AN OBJECTIVE TIME BASED PHYLOGENETIC CLASSIFICATION OF PRIMATES THAT PLACES CHIMPANZEES AND HUMANS IN THE GENUS HOMO

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ABSTRACT. Molecular phylogenetics, a coupling of molecular biology to Hennig's phylogenetic systematics, is bringing about a twofold shift in paradigms, one in systematics and the other in how we view our place in nature. The new paradigm in systematics disbands the traditional use of taxonomic grades and, instead, favors strictly genealogical classifications in which all taxa are monophyletic and are arranged in a hierarchical scheme that reflects the time course of phylogeny. The second new paradigm rejects the traditional anthropological view that we humans are greatly different from all other species and instead emphasizes our commonalities with other species, e.g. our very close genetic identity to chimpanzees. On using DNA evidence on primate phylogeny, complemented by paleontological evidence, a temporal based classification of primates describes objectively, without anthropocentric biases, the taxonomic place of humans among the primates. All living apes and humans belong to subfamily Homininae. Homininae divides into Hylobatini (common and siamang gibbons) and Hominini, the latter into Pongina for *Pongo* (orangutans) and Hominina for *Gorilla* and *Homo*. *Homo* itself divides into the subgenera *H.* (*Homo*) for humans and *H.* (*Pan*) for common and pygmy chimpanzees. Even on disbanding *Australopithecus* and *Ardipithecus* by placing their species into *Homo* (*Homo*), the presumed genealogical relationships of these extinct species to each other and to living humans can be depicted by how the species are listed and indented under the subgenus rank.

KEY WORDS. Molecular phylogenetics, phylogenetic classification, taxonomic ranks, DNA evidence, primate phylogeny, primate clades, bipedal hominids, common and bonobo chimpanzees, *Homo* (*Homo*), *Homo* (*Pan*).

Hennig (1966) observed that one of the more perplexing problems in taxonomy is the assigning of ranks to the groups in a hierarchical taxonomic classification. A partial solution to this problem is to have phylogenetic classifications in which all taxa represent monophyletic groupings, i.e., the names of the taxa can serve as the names of actual

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clades. Clearly, on so naming clades, a younger clade nested within an older clade, taxonomically must always have a rank at a lower hierarchical level than the older clade. For example, all taxa with the rank of family in a cladistic phylogenetic classification of primates should be of younger age than the order Primates, the older more inclusive taxon; similarly all orders of mammals should be of younger age than the class Mammalia. In as much as ranking solely by relative age does not ensure that taxa assigned the same rank represent clades that are equivalent to one another with respect, at least, to some key objective measure, Hennig (1966) reasoned that the optimal yardstick for measuring which clades are equivalent is the absolute age of origin of the clades, i.e., the taxa assigned the same rank should represent clades of about the same absolute age. Perhaps because such a temporal system of classification would be inordinately difficult to achieve across phyla, Hennig (1981) initiated a trend among cladists to abandon the use of ranks altogether (De Queiroz and Gauthier, 1992). Nevertheless, since long established rules in the practice of taxonomy require that taxonomic names with the endings *oidea*, *idae*, *inae*, *ini*, and *ina* designate the ranks of superfamily, family, subfamily, tribe, and subtribe, respectively, and since most systematists and taxonomists still use ranks in their classifications, Hennig's cogent reasons for a rank equals age system of phylogenetic classification still have merit. Moreover, molecular phylogenetic investigations have provided tools along with those of paleontological investigations for dating branch-points in phylogeny and thus for constructing phylogenetic classifications in which taxa at the same rank represent clades of equivalent age (Goodman, 1996; Goodman *et al.*, 1998). Not only have the primates been so classified (Goodman *et al.*, 1998, 1999a,b) but the potential exists from the combined tools of molecular phylogenetics and paleontology for eventually extending a temporal scheme of biological classification to all living phyla (Avise and John, 1999).

Molecular phylogenetic investigations utilize the knowledge that each present-day genome contains a range of DNA sequences from rapidly to extremely slowly evolving. This makes it possible to discover the phylogenetic relationships that exist among living species at all levels of the taxonomic hierarchy from the most recently to the most anciently separated. The advances in doing so are bringing about a two-fold shift in paradigms, one in systematics and the other in how we humans should view our place in nature. The new paradigm in systematics is essentially that first envisioned by Charles Darwin and further developed in a rigorous scientific way by Willig Hennig. It calls for disbanding the use of so-called grade taxa, such as the traditional primate taxa Prosimii and Pongidae with their paraphyletic groupings and instead calls, as sketched out above, for strictly genealogical (*i.e.*, cladistic) classifications that depict

sister-group relationships and, ideally, denote by rank level the clades of equivalent age. The other new paradigm rejects the traditional anthropological view that we humans are greatly different from all other animal species. Instead, the molecular view emphasizes how much we hold in common with other species, especially with our sister-group the common and bonobo chimpanzees. Below we present, in terms of the DNA and paleontological evidence on primate phylogeny, a temporal based phylogenetic classification of primates that describes in an objective, nonanthropocentric way the taxonomic place of humankind among the primates.

D.N.A. EVIDENCE ON PRIMATE PHYLOGENY

Considerable evidence on primate phylogeny already exists, the most objective being the DNA evidence. The main studies that have gathered this DNA evidence are listed in Table 1. The phylogenetic analyses carried out in these studies have utilized DNA hybridization data and both mitochondrial and nuclear DNA sequence data, the latter from a growing number of unlinked nuclear genomic loci. The nonfunctional noncoding sequences of the nuclear loci due to their relatively fast nucleotide substitution rates have provided some of the best evidence on the phylogenetic relationships of humans and other living primates (Goodman *et al.*, 1998). Moreover the patterns of noncoding nucleotide substitution seem to conform to a continuous time Markov chain stochastic process. A model that includes this stochastic process and a putative phylogenetic tree describing the descent of the sequences can be examined by a goodness of fit test to see how close the observed distribution of character states (the four nucleotides A, C, G, T) in the present day sequences agrees with the model's expected distribution. With our datasets of noncoding DNA sequences there is only one tree not rejected by the goodness of fit test; it has the common and bonobo chimpanzee clade and the human clade closest to each other, i.e., as sister-groups. Table 2 presents a simplified example of this result using the binary code (A and G = R, C or T = Y) for transversions (RY) and orthologous human, chimpanzee, gorilla, and orangutan noncoding nucleotide sequences. The phylogenetic classification of primates presented in Table 3 summarizes the results obtained from our larger DNA datasets representing the full range of primate clades. The results of cladistic analyses of morphological characters are congruent with these DNA results and thus provide further evidence that chimpanzees are the sister-group of humans (Shoshani *et al.*, 1996; Goodman *et al.*, 1998*)*.

THE PHYLOGENETIC CLASSIFICATION OF PRIMATE CLADES

This classification (Table 3) was constructed by synthesizing the DNA evidence on phylogenetic relationships with the fossil and molecular evidence on branch times in primate phylogeny. In the classification, each taxon represents a monophyletic group or clade, the hierarchical groupings of lower-ranked taxa into higher-ranked taxa describe the phylogenetic relationships of the clades, and taxa at the same rank represent clades that are roughly equally old, i.e., at an equivalent evolutionary age. The fossil record by itself allowed estimates of the ages of only a scattering of branch-points in primate phylogeny. However, the model of local molecular clocks applied to the branch lengths of phylogenetic trees constructed from our DNA datasets allowed estimates of the ages of all branch-points in these trees. The model of local molecular clocks differs from that of a global molecular clock by not assuming that all lineages accumulate nucleotide substitutions at the same rate; local molecular clock calculations are much more constrained by fossil evidence on branch-times than global molecular clock calculations are (Goodman, 1986; Bailey *et al.*, 1991, 1992; Porter *et al.*, 1997a,b, 1999; Barroso *et al.*, 1997; Meireles *et al.*, 1999; Chaves *et al.*, 1999). Even though nucleotide substitutions in the nonfunctional noncoding DNA tend to accumulate at a less variable rate than positively selected nucleotide substitutions, selectively neutral substitution rates can still show considerable variation between lineages. For example, the nonfunctional noncoding DNA evolution rate is almost twice as fast in loriform strepsirhines than in lemuriform strepsirhines (Bonner *et al.*, 1980, 1981; Koop *et al.*, 1989; Porter *et al.*, 1997a). As another example, leaf-eating Old World monkeys show a faster rate than cheek-pouched Old World monkeys (Page *et al.*, 1999). Local molecular clock estimates of branch-times adjust for such lineage variation in rates by having each base substitution occur over a longer period of time in a more slowly evolving lineage than in a more rapidly evolving lineage.

To use the model of local molecular clocks for estimating lineage divergence dates from the percentages of sequence change on the branches of the molecular phylogenetic trees, reference dates based on fossil evidence (reviewed in Goodman *et al.*, 1998) were used to calibrate the local clocks. This fossil evidence placed the lineage divergence date or last common ancestor (LCA) of Old World monkeys (family Cercopithecidae) and humans and apes (family Hominidae) at 25 Ma (millions of years ago), the LCA of platyrrhines and catarrhines at 40 Ma, and the LCA of strepsirhines and haplorhines (i.e., of all living primates) at 63 Ma. The paleontologically based age of 25 Ma for the LCA of cercopithecids and hominids served as the starting reference date for estimating the divergence dates for lineages within the hominid clade and separately within the cercopithecid clade. The age of 40 Ma for the LCA of platyrrhines and

catarrhines served as the starting date for estimating the divergence dates for lineages within the platyrrhine clade. The age of 63 Ma for the LCA of strepsirhines and haplorhines served as the starting date for estimating the divergence dates for lineages within the strepsirhine clade and also for the haplorhine lineage to tarsiers.

On the basis of the results obtained from the molecular phylogenetic trees on the phylogenetic relationships and ages of the primate clades, the classification in Table 3 portrays a series of phylogenetic branchings during the course of primate evolution from the Paleocene epoch to the present day. The division of a higher-ranked taxon into subordinate lower-ranked taxa denotes a phylogenetic branching. The age (in Ma) placed after the name of a taxon is the estimated age of that taxon treated as a *crown group* but also of that taxon's closest (at a step below in rank) subordinate taxa treated as *total groups*. A crown group includes both the LCA of the extant species in a clade and all descendant species (extinct and extant) of the LCA but does not include the stem of the LCA (Jeffries 1979). The total group includes, in addition to all members of the crown group, the stem of the LCA and all extinct offshoots of the stem. Thus the age of 63 Ma for the LCA of all living primates—that is, the age for Primates as a crown group—is the age for both Strepsirhini and Haplorhini as total groups. In turn, the ages of 50 Ma and 58 Ma listed alongside of Strepsirhini and Haplorhini, respectively, are the ages for these two taxa treated as crown groups.

After this first major branching, in the early Paleocene epoch, into semiordinal clades, subordinal clades emerged. The late Paleocene haplorhines divided into Tarsiiformes and Anthropoidea. The anthropoideans of the middle Eocene epoch (at ~40 Ma) divided into the infraorders Platyrrhini and Catarrhini. As total groups, families originated from superfamilial clades within infraorders in the middle to late Oligocene epoch (~28-25 Ma), subfamilies in the early Miocene epoch (~23-22 Ma), tribes in the early to middle Miocene (~20-15 Ma), subtribes in the middle to late Miocene (~14-10 Ma), genera in the late Miocene (~10-7 Ma), and subgenera in the late Miocene to early Pliocene epoch (~7-4 Ma). Estimated branch times at the infrageneric level for the species examined at the DNA level in this study ranged from 7 to <1 Ma.

In this primate classification, in which taxa represent clades and the ages of the clades determine the ranks of the taxa, many of the names for taxa are the same as those commonly used in other primate classifications. This is possible because in traditional primate classifications, despite the use of the grade concept to name some of the taxa, most taxa do represent monophyletic groups. For example, in the traditional primate classification used by Martin (1990), there are extant members in 5 infraorders, 6 superfamilies, 12 families, and 13 subfamilies. The molecular evidence shows

that all these extant infraorders and superfamilies, 9 of the 12 extant families and 10 or, possibly, 11 of the 13 extant subfamilies are monophyletic taxa. However, sister-group relationships are not well depicted, nor are taxa at the same rank necessarily at an equivalent age in traditional primate classifications. However, a crude correlation does exist between age of origin of a taxon and its rank. As Romer (1962, p. 32) observed, the rise of modern orders and suborders of mammals occurred in the Eocene epoch, the rise of modern families in the Oligocene epoch, and the rise of modern subfamilies in the Miocene epoch. In correlation, the strictly phylogenetic classification of primate taxa, with its age equivalence among taxa at the same rank, places suborders, families, and subfamilies, when treated as total groups, in the Eocene, Oligocene, and Miocene geologic epochs, respectively. The names for genera used in tabulations of the living primates (e.g., see Groves 1993) are also used in the phylogenetic classification (Table 3), in most cases as full generic names but in a few cases as subgeneric names. An exception is that Groves (1993) treats gibbons and siamangs as members of the same genus, *Hylobates*. However, the estimated LCA age for gibbons and siamangs is 8 Ma. Thus in this case, the phylogenetic classification places these two apes in separate genera but groups them together in the same subtribe.

In contrast with the traditional family Hominidae, which has *Homo sapiens* as its only living species, the age-equals-rank system places all living apes and humans in subfamily Homininae. A phylogenetic branching (at ~18 Ma) divided this subfamily into tribes Hylobatini and Hominini. Within Hylobatini, the phylogenetic branching (at ~8 Ma) in the subtribe Hylobatina separated *Symphalangus* (siamangs) from *Hylobates* (gibbons). Within Hominini, a phylogenetic branching (at ~14 Ma) separated the monogeneric subtribe Pongina for *Pongo* (orangutans) from Hominina. Within Hominina, a phylogenetic branching (at ~7 Ma) separated *Gorilla* from *Homo*. Within *Homo*, a phylogenetic branching (at ~6 Ma) separated the subgenus for common chimpanzees and bonobos —that is, *H.* (*Pan*)—from the subgenus for humans—that is, *H.* (*Homo*). Thus, the principle of rank equivalence with other primate clades of the same age requires grouping the chimpanzee clade with the human clade within the same genus.

Humans and chimpanzees are more than 98.3 percent identical in their typical nuclear noncoding DNA and more than 99.5 percent identical in the active coding nucleotide sequences of their functional nuclear genes (Goodman *et al.*, 1989, 1990). In mammals such high genetic correspondence is commonly found between sibling species below the generic level but not between species in different genera. The genetic and phylogenetic evidence that groups humans and chimpanzees together as sister subgenera of the same genus justifies the belief that the two chimpanzee species

can provide insights into distinctive features of humankind's own evolutionary origins. Indeed chimpanzees use tools, have material cultures, are ecological generalists, and are highly social (McGrew, 1992; DeWaal, 1995; Goldberg, 1998). Their anatomical inability to produce most of the sounds of human speech long obscured the fact that they are also capable of understanding and using rudimentary forms of language, as shown by recent studies on communication via sign language and lexigrams (Fouts and Mills, 1997; Savage-Rumbaugh, Shanker, and Taylor, 1998).

THE BIPEDAL HOMINIDS: SUBGENUS *HOMO* (*HOMO*)

Placing all living apes and humans in the subfamily Homininae and including common and bonobo chimpanzees with humans in the genus *Homo* conflicts with the entrenched usage of the term "hominids" for the clade which contains only humans and fossils that are cladistically closer to humans than to any other living primates. To acknowledge the scientific merit of classifying humans close to apes and especially close to chimpanzees and still have a vernacular term for the clade that contains humans and that traces back to the LCA of humans and chimpanzees, the term "bipedal hominids" (e.g., as used by Kohler and Moya-Sola, 1997) could substitute for the term "hominids". In this regard one could also use the vernacular term "proto-humans" when referring to the fossil forms that are cladistically closer to humans than to any other living primates. However, the problem would still remain as to how a genealogical classification could place the extinct species of bipedal hominids, i.e., the proto-humans, as well as *Homo sapiens* in the subgenus *Homo* (*Homo*) and still display the sister-group relationships of these species. The following repeats verbatim an exercise (Goodman *et al.*, 1999a) that shows how this can be done.

In this exercise we focus on the genealogical relationships of ten extinct species to one another and to modern humans as portrayed by Yoon (1995) in her news account of the views of paleoanthropologists following the discovery of the 3.9 – 4.2 Ma fossil species named *Australopithecus anamensis*. The other fossil species are *Ardipithecus ramidus*, four *Australopithecus* species (*A. afarensis, A. africanus, A. robustus,* and *A. boisei*), and three *Homo* species (*H. habilis, H. erectus,* and *H. neanderthalensis*). Our genealogical classification for the extinct species and extant *Homo sapiens* places them all in *Homo* (*Homo*) as the sister of *Homo* (*Pan*) (Table 4). For each species listed in Table 4 under *H.* (*Homo*) the species name and age from Yoon (1995) is given in parenthesis after its species name as a member of the subgenus *Homo* (*Homo*). Our classification, by the way it sequentially lists and indents the species, portrays the same relationships among them as portrayed by Yoon. Thus *ramidus*, the first listed and least indented

member of the subgenus is treated as if it represented the clade that contains *ramidus* and all the species listed below it at more indented positions. At age 4.4 Ma, *ramidus* could be viewed either as the LCA of the members of the clade or as a close relative of the LCA. The next listed species *anamensis* (at age 4.2–3.9 Ma and at a more indented position than *ramidus*) may be viewed as a lineal descendant of the LCA represented by *ramidus*, thus *anamensis* represents a clade that originated closer to the present than the clade represented by *ramidus*. Again, the next listed species, *afarensis* (at age 3.6 – 2.8 Ma and at a more indented position than *anamensis*) represents a clade closer to the present than the clade represented by *anamensis*. From a basal population within the *afarensis* clade two diverging descendant clades emerged, one represented by *africanus* (at age 2.8 – 2.4 Ma) and the other by *habilis* (at age 1.9–1.8 Ma). The extinct species *boisei* (at age 2.4–1.3 Ma) and *robustus* (at age 2.0–1.6 Ma) are members of the *africanus* clade, while *erectus* (at age 1.8–0.9 Ma) is a member of the *habilis* clade. The two *sapiens* subspecies, i.e., extinct *s. neanderthalensis* (at age 0.5–0.1 Ma) and extant *s. sapiens* (at age 0.5 – 0.0 Ma) are members of the *erectus* clade.

If *afarensis* and the *africanus* and *habilis* members of *afarensis* clade all share a more recent common ancestor or LCA with one another than with *anamensis*, as portrayed by Yoon (1995) and displayed in Table 4, then the paleoanthropological genus *Australopithecus* (which includes *anamensis*, *afarensis*, and the members of the *africanus* clade but not the members of the *habilis* clade) is a paraphyletic taxon. In contrast, our subgenus *Homo* (*Homo*) (which includes all members of the paleoanthropological *Ardipithecus*, *Australopithecus*, and *Homo* genera) is a monophyletic taxon. Moreover our classification, as illustrated in Table 4, displays the presumed genealogical relationships of the extinct species to one another as well as to living humans.

TABLE 1

DNA STUDIES THAT ELUCIDATE PRIMATE PHYLOGENY

Major Clades	Platyrrhine Clades	Cercopithecid Clades
Bailey *et al.* (1991)	Barroso *et al.* (1997)	Benveniste (1985)
Bailey *et al.* (1992)	Benveniste (1985)	Disotell *et al.* (1992)
Goodman *et al.* (1998)	Canavez *et al.* (1999)	Goodman *et al.* (1998)
Koop *et al.* (1989)	Chaves *et al.* (1999)	Harris and Disotell (1998)
Porter *et al.* (1995)	Chiu (1997)	Messier and Stewart (1997)
Porter *et al.* (1997a)	Goodman *et al.* (1998)	Page *et al.* (1999)
Zietkiewicz *et al.* (1999)	Harada *et al.* (1995)	Van der Kuyl *et al.* (1995)
	Horovitz and Meyer (1995)	
Strepsirhine Clades	Horovitz *et al.* (1998)	**Hominid Clades**
Bailey *et al.* (1991)	Meireles *et al.* (1999)	Arnason *et al.* (1998)
Bailey *et al.* (1992)	Porter *et al.* (1995)	Bailey *et al.* (1991)
Bonner *et al.* (1980)	Porter *et al.* (1997a)	Bailey *et al.* (1992)
Bonner *et al.* (1981)	Porter *et al.* (1997b)	Benveniste (1985)
Goodman *et al.* (1998)	Porter *et al.* (1999)	Caccone and Powell (1989)
Porter *et al.* (1995)	Schneider *et al.* (1993)	Goodman *et al.* (1998)
Porter *et al.* (1997a)	Schneider *et al.* (1996)	Horai *et al.* (1995)
Yoder *et al.* (1996)	Tagliaro *et al.* (1997)	Perrin-Pecontal *et al.* (1992)
Yoder (1997)	von Dornum (1997)	Porter *et al.* (1997a)
	von Dornum and Ruvulo (1999)	Ruvolo (1997)
		Sibley and Ahlquist (1987)
		Takahata and Satta (1997)
		Satta *et al.* (2000)

TABLE 2

OBSERVED AND EXPECTED COUNTS OF PURINE R AND PYRIMIDINE Y CHARACTER
PATTERNS FOR ALIGNED HUMAN (H), CHIMPANZEE (C) GORILLA (G), AND
ORANGUTAN (O) γ SEQUENCES [a]

CHARACTER STATE PATTERN	OBSERVED	EXPECTED (H, C), (G, O)	EXPECTED (H, O), (C, G)	EXPECTED (H, G), (C, O)
RRRR	3659	3658.413976	3657.087016	3656.47514
RRRY	31	31.618508	10.888444	33.50574
RRYR	9	8.971724	3.02252	3.02252
RRYY	3	3.000404	0.159919	0.08406
RYRR	3	2.963544	32.893864	10.881072
RYRY	0	0.071858	0.145427	0.148346
RYYR	0	0.142626	0.078821	0.156321
RYYY	15	14.81772	15.731848	15.731848
YRRR	9	9.62046	9.0307	9.642576
YRRY	1	0.114754	0.12828	0.125575
YRYR	0	0.116246	0.117714	0.120585
YRYY	10	10.151244	33.57946	12.031104
YYRR	1	1.002592	1.002592	0.136184
YYRY	11	11.198068	10.829468	11.087488
YYYR	33	32.76854	11.773084	33.572088
YYYY	3587	3587.0309	3585.534384	3585.283736
G^2		3.28 (22%)	16.32 (0%)	18.79 (0%)

[a] These are noncoding orthologous DNA sequences, each flanking 5′ and 3′ the
tandemly duplicated γ¹ and γ² globin genes; any γ¹ and γ² sequences with a history of
gene conversions were removed from the alignment. A character pattern is the array of
characters at an aligned orthologous sequence position in species order h, c, g, and o.
For example, the character pattern RRYY represents alignment positions at which h is
R, c is R, g is Y, and o is Y. Each of the observed counts is the number of alignment
positions at which a character pattern occurs. The expected count of each character
pattern comes from multiplying the total number of sites 7372 by the multinominal
probability of that particular character pattern calculated by the model. For each of the
three alternative trees, the likelihood ratio G^2 goodness of fit criterion was minimized
in finding the expected counts of character patterns. The resulting G^2 values are shown
in the row labelled G^2; in parentheses this row also shows the estimated P values
(number of Monte Carlo replicates out of 1000 having G^2 greater than that of the
observed). The nature of these calculations are described in Czelusniak and Goodman
(1995).

TABLE 3: DNA BASED PHYLOGENETIC CLASSIFICATION[a] OF PRIMATES

Order Primates (63 Ma)
Semiorder Strepsirhini (50 Ma)
Suborder Lemuriformes (45 Ma)
Infraorder Chiromyiformes
Family Daubentoniidae
Daubentonia madagascariensis: aye-aye
Infraorder Eulemuriformes
Superfamily Lemuroidea (28 Ma)
Family Cheirogaleidae (22 Ma)
Subfamily Microcebinae
Microcebus murinus: gray mouse lemur
Subfamily Cheirogaleinae
Cheirogaleus medius: fat-tailed dwarf lemur
Family Indridae
Propithecus verreauxi: verreaux's sifaka
Family Lemuridae
Eulemur fulvus: brown lemur
Suborder Loriformes
Family Loridae (23 Ma)
Subfamily Galagoninae
Otolemur crassicaudatus: thick-tailed greater bush baby
Subfamily Perodicticinae
Perodicticus potto: potto
Subfamily Lorinae
Nycticebus coucang: slow loris
Semiorder Haplorhini (58 Ma)
Suborder Tarsiiformes
Family Tarsiidae
Tarsius (6 Ma)
T. syrichta: Philippine tarsier
T. bancanus: western tarsier
Suborder Anthropoidea (40 Ma)
Infraorder Platyrrhini
Superfamily Ceboidea (26 Ma)
Family Cebidae (22 Ma)
Subfamily Cebinae (20 Ma)
Tribe Cebini
C. albifrons: white-fronted capuchin
C. olivaceus: weeper capuchin
C. kaapori: capuchin
Tribe Saimiirini
Saimiri (2 Ma)
S. sciureus: common squirrel monkey
S. boliviensis: Bolivian squirrel monkey
Subfamily Aotinae
Aotus (3 Ma)
A. azarae: red-necked night monkey
A. nancymai: red-necked night monkey

Subfamily Callitrichinae
Tribe Callitrichini (14 Ma)
Subtribe Saguina
Saguinus (6 Ma)
S. fuscicollis: saddleback tamarin
S. bicolor: bare-faced tamarin
S. midas: golden-handed tamarin
Subtribe Leontopithecina
Leontopithecus rosalia: golden lion tamarin
Subtribe Callimiconina
Callimico goeldii: goeldi's monkey
Subtribe Callitrichina
Callithrix (5 Ma)
C. (Callithrix) (<1 Ma)
C. (C.) jacchus: common marmoset
C. (C.) geoffroyi: geoffroy's tufted-eared marmoset
C. (Cebuella) pygmaea: pygmy marmoset
C. (Mico) (3 Ma)
C. (M.) argentata: bare-ear marmoset
C. (M.) humeralifer: tassel-eared marmoset
C. (M.) mauesi: maues marmoset
Family Pitheciidae
Subfamily Pitheciinae (19 Ma)
Tribe Callicebini
Callicebus (7 Ma)
C. moloch: dusky titi monkey
C. torquatus: collared titi monkey
Tribe Pitheciini
Subtribe Pitheciina (11 Ma)
Pithecia irrorata: bald-faced saki
Chiropotes (6 Ma)
C. (Cacajao) calvus: bald uacari
C. (Chiropotes) satanas: bearded saki
Family Atelidae
Subfamily Atelinae (17 Ma)
Tribe Alouattini
Alouatta (3 Ma)
A. caraya: black-and-gold howler
A. belzebul: red-handed howler
A. seniculus: red howler
Tribe Atelini (12 Ma)
Subtribe Atelina
Ateles (4 Ma)
A. paniscus: black spider monkey
A. geoffroyi: black-handed spider monkey
Subtribe Brachytelina (10 Ma)
Lagothrix lagotricha: woolly monkey
Brachyteles arachnoides: woolly spider monkey

Infraorder Catarrhini
Superfamily Cercopithecoidea (25 Ma)
Family Cercopithecidae
Subfamily Cercopithecinae (15 Ma)
Tribe Colobini (10 Ma)
Subtribe Colobina
Colobus guereza: Abyssinian colobus
Subtribe Presbytina (7 Ma)
Trachypithecus obscurus: spectacled leaf monkey or langur
Nasalis larvatus: proboscis monkey
Tribe Cercopithecini (10 Ma)
Subtribe Cercopithecina (9 Ma)
Cercopithecus
C. cephus: mustached guenon
Erythrocebus
E. patas: patas monkey
Chlorocebus
C. aethiops: green monkey
Subtribe Papionina (9 Ma)
Macaca (4 Ma)
M. mulatta: rhesus macaque
M. nigra: Celebes macaque
Cercocebus (5 Ma)
C. (Mandrillus) (4 Ma)
C. (M.) sphinx: mandrill
C. (M.) leucophaeus: drill
C. (Cercocebus) galeritus: Tana river mangabey
Papio (4 Ma)
P. (Papio) hamadryas cynocephalus: yellow baboon
P. (Theropithecus) gelada: gelada baboon
P. (Lophocebus) aterrimus: black mangabey
Family Hominidae
Subfamily Homininae (18 Ma)
Tribe Hylobatini
Subtribe Hylobatina (8 Ma)
Symphalangus syndactylus: siamang
Hylobates lar: white-handed gibbon
Tribe Hominini (14 Ma)
Subtribe Pongina
Pongo pygmaeus: Borneo orangutan
Subtribe Hominina (7 Ma)
Gorilla gorilla: gorilla
Homo (6 Ma)
H. (Pan) (3 Ma)
H. (P.) troglodytes: chimpanzee
H. (P.) paniscus: pygmy chimpanzee or bonobo
H. (Homo) sapiens: humankind

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[a] An age placed in parentheses after the name of a higher taxon in this hierarchical classification represents the estimated age of that higher taxon, treated as a *crown group*, but also of the next lower ranking taxa, treated as *total groups*. Common names for extant species are from Rowe (1996). Estimated ages are either the same or very close to previous estimates (Goodman *et al.*, 1998, 1999). Additional information from the molecular phylogenetic trees produced in recent studies was used in recalculating the estimated ages for taxa within Platyrrhini (Meireles *et al.*, 1999; Chaves *et al.*, 1999) and within Cercopithecidae (Page *et al.*, 1999). Subgeneric names are used here for any collection of species with an estimated LCA age of 6 Ma or less and with at least some species in the collection having different full generic names (Groves (1993), also in Rowe (1996) who follows Groves in his use of generic names. In fact to have a rough equivalence for taxa at the same rank, subgeneric names should also have been used for the subdivisions within *Tarsius*, *Cebus*, *Saguinus*, *Callicebus*, *Ateles*, and *Macaca* as the estimated crown group ages of these genera are 6, 5, 6, 7, 4, and 4 Ma, respectively.

TABLE 4

A GENEALOGICAL CLASSIFICATION OF EXTANT AND EXTINCT
SPECIES WITHIN THE GENUS *HOMO*[a]

Homo
  H. (Pan)
    H. (P.) paniscus
    H. (P.) troglodytes
  H. (Homo)
    H. (H.) ramidus (Ardipithecus ramidus, 4.4 Ma)[a]
     H. (H.) anamensis (Australopithecus anamensis, 4.2-3.9 Ma)[a]
      H. (H.) afarensis (Australopithecus afarensis, 3.6-2.8 Ma)[a]
       H. (H.) africanus (Australopithecus africanus, 2.8-2.4 Ma)[a]
        H. (H.) boisei (Australopithecus boisei, 2.4-1.3 Ma)[a]
        H. (H.) robustus (Australopithecus robustus, 2.0-1.6 Ma)[a]
      H. (H.) habilis (Homo habilis, 1.9-1.8 Ma)[a]
       H. (H.) erectus (Homo erectus, 1.8-0.9 Ma)[a]
        H. (H.) sapiens neanderthalensis (Homo neanderthalensis, 0.5-0.1 Ma)[a]
        H. (H.) sapiens sapiens (Homo sapiens, 0.5-0.0 Ma)[a]

[a] Shown in parenthesis is the species' name and age from Yoon (1995) for each species
that we treat as a member of subgenus *Homo (Homo)*.

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