, *Palevol* 3 (2004).
- [25] T. Disotell, Phylogeny of Old World monkeys, *Evol. Anthropol.* 5 (1996) 18–24.
- [26] P. Dolhinow, A. Fuentes, *The nonhuman primates*, Mayfield Publishing Company, Mountain View, 1999. 340 p.
- [27] M. von Dornum, DNA Sequence Data from Mitochondrial COII and Nuclear G6PD Loci and a Molecular Phylogeny of the New World Monkeys (Primates, Platyrrhini), PhD thesis, Harvard University, 1997.
- [28] G.E. Erikson, Brachiation in New World Monkeys and in Anthropoid Apes, *Symp. Zool. Soc. Lond.* 10 (1963) 135–164.
- [29] J. Fleagle, Locomotion and Posture, in: D.J. Chivers (Ed.), *Malayan Forest Primates*, Plenum Press, New York, pp. 191–207.

- [30] P. Gagneux, C. Wills, U. Gerloff, D. Tautz, P.A. Morin, C. Boesch, B. Fruth, G. Hohmann, O.A. Ryder, D.S. Woodruff, Mitochondrial sequences show diverse evolutionary histories of African hominoids, *Proc. Natl Acad. Sci. USA* 96 (1999) 5077–5082.
- [31] D. Gebo, Climbing, Brachiation and Terrestrial Quadrupedalism: Historical Precursors of Hominid Bipedalism, *Am. J. Phys. Anthropol.* 101 (1996) 55–92.
- [32] D. Gebo, L. MacLatchy, R. Kityo, A. Deino, J. Kingston, D. Pilbeam, A hominoid genus from the Early Miocene of Uganda, *Science* 276 (1997) 401–404.
- [33] S. Gibbs, M. Collard, B. Wood, Soft-tissue characters in higher primate phylogenetics, *Proc. Natl Acad. Sci. USA* 97 (2000) 11130–11132.
- [34] G.V. Glazko, M. Nei, Estimation of divergence times for major lineages of primate species, *Mol. Biol. Evol.* 20 (2003) 424–434.
- [35] M. Goodman, Immunochemistry of the primates and primate evolution, *Ann. NY Acad. Sci.* 102 (1962) 219–234.
- [36] M. Goodman, A.E. Romero-Herrera, H. Dene, J. Czelusniak, R.E. Tashian, Amino acid sequence evidence on the phylogeny of Primates and other Eutherians, in: M. Goodman (Ed.), *Macromolecular sequences in systematic and evolutionary biology*, Plenum Press, New York, 1982, pp. 115–191.
- [37] M. Goodman, C.A. Porter, J. Czelusniak, S.L. Page, H. Schneider, J. Shoshani, G. Gunnell, C.P. Groves, Toward a phylogenetic classification of primates based on DNA evidence complemented by fossil evidence, *Mol. Phylogenet. Evol.* 9 (1998) 585–598.
- [38] C.P. Groves, *Gorillas*, Arthur Baker, London, 1970 96 p.
- [39] C.P. Groves, Systematics of the Great Apes, in: D. Swindler, S. Erwin (Eds.), *Comparative Primate Biology*, vol. 1, Systematics, Evolution, and Anatomy, Alan R. Liss, New York, 1986, pp. 187–217.
- [40] C.P. Groves, J.D. Paterson, Testing hominoid phylogeny with the PHYLIP programs, *J. Hum. Evol.* 20 (1991) 167–183.
- [41] T. Harrison, A Reassessment of the Phylogenetic Relationships of *Oreopithecus bambolii* Gervais, *J. Hum. Evol.* 15 (1986) 541–583.
- [42] T. Harrison, L. Rook, Enigmatic anthropoid or misunderstood ape? The phylogenetic status of *Oreopithecus bambolii* reconsidered, in: D.R. Begun, C.V. Ward, M.D. Rose (Eds.), *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations*, Plenum Press, New York, 1997, pp. 327–363.
- [43] S. Hartwig-Scherer, Allometry in Hominoids: A Comparative Study of Skeletal Growth Trends, PhD thesis, University of Zürich, Switzerland, 1993, 163 p.
- [44] B. Hedges, personal communication.
- [45] B. Hedges, S. Kumar, *Trends Genet.* 19 (2003) 200–206.
- [46] S. Horai, K. Hayasaka, R. Kondo, K. Tsugane, N. Takahata, Recent African origin of modern humans revealed by complete sequences of hominoid mitochondrial DNAs, *Proc. Natl Acad. Sci. USA* 92 (1995) 532–536.
- [47] T.H. Huxley, *Man's Place in Nature*, Ann Arbor Paperbacks, Ann Arbor, 1959 184 p.
- [48] A. Keith, Man's posture: its evolution and disorders, *Brit. Med. J.* (1923) 451–454 499–502, 545–8, 587–90, 624–6, 669–72.
- [49] A.G. Kluge, Cladistics and the Classification of the Great Apes, in: R. Ciochon, R. Corruccini (Eds.), *New Interpretations of Ape and Human Ancestry*, Plenum Press, New York, 1983, pp. 151–177.
- [50] C.D. Knott, Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability, *Int. J. Primatol.* 19 (1998) 1061–1079.
- [51] M. Köhler, S. Moyà-Solà, Ape-like or hominid-like? The positional behavior of *Oreopithecus bambolii* reconsidered, *Proc. Natl Acad. Sci. USA* 94 (1997) 11747–11750.
- [52] S. Kumar, B. Hedges, A molecular timescale for vertebrate evolution, *Nature* 392 (1998) 917–920.
- [53] S. Larson, Parallel evolution in the hominoid trunk and forelimb, *Evol. Anthropol.* 6 (1998) 87–99.
- [54] M. Leighton, Modelling dietary selectivity by Bornean orangutans: evidence for integration of multiple criteria in fruit selection, *Int. J. Primatol.* 14 (1993) 257–313.
- [55] W. Li, personal communication.
- [56] Y. Lin, P.A. McLenachan, A.R. Gore, M.J. Phillips, R. Ota, M.D. Hendy, D. Penny, Four New Mitochondrial Genomes and the Increased Stability of Evolutionary Trees of Mammals from Improved Taxon Sampling, *Mol. Biol. Evol.* 19 (2002) 2060–2070.
- [57] E.R. Miller, Faunal correlation of Wadi Moghara, Egypt: implications for the age of *Prohylobates tandyi*, *J. Hum. Evol.* 36 (1999) 519–533.
- [58] S. Moyà-Solà, M. Köhler, New partial cranium of *Dryopithecus lartet*, 1863 (Hominoidea, Primates) from the Upper Miocene of Can Llobateres, Barcelona, Spain, *J. Hum. Evol.* 29 (1995) 101–139.
- [59] M. Nei, G.V. Glazko, Estimation of divergence times for a few mammalian and several primate species, *J. Hered.* 93 (2002) 157–164.
- [60] S.V. Nelson, Faunal and Environmental Change Surrounding the Extinction of *Sivapithecus*, A Miocene Hominoid, in the Siwaliks of Pakistan, PhD thesis, Harvard University, 2002.
- [61] S.V. Nelson, *The Extinction of Sivapithecus: Faunal and Environmental Changes Surrounding the Disappearance of a Miocene Hominoid in the Siwaliks of Pakistan*, Brill Academic Publishers, Boston, 2003 138 p.
- [62] D. Pilbeam, Genetic and morphological records of the Hominoidea and hominid origins: a synthesis, *Mol. Phylogenet. Evol.* 5 (1996) 155–168.
- [63] D. Pilbeam, Research on Miocene hominoids and hominid origins: the last three decades, in: D.R. Begun, C.V. Ward, M.D. Rose (Eds.), *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations*, Plenum Press, New York, 1997, pp. 13–28.
- [64] D. Pilbeam, Hominoid systematics: the soft evidence, *Proc. Natl Acad. Sci. USA* 97 (2000) 10684–10686.
- [65] D. Pilbeam, Perspectives on the Miocene Hominoidea, in: W. Hartwig (Ed.), *The Primate Fossil Record*, Cambridge University Press, Cambridge, 2002, pp. 303–310.
- [66] C. Poux, T. van Rheede, O. Madsen, W. de Jong, Sequence gaps join mice and men phylogenetic evidence from deletions in two proteins, *Mol. Biol. Evol.* 19 (2002) 2035–2037.



- [67] PRISM, Middle Pleistocene environments of the Northern Hemisphere, in: E.S. Vrba, G.H. Denton, T.C. Partridge, L.H. Burckle (Eds.), *Paleoclimate and Evolution*, Yale University Press, New Haven, 1995, pp. 197–212.
- [68] J. Quade, T.E. Cerling, P. Andrews, B. Alpagut, Paleodietary reconstruction of Miocene faunas from Paçalar, Turkey using stable carbon and oxygen isotopes of fossil tooth enamel, *J. Hum. Evol.* 28 (1995) 373–384.
- [69] D.T. Rasmussen, Early catarrhines of the African Eocene and Oligocene, in: W.C. Hartwig (Ed.), *The Primate Fossil Record*, Cambridge University Press, Cambridge, 2002, pp. 203–220.
- [70] M. Ruvolo, Molecular phylogeny of the hominoids: inference from multiple independent DNA sequence data sets, *Mol. Biol. Evol.* 14 (1997) 248–265.
- [71] M. Ruvolo, Genetic Diversity in Hominoid Primates, *Annu. Rev. Anthropol.* 26 (1997) 515–540.
- [72] V.M. Sarich, Retrospective on hominoid macromolecular systematics, in: R.L. Ciochon, R.S. Corruccini (Eds.), *New Interpretations of Ape and Human Ancestry*, Plenum Press, New York, 1983, pp. 137–150.
- [73] V.M. Sarich, Mammalian systematics: twenty-five years among their albumins and transferrins, in: F. Szalay, M. Novacek, M. McKenna (Eds.), *Mammal Phylogeny: Placentals*, Springer-Verlag, New York, 1993, pp. 103–114.
- [74] Y. Satta, J. Klein, N. Takahata, DNA archives and our nearest relative: the trichotomy problem revisited, *Mol. Phylogenet. Evol.* 14 (2000) 259–275.
- [75] A.H. Schultz, The skeleton of the trunk and limbs of higher primates, *Hum. Biol.* 2 (1930) 303–438.
- [76] A.H. Schultz, The Recent Hominoid Primates, in: S.L. Washburn, P.C. Jay (Eds.), *Perspectives on Human Evolution*, Holt, Rinehart, and Winston, New York, 1968, pp. 122–195.
- [77] J.H. Schwartz, The evolutionary relationships of man and orang-utans, *Nature* 308 (1984) 501–505.
- [78] J.H. Schwartz, *Lufengpithecus* and hominoid phylogeny: problems in delineating and evaluating phylogenetically relevant characters, in: D.R. Begun, C.V. Ward, M.D. Rose (Eds.), *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations*, Plenum Press, New York, 1997, pp. 363–388.
- [79] B.T. Shea, An allometric perspective on the morphological and evolutionary relationships between pygmy (*Pan paniscus*) and common (*Pan troglodytes*) chimpanzees, in: R. Susman (Ed.), *The Pygmy Chimpanzee*, Plenum Press, New York, 1984, pp. 89–130.
- [80] C.G. Sibley, J.A. Comstock, J.E. Ahlquist, DNA hybridization evidence of hominoid phylogeny – a reanalysis of the data, *J. Mol. Evol.* 30 (1990) 202–236.
- [81] G.G. Simpson, The meaning of taxonomic statements, in: S.L. Washburn (Ed.), *Classification and human evolution*, Viking Fund Publications in Anthropology, No. 37, Wenner-Gren Foundation, New York, 1963, pp. 1–31.
- [82] M. Springer, W. Murphy, E. Eizirik, S. O'Brien, Placental mammal diversification and the Cretaceous–Tertiary boundary, *Proc. Natl Acad. Sci.* 100 (2003) 1056–1061.
- [83] R.L. Stauffer, A. Walker, O.A. Ryder, M. Lyons-Weiler, S. Hedges, Human and ape molecular clocks and constraints on paleontological hypotheses, *J. Hered.* 92 (2001) 469–474.
- [84] C. Stewart, T.R. Disotell, Primate evolution – in and out of Africa, *Curr. Biol.* 8 (1998) 582–588.
- [85] S. Tavaré, C.R. Marshall, O. Will, C. Soligo, M. Martin, Using the fossil record to estimate the age of the last common ancestor of extant primates, *Nature* 416 (2002) 726–729.
- [86] R.H. Tuttle, Parallelism, brachiation, and hominoid phylogeny, in: Luckett, F. Szalay (Eds.), *Phylogeny of the Primates: a multidisciplinary approach*, Plenum Press, New York, 1975, pp. 447–480.
- [87] A. Uchida, Design of the mandibular molar in the extant great apes and Miocene fossil hominoids, *Anthropol. Sci.* 106 (1998) 119–126.
- [88] P. Vignaud, P. Düringer, T.M. Hassane, A. Likius, C. Blondel, J.-R. Boisserie, L. de Bonis, V. Eisenmann, M.-E. Étienne, D. Geraadsk, F. Guy, T. Lehmann, F. Lihoreau, N. Lopez-Martinez, C. Mourer-Chauvire, O. Otero, J.C. Rage, M. Schuster, L. Viriot, A. Zazzo, M. Brunet, Geology and palaeontology of Miocene Toros-Menalla hominid locality, *Chad, Nature* 418 (2002) 152–155.
- [89] A. Walker, *Proconsul*: function and phylogeny, in: D.R. Begun, C.V. Ward, M.D. Rose (Eds.), *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations*, Plenum Press, New York, 1997, pp. 209–224.
- [90] R.W. Wrangham, N. Conklin-Brittain, K. Hunt, Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants, *Int. J. Primatol.* 19 (1998) 949–970.
- [91] C. Wu, W. Li, Evidence for higher rates of nucleotide substitution in rodents than in man, *Proc. Natl Acad. Sci. USA* 82 (1985) 1741–1745.
- [92] J. Yamagiwa, T. Maruhashi, T. Yumoto, N. Mwanza, Dietary and ranging overlap in sympatric gorillas and chimpanzees in Kahuzi-Biega National Park, Zaïre, in: W.C. McGrew, L.F. Marchant, T. Nishida (Eds.), *Great Ape Societies*, Cambridge University Press, Cambridge, 1999, pp. 82–100.
- [93] N.M. Young, Homology and Homoplasy in the Evolution of the Hominoid Postcranium, PhD thesis, Harvard University, 2002, 289 p.
- [94] N.M. Young, A reanalysis of variability in the hominoid postcranium: implications for ape evolution, *J. Hum. Evol.* 45 (2003) 441–464.
- [95] N.M. Young, L. MacLachy, The Phylogenetic Position of *Morotopithecus*, *J. Hum. Evol.* (in press).