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Toward a Phylogenetic Classification of Primates Based on DNA Evidence Complemented by Fossil Evidence

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A highly resolved primate cladogram based on DNA evidence is congruent with extant and fossil osteological evidence. A provisional primate classification based on this cladogram and the time scale provided by fossils and the model of local molecular clocks has all named taxa represent clades and assigns the same taxonomic rank to those clades of roughly equivalent age. Order Primates divides into Strepsirhini and Haplorhini. Strepsirhines divide into Lemuriformes and Loriformes, whereas haplorhines divide into Tarsiiformes and Anthropoidea. Within Anthropoidea when equivalent ranks are used for divisions within Platyrrhini and Catarrhini, Homininae divides into Hylobatini (common and siamang gibbon) and Hominini, and the latter divides 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 chimpanzees and bonobos. The differences between this provisional age related phylogenetic classification and current primate taxonomies are discussed. © 1998 Academic Press

INTRODUCTION

A recent tabulation of the living mammal species of the world (Wilson and Reeder, 1993) lists 4629 species of which 3 belong to the order Monotremata, 270 belong to 6 marsupial (metatherian) orders, and 4356 belong to 18 placental (eutherian) orders. The order Primates with 233 species is the fifth most speciose placental order, outnumbered only by Rodentia, Chiroptera, Insectivora, and Carnivora which have 2015, 925, 428, and 271 species, respectively. Among the 233 living primate species is *Homo sapiens*. Not surprisingly, studies of the phylogeny and systematics of primates are being actively pursued. As our study will show, parsimony analyses of sizeable bodies of character state data are yielding congruent molecular and morphological results on the sister-group relationships among primate clades. However, sharply differing views exist as to whether knowledge on sister-group relationships should be the main determinant of how organisms are classified in a formal taxonomic classification. What is at issue is whether all taxa in the classification should represent monophyletic groupings, i.e., actual clades (the cladistic view) or whether paraphyletic groupings, so-called primitive grade taxa should be preferred if they give stability to the classification (the traditional view).

This is an especially contentious issue for primate taxonomy for the very reason that our own species *H. sapiens* is a primate. The traditional view considers humans to be very different from all other forms of life. Thus, this view favors retaining the paraphyletic family Pongidae for apes (Simpson, 1945, 1963), in order that humans may remain as the only living primate in the family Hominidae. In contrast, the cladistic evidence from both DNA sequences (reviewed in Goodman, 1996) and morphology (Shoshani *et al.*, 1996) demonstrate that the African apes (chimpanzees and gorillas) are more closely related to humans than to the Asiatic apes (orangutans and gibbons) and further that chimpanzees are the sister group of humans rather than of gorillas. Thus, the cladistic view favors merging the traditional Pongidae and Hominidae into a single monophyletic family in which the subordination of its subfamilies, tribes, subtribes, genera, and subgenera is meant to represent the series of clades that arose from progressively more recent common ancestors during evolutionary descent from the stem of the family to the present. In terms of this cladistic system, if rank equivalence is sought with other primate clades, the molecular evidence from DNA sequences favors a taxonomic classification that barely separates humans from chimpanzees, placing the two sister lineages either in the same subtribe (Goodman, 1996) or even in the same genus (this paper).

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Here we review the DNA evidence on primate phylogeny, emphasizing results provided by orthologous nuclear genomic sequences. Then we update the morphological analysis of Shoshani *et al.* (1996) by enlarging the previous dataset for 22 extant species with characters from two additional extant species and 18 extinct (fossil) species. The fossil evidence on primate phylogeny, in conjunction with so-called local molecular clock estimates of divergence times allows us to date the ages of primate clades in units of millions of years before the present or Ma (Mega annum, million years before present). Finally, utilizing this information, we present a provisional phylogenetic classification of primates in which the taxa represent actual clades and in which the ages of the clades determine the ranks of the taxa.

DNA EVIDENCE ON PRIMATE PHYLOGENY

Extensive comparative DNA sequence data exist for the 60- to 80-kilobase (kb) nuclear genomic region called the β-globin gene cluster that in mammals spans a series of β-type globin genes including ϵ, γ, η, δ, and β. The γ gene was deleted in artiodactyls, whereas the η gene was deleted in rodents and lagomorphs and became a pseudogene (ψη) in the stem of the primates (Goodman *et al.*, 1984). This pseudogene, the noncoding introns of the functional genes, and the long stretches of noncoding sequence surrounding each gene all evolve at a much more rapid rate than the coding exons of the functional genes. Each β-type globin gene has three exons and two introns but the sum of the lengths of the introns is more than twice that of the exons. Thus each β-type globin gene, even without its flanking regions, has a high proportion of relatively rapidly evolving sequence. Probably because of this, the maximum parsimony (MP) trees constructed for aligned orthologous β-globin gene cluster sequences have provided a fairly well resolved picture of the branching pattern (i.e., sister-group relationships) among primate clades (Koop *et al.*, 1989; Bailey *et al.*, 1992; Porter *et al.*, 1997a,b). Moreover, neighbor-joining (NJ) trees, constructed from matrices of pairwise distances among the aligned sequences, have depicted the same sister-group relationships among primate clades as depicted in the MP trees.

Major Clades

The MP trees for separate datasets of ϵ, γ, ψη, δ, and β sequences all congruently divide the primates first into haplorhine and strepsirhine branches and then the haplorhines into tarsier and simian (Anthropoidea) branches. Also strepsirhines divide into lemuriform and loriform branches in those MP trees in which both clades are represented by sequences (ϵ, γ, ψη). In turn the ϵ, γ, ψη, and δ data set (Porter *et al.*, 1995, 1997a,b; Bailey *et al.*, 1992; Koop *et al.*, 1989) each have sequences representing the three major simian groups that in the traditional taxonomy of primates are the superfamilies Ceboidea (New World monkeys), Cercopithecoidea (Old World monkeys), and Hominoidea (apes and humans). The MP trees for these four sets of sequences all congruently divide Anthropoidea (the simians) first into platyrrhine (ceboid) and catarrhine branches and then the catarrhines into cercopithecoid and hominoid branches.

The ϵ-globin locus has been sequenced for more primate species than has any other nuclear genomic locus. The gene proper region of the ϵ locus (a 1.7-kb region spanning primarily the gene's three exons and two introns) has been sequenced in 43 primates, and in 16 of the 43 primates a further 2-kb region immediately upstream of exon 1 has also been sequenced. The alignment of all these primate ϵ sequences along with rabbit and goat orthologues can be accessed through the internet at http://ns.med.wayne.edu/. An alignment with 34 of these sequences was published in Porter *et al.* (1995) and sequences gathered since then are shown in Harada *et al.* (1995) and Porter *et al.* (1997a,b). The MP tree constructed for these 45 ϵ sequences (Fig. 1) well supports, as judged by bootstrap proportions (BP) and Bremer support (BS) values, the monophyly of order Primates. With regard to major subdivisions within the order, this MP tree supports Strepsirhini, Loriformes, Lemuriformes, Haplorhini, Anthropoidea, Platyrrhini, and Catarrhini.

Strepsirhine Clades

Among the 43 primate ϵ sequences, 3 are from loriform strepsirhines and 5 are from Malagasy strepsirhines. The 3 loriforms are the African greater bushbaby (*Otolemur*), the African potto (*Perodicticus*), and the Asian slow loris (*Nycticebus*). The five Malagasy strepsirhines are the aye-aye (*Daubentonia*), dwarf lemur (*Cheirogaleus*), mouse lemur (*Microcebus*), sifaka (*Propithecus*), and brown lemur (*Eulemur*). A current taxonomy of living primates (Rowe, 1996) places these Malagasy strepsirhines in families Daubentoniidae (*Daubentonia*), Cheirogaleidae (*Cheirogaleus* and *Microcebus*), Indridae (*Propithecus*), and Lemuridae (*Eulemur*). The strepsirhine region of the MP tree (Fig. 1A) not only very strongly groups together *Otolemur, Perodicticus,* and *Nycticebus* into the loriform clade, but also at lesser strength groups all five Malagasy strepsirhines together into the lemuriform clade. Within Lemuriformes, the two cheirogaleids (*Cheirogaleus* and *Microcebus*) strongly group together, and then the cheirogaleid, indrid, and lemurid clades very strongly group together. The sister group of this lemuroid three-family clade is the lineage to *Daubentonia*. Loriforms and lemuriforms are well represented by mitochondrial cytochrome *b* sequences, and the MP tree constructed for these sequences (Yoder *et al.*, 1996) depicts cladistic relationships that are congruent with those depicted by our MP trees for ϵ sequences. In the cytochrome *b* MP tree, *Daubentonia* is the sister-group of a strongly supported indrid-cheirogaleid-lemurid clade. Loriforms, cheirogaleids, an indrid, and lemurids are also represented by DNA hybridization data, and the degrees of hybridization among these DNA samples support the close placement of cheirogaleids with the other lemuriforms rather than with loriforms (Bonner *et al.*, 1980, 1981). Similarly, the morphological evidence gathered by Yoder (1994) in congruence with molecular evidence shows that the Malagasy cheirogaleids are lemuroids and not, as some workers have proposed (Schwartz, 1986; Fleagle, 1988), more closely related to mainland loroids than to other Malagasy strepsirhines.

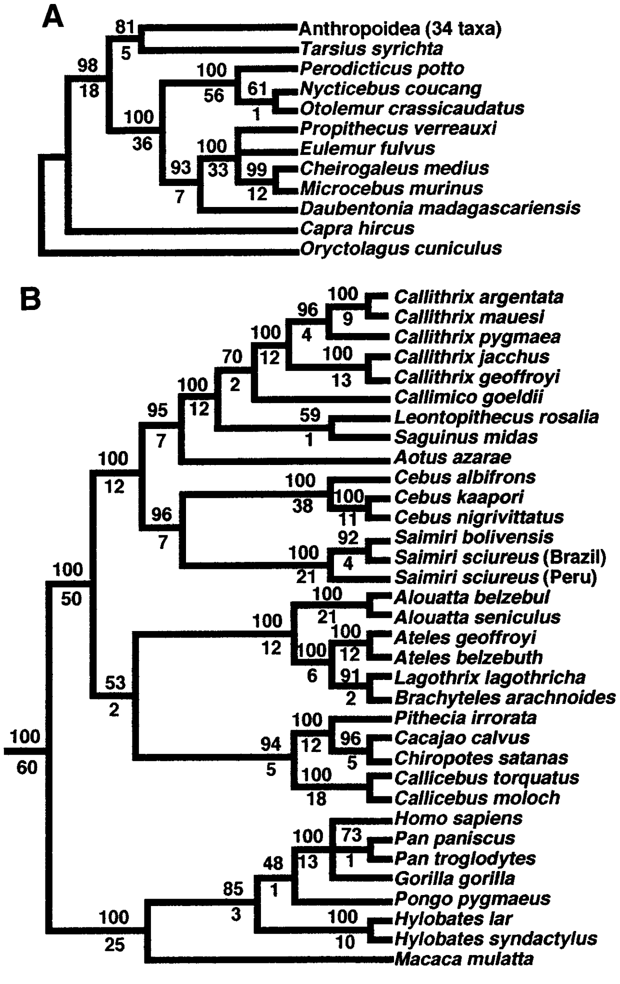

FIG. 1. Consensus of four MP trees for 45 ϵ-globin gene sequences. All sequences span a 1.7-kb gene proper region extending 5′ to 3′ from within the proximal promotor across the exons and introns to the polyadenylation site, and 17 of these sequences encompass at the 5′ side a further 2 kb of upstream flanking DNA. The detailed procedures used to generate and analyze this data set are given in Porter *et al.* (1997a,b). Nucleotide substitution (NS) score for each MP tree is 4361 (each indel, i.e., insertion or deletion, is treated as a single NS and is counted as part of the total NS score). Bootstrap proportions (percentage of 1000 replications) are shown above internal nodes. Bremer support values are shown below the nodes. (A) The portion of the consensus MP tree showing the cladistic relationships of 11 nonsimian taxa to one another and to Anthropoidea. (B) The portion of the consensus MP tree showing the cladistic relations of 34 simian taxa to one another within Anthropoidea.

TABLE 1

Bootstrap Proportions (BP) and Bremer Support (BS) Values for Ceboid Clades Congruently Identified by ϵ-Globin Gene and IRBP Intron 1 Sequences

	ϵ		IRBP	
Taxon	BP	BS	BP	BS
Cebid clades				
Cebidae: Cebinae, Aotinae (*Aotus*), Callitrichinae	100	12	99	12
Cebinae: *Cebus, Saimiri*	96	7	77	4
Callitrichinae: *Saguinus, Leontopithecus, Callimico, Callithrix*	100	12	100	20
Callithrix: argentata, cebuella, and *jacchus* groups	100	12	100	19
Callithrix (Mico): C. argentata, C. mauesi,	100	9		
C. argentata, C. humeralifer			99	6
Callithrix (Callithrix): C. jacchus, C. geoffroyi	100	13	98	6
Pitheciid clades				
Pitheciidae: Callicebini (*Callicebus*), Pitheciini	94	5	100	16
Callicebus: C. moloch, C. torquatus	100	18	100	32
Pitheciini: Pitheciina (*Pithecia*), Chiropotina	100	12	100	22
Chiropotina: *Cacajao, Chiropotes*	96	5	100	15
Atelid clades				
Atelidae: Alouattini (*Alouatta*), Atelini	100	12	100	12
Atelini: Atelina (*Ateles*), Brachytelina	100	6	72	2
Brachytelina: *Lagothrix, Brachyteles*	91	2	76	4

Platyrrhine Clades

The branching pattern of platyrrhine clades in the MP tree for ϵ sequences (Fig. 1B) is congruent in most features with the branching pattern in the MP tree for a series of noncoding sequence orthologues at another nuclear genomic locus, the 1.8-kb intron 1 of the interstitial retinol-binding protein gene (IRBP) (Schneider *et al.*, 1996; Barroso *et al.*, 1997). Since in humans IRBP is on chromosome 10 (Fong *et al.*, 1990) whereas the ϵ-globin gene is located on chromosome 11 (Bunn and Forget, 1986), the two nuclear genes are probably unlinked in New World monkeys as well.

Table 1 lists BP and BS values for ceboid clades that have been congruently identified by the MP trees for ϵ and IRBP sequences, the former tree shown in Porter *et al.* (1997b) as well as in our present paper and the latter tree shown in Barroso *et al.* (1997). A cladistic classification (Barroso *et al.*, 1997), based on these congruent results divides Ceboidea into the monophyletic families, Cebidae, Pitheciidae, and Atelidae. Cebidae has three subfamilies, Cebinae for the sister genera *Cebus* (capuchin monkeys) and *Saimiri* (squirrel monkeys), Aotinae for *Aotus* (night monkeys), and Callitrichinae consisting of *Saguinus* (tamarins), *Leontopithecus* (lion tamarins), *Callithrix* (common and pygmy marmosets), and *Callimico* (Goeldi's monkeys). Pitheciidae has a single subfamily, Pitheciinae, which divides into tribes Callicebini for *Callicebus* (titi monkeys) and Pitheciini for *Pithecia* (saki monkeys), *Chiropotes* (bearded saki monkeys), and *Cacajao* (uacari monkeys). *Chiropotes* and *Cacajao* are sister groups and thus cladistically should be grouped apart from *Pithecia* either in a separate subtribe (Harada *et al.*, 1995; Barroso *et al.*, 1997) or even in the same genus as the subgenera *Chiropotes* (*Chiropotes*) and *Chiropotes* (*Cacajao*) (this paper). Atelidae has a single subfamily, Atelinae, which divides into subtribes Atelina for *Ateles* (spider monkeys) and Brachytelina for *Lagothrix* (woolly monkeys) and *Brachyteles* (woolly spider monkeys).

With three exceptions these monophyletic taxa within Ceboidea have high BP and BS values from both ϵ and IRBP sequences (Table 1). The three exceptions are the cebine clade (the sister grouping of *Cebus* and *Saimiri*), the atelin clade (the sister grouping of Atelina and Brachytelina), and the brachytelan clade (the sister grouping of *Lagothrix* and *Brachyteles*). Cebinae is well supported by ϵ sequences but weakly supported by IRBP sequences. Atelini is also well supported by ϵ sequences but weakly supported by IRBP sequences. Brachytelina is only weakly supported by each of the two sets of sequences. However, atelid γ-globin sequences in an alignment spanning more than 7000 nucleotide positions yield an MP tree with high BP and BS values for both Atelini and Brachytelina (Meireles, 1997). Congruent features of the ceboid phylogenetic branching pattern in the MP trees for ϵ and IRBP sequences are also found by MP trees for two other sets of orthologous DNA sequences, a mitochondrial set consisting of cytochrome oxidase II gene (COII) sequences and an X chromosomal set consisting of glucose-6-phosphate dehydrogenase gene (G6PD) sequences (von Dornum, 1997). Moreover, the MP trees for COII and G6PD agree with the ϵ tree in placing *Callimico* as the sister group of *Callithrix* (von Dornum, 1997).

While the MP trees for ϵ and IRBP sequences congruently support all clades listed in Table 1, these trees differ with regard to sister-group relationships among the three *Callithrix* subgenera, the four callitrichin genera, the three cebid subfamilies, and the three ceboid families. We anticipate that the few uncertainties on sister-group relationships will be resolved by enlarging the DNA sequence data from additional species and from additional genomic loci. Indeed, a case in point concerns the subgenera (species groups) of *Callithrix*. In addition to the ϵ and IRBP sequences there are now two other datasets of orthologous DNA sequences that not only strongly support the previously proposed (Hershkovitz, 1977; Mittermeier *et al.*, 1988) division of *Callithrix* into an argentata group (to which *C. argentata*, *C. humeralifer*, and *C. mauesi* belong) and a jacchus group (to which *C. jacchus* and *C. geoffroyi* belong), but also show that for *Callithrix* to be a monophyletic taxon it must include *Cebuella pygmaea*, i.e., *Callithrix (Cebuella) pygmaea*, as a third species group. One of these two sets of orthologues consists of mitochondrial control region sequences (Tagliaro *et al.*, 1997) and the other consists of von Willebrand intron 11 gene sequences (R. Chaves, unpublished data). The MP tree for each of these two sets of orthologues, like the MP tree for ϵ sequences, places the pygmy marmoset *Callithrix (Cebuella) pygmaea* as sister to the argentata group of marmoset species.

Catarrhine Clades

All extant genera of the hominoid branch of catarrhines are represented by ϵ sequences. However, in the alignment of ϵ sequences, *Gorilla* and the two species of *Pan* (*P. troglodytes, P. paniscus*) are represented over only the 1.7-kb gene proper region. This may account for why the MP tree for ϵ sequences (Fig. 1B) failed to identify among the three most closely related genera (*Gorilla, Pan, Homo*), the two that share the closest kinship. A failure to sharply resolve the trichotomous branching of the three genera into two dichotomous branchings occurred with $\psi\eta$-globin sequences when only a 2.1-kb region had been sequenced in each species (Koop *et al.*, 1986). However, when extensive upstream (5′) and downstream (3′) regions flanking the $\psi\eta$ locus were sequenced such that the full alignment spanned a 7-kb region, the MP tree for these sequences then placed *Pan* and *Homo* closest to each other. The support for this sister grouping became stronger when further downstream sequences obtained by Maeda *et al.* (1988) were added such that the full alignment now spanned a 10.1-kb region (Bailey *et al.*, 1992). We have reanalyzed this data set in order to determine BP as well as BS values for the clades in the MP tree. Table 2 shows these results. It also shows the corresponding results for the data set of γ sequences (Bailey *et al.*, 1992) on similarily reanalyzing it. The simian sequences in this γ data set were obtained by first sequencing all or most of a 12-kb genomic region spanning the tandemly duplicated γ^1 and γ^2 loci and then removing sequences involved in gene conversions. On doing so, each simian species was still represented in most cases by about 8 kb of nonconverted noncoding γ^1 and γ^2 sequences. The results for the $\psi\eta$ and γ datasets (Table 2) reveal that a series of dichotomous branchings separate the five

TABLE 2

(BP) and (BS) Values for Primate Clades Congruently Identified by ψη- and γ-Sequences

	ψη		γ	
Taxon	BP	BS	BP	BS
Haplorhini	61	2	97	20
Anthropoidea	100	61	100	136
Platyrrhini	100	53	100	44
Catarrhini	100	35	100	48
Hominoidea	100	60	100	70
Pongo–Gorilla–Pan–Homo	100	24	100	25
Gorilla–Pan–Homo	100	68	100	63
Pan–Homo	89	5	99	11
Pan troglodyets–P. paniscus[a]	100	44	100	12

[a] The 4919 bp of the *P. paniscus* ψη sequence determined by Bailey *et al.* (1992) was increased to the 7004 bp determined by Barriel (1997) by adding that portion of the Barriel ψη *P. paniscus* sequence missing from the orthologous Bailey *et al.* sequence.

hominoid genera from one another, with strong to very strong bootstrap and strength of grouping support at each branch point. *Hylobates* separates out first, next *Pongo,* then *Gorilla,* and finally *Pan* and *Homo* separate from each other. The DNA hybridization results of Sibley and Ahlquist (1984, 1987) and Caccone and Powell (1989) show this same series of dichotomous branchings or sister-group relationship, including that between *Homo* and *Pan.* A data set of orthologous β-globin gene cluster sequences, each spanning the 3.9 kb δ–β intergenic region, also supports the sister grouping of *Pan* and *Homo* (Perrin-Pecontal *et al.,* 1992). From all available DNA sequence data showing phylogenetic resolution among the hominoids, Ruvolo (1997) identified 14 independent data sets, each belonging to a different genetic linkage group. Among these 14 datasets, 11 support a *Homo–Pan* clade, 2 support a *Pan–Gorilla* clade, and 1 supports a *Homo–Gorilla* clade. Clearly, as Ruvolo (1997) concluded, the existing DNA sequence data are already providing overwhelming evidence that *Pan* and *Homo* are sister groups.

As yet the cercopithecoid branch of catarrhines is not nearly as well represented by DNA sequence data as is the hominoid branch. In fact the only cercopithecoid species represented in the published ϵ, ψη, and γ data sets is the rhesus monkey (*Macaca mulatta*). However, the two traditional cercopithecid subfamilies, Colobinae and Cercopithecinae, are represented by DNA hybridization data (Benveniste, 1985) and COII nucleotide sequences (von Dornum, 1997). DNA samples from *Colobus* and *Presbytis* represent the two extant colobine subtribes (Colobina and Presbytina) in the DNA hybridization data; in turn samples from *Papio, Theropithecus, Mandrillus, Cercocebus,* and *Macaca* represent the cercopithecine tribe Papionini, while samples from *Cercopithecus* and *Erythrocebus* represent Cercopithecini, the other cercopithecine tribe. The degrees of hybridization among these DNA samples (Benveniste, 1985) correlate exactly with the traditional divisions (Delson, 1992) of Cercopithecidae into Colobinae and Cercopithecinae, Colobinae into Colobina and Presbytina, and Cercopithecinae into Papionini and Cercopithecini. The MP tree for the COII dataset of von Dornum (1997) provides cladistic evidence for these cercopithecid subfamilial, tribal, and subtribal clades, except that *Theropithecus, Mandrillus,* and cercopithecins are not represented in this study. MP and maximum likelihood (ML) trees have also been constructed for a data set consisting of papionin COII sequences and a cercopithecin orthologue (*Cercopithecus*) as the outgroup (Disotell *et al.,* 1992); the MP and ML results depict three papionin subclades: one for *Macaca,* another for *Papio* and *Theropithecus,* and the third for *Cercocebus* and *Mandrillus.* Moreover *Colobus, Cercopithecus, Mandrillus, Cercocebus, Papio,* and *Theropithecus* orthologues of a 1.2-kb region of the β-globin gene cluster, extending from about 0.6 to 1.8 kb upstream of the γ^1-globin gene locus, has now been sequenced (S. Page, unpublished data) and added to a data set containing the previously determined *Macaca* sequence along with other simian γ sequences. The MP tree constructed for these noncoding DNA orthologues is congruent with both the COII results (von Dornum, 1997; Disotell *et al.,* 1992) and DNA hybridization results (Benveniste, 1985).

MORPHOLOGICAL ANALYSIS OF PRIMATE PHYLOGENY

Previously, Shoshani *et al.* (1996) employed a data set of up to 264 morphological characters from 22 extant genera of which 18 were primates and 4 were nonprimate eutherians. In the present analysis two additional extant primates (the pitheciins *Chiropotes* and *Pithecia*) and 18 fossils ranging in age from 13 to 64 Ma were added to the dataset. The genera and number of characters studied for each are listed in Table 3. Not only is the total number of characters listed but also the number coded as zero (inferred to be primitive) versus the number coded as nonzero (inferred to be derived). Further information on the fossil primate taxa, such as geological age and distribution, are given in Table 4. Because of the fragmentary nature of the fossils only up to 42 characters were studied for them. Also, so far, only 85 and 87 characters have been studied for the newly added extant taxa (*Chiropotes* and *Pithecia*). A full description of the 264 morphological characters and the codes used for the character states (0, 1, 2, 3, 4, 5) is presented in Appendix 2 of Shoshani *et al.* (1996), and the data matrix for the original 22 extant genera is presented in Appendix 3 of that paper. The enlarged data matrix for the 24 extant and 18 extinct genera can

TABLE 3

Extant and Extinct Taxa and Number of Morphological Characters Studied (Maximum of 264 Characters are from Shoshani *et al.* (1996)

Taxon extant	No. of characters studied[a]	Taxon extinct	No. of characters studied[a]
Solenodon	143; 134/9	*Purgatorius*	11; 11/0
Tupaia	143; 122/21	*Plesiadapis*	42; 32/10
Cynocephalus	144; 112/32	*Adapis*	34; 19/15
Pteropus	175; 140/35	*Notharctus*	42; 30/12
Lemur	187; 145/42	*Komba*	12; 6/6
Daubentonia	179; 133/46	*Shoshonius*	27; 20/7
Loris	156; 118/38	*Tetonius*	31; 22/9
Nycticebus	159; 119/40	*Necrolemur*	30; 20/10
Tarsius	186; 128/58	*Afrotarsius*	5; 5/0
Leontopithecus	219; 133/86	*Eosimias*	11; 11/0
Aotus	186; 116/70	*Homunculus*	18; 9/9
Cebus	220; 132/88	*Dolichocebus*	11; 3/8
Saimiri	217; 128/89	*Tremacebus*	16; 6/10
Pithecia	85; 43/42	*Cebupithecia*	23; 15/8
Chiropotes	87; 43/44	*Catopithecus*	19; 7/12
Macaca	219; 139/80	*Aegyptopithecus*	29; 13/16
Papio	219; 139/80	*Victoriapithecus*	18; 3/15
Colobus	216; 129/87	*Proconsul*	34; 11/23
Presbytis	219; 134/85		
Hylobates	256; 132/124		
Pongo	254; 94/160		
Gorilla	256; 90/166		
Pan	256; 82/174		
Homo	255; 81/174		

[a] First number refers to total numbers of characters studied for this taxon, followed by number of characters coded as “0” (before slash) and all other characters (after slash). For example, 11; 11/0 means total number of characters studied = 11; 11 characters coded as “0,” and zero characters coded for all other character states [1, 2, 3, 4, 5].

be accessed through our internet address (http://ns.med.wayne.edu).

Cladistic Branching Pattern

The MP tree found for the 24 extant genera is shown in Fig. 2 and the MP tree found for all 42 genera is shown in Fig. 3. The phylogenetic relationships depicted by the morphological cladogram for the data set consisting of only the extant genera (Fig. 2) agree in virtually all respects with the DNA evidence on primate phylogeny. Primates, Strepsirhini, Lemuriformes, Loriformes, Haplorhini, Tarsiiformes, Anthropoidea, Ceboidea, Cebidae, Pitheciidae, Catarrhini, Cercopithecoidea, Cercopithecinae, Colobinae, and Hominoidea are all depicted as monophyletic taxa. Moreover, within Hominoidea in further agreement with the DNA evidence, a series of cladistic divisions separates out first *Hylobates,* next *Pongo,* then *Gorilla,* and finally *Pan* and *Homo* from each other. However, at most nodes the morphological MP tree for extant genera (Fig. 2) provides much weaker BP support than the molecular MP trees (Fig. 1, Tables 1 and 2) provide.

The consensus of the 12,300 MP trees found for the morphological data set consisting of all 42 genera (the 18 extinct as well as 24 extant) shows that, except for the catarrhine (9 extant and 4 extinct) and 2 extant loriform genera, all other genera form a bush (i.e., polytomy) at the base of the tree (Fig. 3). This anamologous result may be attributed to the small number of total characters and the high proportion of them that are primitive (coded as 0) in the fossil genera. To see if we could obtain a more resolved tree that still included most of the fossil genera, we removed from the dataset five genera (*Purgatorius, Komba, Afrotarsius, Eosimias,* and *Dolichocebus*) that were represented by fewer characters (only from 5 to 12) than any of the other fossils. After doing so, the remaining 37 genera

TABLE 4

Extinct Primate Taxa for which Data for 42 Characters Were Collected

Taxon	Geological age Distribution	Notes
Purgatorius unio	Early Paleocene, 64 Ma North America	Most primitive Possible primate
Plesiadapis cookei	Late Paleocene, 56 Ma North America	Plesiadapiform
Adapis parisiensis	Eocene/Oligocene, 34 Ma Europe	Adapiform
Notharctus tenebrosus	Middle Eocene, 49 Ma North America	Adapiform
Komba robustus	Early Miocene, 22 Ma Africa	Loriform
Shoshonius cooperi	Early Eocene, 51 Ma North America	Omomyiform
Tetonius homunculus	Early Eocene, 52 Ma North America	Omomyiform
Necrolemur antiquus	Eocene/Oligocene, 34 Ma Europe	Omomyiform
Afrotarsius chatrathi	Early Oligocene, 31 Ma Africa	Possible tarsiiform
Eosimias sp.	Middle Eocene, 48 Ma China	Most primitive Possible simian
Homunculus ameghini	Early Miocene, 20 Ma South America	Primitive platyrrhine
Dolichocebus gaimanensis	Late Oligocene, 24 Ma South America	Primitive platyrrhine
Tremacebus harringtoni	Late Oligocene, 24 Ma South America	Primitive platyrrhine
Cebupithecia sarmientoi	Middle Miocene, 13 Ma South America	Primitive pitheciin
Catopithecus browni	Late Eocene, 35 Ma Egypt	Primitive catarrhine
Aegyptopithecus zeuxis	Early Oligocene, 31 Ma Egypt	Primitive catarrhine
Victoriapithecus maccenniesi	Early Miocene, 22 Ma Kenya	Primitive cercopithecoid
Proconsul africanus	Early Miocene, 22 Ma Africa	Primitive hominoid

Note. The geological dates are after Berggren *et al.* (1995) (SEPM Special Publication Number 54).

(13 extinct and 24 extant) yielded a reduced number (4450) of MP trees, and the consensus of these MP trees was indeed better resolved. Aside from a monophyletic Catarrhini (including the 9 extant and 4 extinct catarrhine genera), the tree depicted a monophyletic Ceboidea (including just extant ceboids), Anthropoidea (including all extant and fossil simian genera), Haplorhini, and Strepsirhini. Otherwise, the haplorhine branch, the strepsirhine branch, and all nonsimian fossil genera (each as a separate branch) formed a bush along with nonprimate branches.

We then established 13 separate datasets, each consisting of the 24 extant genera and a fossil genus represented by more than 12 characters. The MP trees for these data sets always depicted a monophyletic primate clade that included all extant primate genera. The most primitive fossil, 56 Ma *Plesiadapis,* fell outside the primate clade at the base of the consensus MP tree in a polytomy with the 4 nonprimate extant genera. Each of the 12 euprimate fossils was always included within the primate clade. *Necrolemur,* one of the three omomyiforms, joined the haplorhine stem, a position that agrees with the view that omomyiforms are haplorhines (Kay *et al.,* 1997). However, each of the two other omomyiforms joined the primate stem rather than the haplorhines. Moreover, the view that adapiforms are strepsirhines was not supported in that each of the two adapiforms joined the primate stem rather than the strepsirhines. With regard to the platyrrhine fossils, *Tremacebus* joined the pitheciid clade of extant platyrrhines and *Cebupithecia* joined the pitheciin lineage but *Homunculus* in a polytomy with *Chiropotes* and *Pithecia* joined the stem of Anthropoidea. With regard to the catarrhine fossils, the 35 Ma *Catopithecus* joined basal catarrhines; so did the 31 Ma *Aegyptopithecus.* The 22 Ma *Victoriapithecus* joined the extant cercopithecoids, whereas the 22 Ma *Proconsul* joined the extant hominoids.

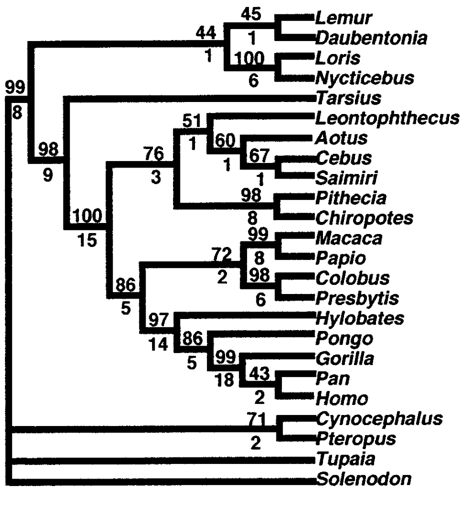

FIG. 2. Consensus of two MP trees for 24 extant taxa (20 primates and 4 outgroups) obtained from PAUP analysis of morphological characters. Each MP tree has a length of 628 steps (character state changes). Bootstrap proportions (percentage of 1000 replications) are shown by internal nodes.

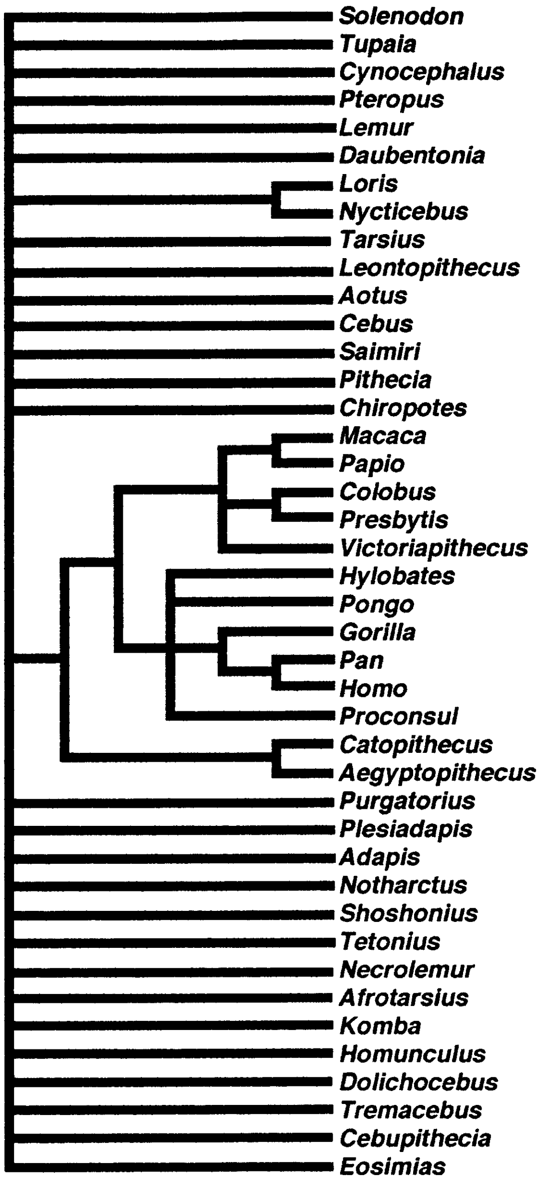

FIG. 3. Consensus of 12,300 MP trees for 42 taxa (24 extant and 18 extinct) from PAUP analysis of morphological characters. Each MP tree has a length of 672 steps.

Reference Times for Dating Branch Points in Primate Phylogeny

The ages of the catarrhine fossils, along with their positions in the consensus MP tree (Fig. 3) for the full morphological data set, allow us to identify two reference ages, one for the cercopithecoid–hominoid split and the other for the catarrhine–platyrrhine split. The basal cercopithecoid position of *Victoriapithecus* along with the basal hominoid position of *Proconsul* suggests that these 22 Ma fossils could have been close in time to the last common ancestor of cercopithecoids and hominoids. The age of 25 Ma has previously been used as a reference date for calibrating branch points in catarrhine phylogeny. As this age just precedes the age of the earliest fossils that provide evidence of the cercopithecoid–hominoid split, we considered it an appropriate age to continue to use for the branch point separating the two main catarrhine branches. Similarly, the earliest fossil evidence that catarrhines had split from platyrrhines is provided by the 35 Ma age of the late Eocene Fayum fossil *Catopithecus.* Since the actual split between catarrhines and platyrrhines must have preceded the earliest fossil that shows the split had taken place, we multiplied 35 Ma by the same factor (25/22) used to derive the age of the cercopithecoid–hominoid divergence node from the 22 Ma age of the basal cercopithecoid and hominoid fossils. On doing so, we obtain the date of 40 Ma for the catarrhine–platyrrhine divergence node.

Omomyiform (Gingerich, 1993) and adapiform (Gingerich, 1986) remains as old as 55 Ma are present in the fossil record but as yet there are no reports of euprimate fossils older than this age. The oldest euprimates in our data set, the omomyiforms *Tetonius* and *Shoshonius* and the adapiform *Notharctus,* have ages of 52, 51, and 49 Ma, respectively. Our analysis neither supports nor strongly opposes the widely held view (Martin, 1990; Kay *et al.,* 1997) that omomyiforms are haplorhines and that adapiforms are strepsirhines. Nevertheless, the euprimate fossils from early Eocene times probably represent close descendant relatives of the last common ancestor of all living primates. Thus, on multiplying 55 Ma by the factor 25/22, we can place the time of the haplorhine–strepsirhine divergence node at 63 Ma. This date is not as ancient as that proposed by Martin (1993) when he attempted to correct for the low sampling level of the primate fossil record over the past 55 million years. On employing a coalescence model in which species diversity decreased at a constant rate as time receded from the present backward, Martin (1993) estimated the Mesozoic age of 80 Ma for the origin of primates of modern aspect. However, Gingerich and Uhen (1994), using Martin's own model, estimated the probability that primates originated as early as 80 Ma was only five chances in a billion. At 63 Ma, 8 million years before the first known euprimate fossils, the probability was 0.05. Thus, Gingerich and Uhen (1994) concluded that a postulated time of euprimate origins older than 63 Ma can be rejected.

AGE-RELATED TAXONOMIC CLASSIFICATION OF PRIMATE CLADES

In conjunction with the fossil evidence on branch times in primate phylogeny, molecular phylogenetic trees (either MP or NJ trees) can provide information on the ages of primate clades. To do so the percentages of sequence change on the tree branches are used to estimate lineage divergence dates by the model of local molecular clocks. This model focuses on a localized set of branch points or region of the phylogenetic tree and uses one or more well-established paleontological time points in that region to calibrate the local clock (Goodman, 1986). The way the local clock calculation of divergence dates is performed is described in detail in Bailey *et al.* (1991, 1992), also in Schneider *et al.* (1993), and as applied to strepsirhines in Porter *et al.* (1997a,b). The NJ trees for the noncoding sequences of the ϵ data sets illustrate the reason for using the model of local molecular clocks to estimate divergence dates rather than the model of a global clock in which all lineages are assumed to evolve at the same rate. The percentage of nucleotide change from the loriform–lemuriform divergence node to each loriform is about twice that to each lemuriform (Figs. 4 and 5), confirming the difference in rates between loriforms and lemuriforms found in the DNA hybridization studies of Bonner *et al.* (1980, 1981). Moreover, if we accept the reference dates of 63 and 40 Ma for the strepsirhine–haplorhine and platyrrhine–catarrhine divergence nodes, then the rate of nucleotide change between these two nodes is considerably faster than the average rate from the platyrrhine–catarrhine divergence node to the present, as is apparent from the branch-lengths in the NJ trees.

Ages of Last Common Ancestors (LCAs)

The ages of origin of euprimate taxa calculated by the local molecular clock are shown in parentheses in the provisional age related taxonomic classification of primate clades (Table 5). Each age for a higher taxon in this hierarchical classification represents the estimated age of the LCA of the lower monophyletic taxa included under that rank. Thus this estimated age represents the age of origin of the higher taxon, treated as a *crown group,* and also of the descendant next lower ranking taxa, treated as *total groups.* A *crown group* is an extant monophyletic taxon defined by its LCA; therefore, it includes the LCA and all lineages that descend from this LCA to both extinct and extant species, but it does not include the stem of the LCA, whereas the *total group* does include the stem (Smith, 1994; Carrol, 1997). For example, Strepsirhini, treated as a *crown group,* includes all lineages to extinct and extant lemuriforms and loriforms and the node (LCA) from which these lineages descend. Treated as a *total group,* Strepsirhini also includes the stem of this LCA. So treated, Strepsirhini is the sister of Haplorhini when it too is treated as a *total group.*

The ages for the strepsirhine taxa shown in this classification were derived from local molecular clock estimates carried out not only on the 45 species NJ tree for ϵ noncoding sequences (Fig. 4) but also on the 17 species tree (Fig. 5), this latter tree being constructed

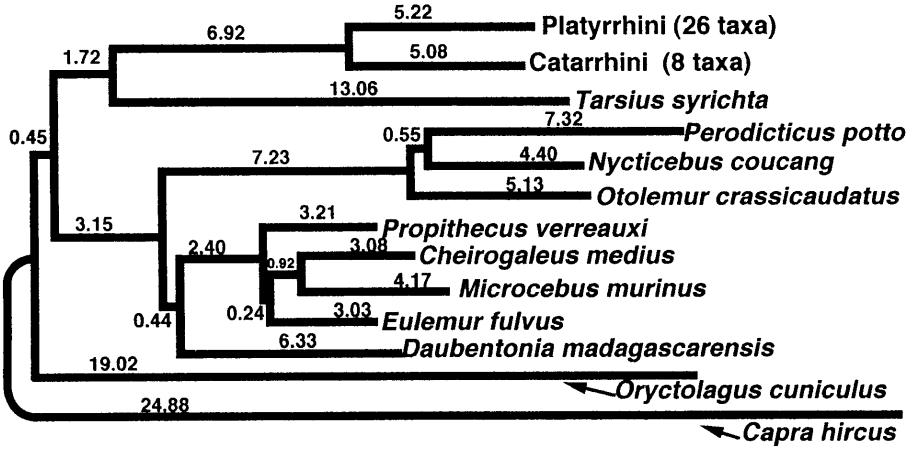

FIG. 4. NJ tree for 45 noncoding ϵ-globin gene sequences, each from only the gene proper region with exons removed. Numbers on the branches represent percentage nucleotide change. Number on the Platyrrhini branch is the average percentage of nucleotide change for all 26 platyrrhine taxa, and number on the Catarrhini branch is the average percentage of nucleotide change for all 8 catarrhine taxa. The full NJ tree with percentages nucleotide change on the branches of the 26 platyrrhine lineages and 8 catarrhine lineages is shown in Porter *et al.* (1997b).

for sequences that include the 2-kb 5′ flanking region as well as the introns and 3′ untranslated region of the ϵ-globin gene locus. When a stepsirhine taxon is represented in both trees the average age from the two estimates is shown in Table 5.

The quite fast rate from 63 Ma (haplorhine–strepsirhine node) to 40 Ma (platyrrhine–catarrhine node) was used to estimate the date of 58 Ma for the LCA of living haplorhines, i.e., Tarsiiformes and Anthropoidea. Similarly, starting with the reference date of 40 Ma for the last common ancestor of platyrrhines and catarrhines, the NJ trees for ϵ sequences and that shown in Barroso *et al.* (1997) for IRBP intron 1 sequences were used to estimate the ages of the monophyletic taxa to the subgeneric level within the platyrrhine clade.

Dates shown in Table 5 for the ages of the LCAs of hominid clades are taken from Bailey *et al.* (1992) who constructed MP and NJ trees for γ and $\psi\eta$ data sets consisting of very extensive stretches of aligned orthologous noncoding sequences. Typically each anthropoid sequence contained about 8000 nucleotides in the γ data set and about 10,000 in the $\psi\eta$ dataset. Molecular

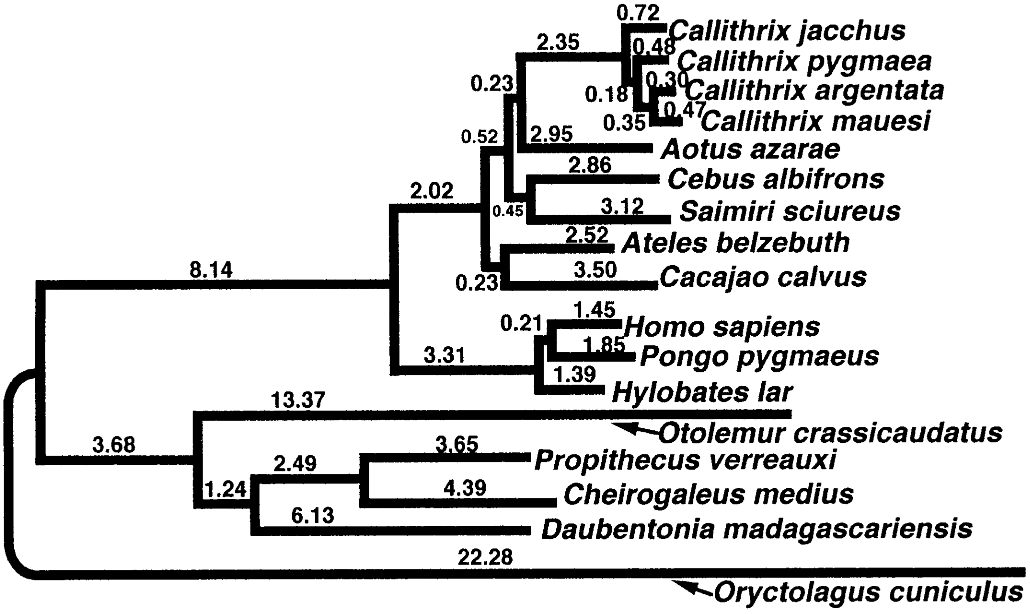

FIG. 5. NJ tree for 17 noncoding ϵ sequences, each from both the gene proper region with exons removed and the adjacent 2-kb 5′ flanking region. Branch lengths shown represent percentages nucleotide change.

TABLE 5

Provisional Age-Related Primate Classification[a]

- Order Primates (63 Ma)
  - Plesion Adapiformes: *Notharctus, Adapis*
  - Semiorder Strepsirhini (50 Ma)
    - Suborder Lemuriformes (45 Ma)
      - Infraorder Chiromyiformes
        - *Daubentonia:* aye-aye
      - Infraorder Eulemurides
        - Superfamily Lemuroidea (28 Ma)
          - Family Cheirogaleidae (22 Ma)
            - Subfamily Microcebinae
              - *Microcebus:* mouse lemurs
            - Subfamily Cheirogaleinae
              - *Cheirogaleus:* dwarf lemurs
          - Family Indridae
            - *Propithecus:* sifakas
          - Family Lemuridae
            - *Eulemur:* brown lemurs
    - Suborder Loriformes
      - Family Loridae (23 Ma)
        - Subfamily Galagoninae
          - *Otolemur:* bush babies
        - Subfamily Lorinae
          - *Nycticebus:* slow lorises
        - Subfamily Perodicticinae
          - *Perodicticus:* pottos
  - Plesion Omomyiformes: *Tetonius, Shoshonius, Necrolemur*
  - Semiorder Haplorhini (58 Ma)
    - Suborder Tarsiiformes
      - *Tarsius:* tarsiers
    - Suborder Anthropoidea (40 Ma)
      - Infraorder Platyrrhini
        - Superfamily Ceboidea (25 Ma)
          - Plesion Homunculidae: *Homunculus*
          - Family Cebidae (22 Ma)
            - Subfamily Cebinae (20 Ma)
              - Tribe Cebini
                - *Cebus:* capuchin monkeys
              - Tribe Saimiriini
                - *Saimiri:* squirrel monkeys
            - Subfamily Aotinae
              - *Aotus:* night monkeys
            - Subfamily Callitrichinae
              - Tribe Callitrichini (13 Ma)
                - Subtribe Saguinina
                  - *Saguinus:* tamarins
                - Subtribe Leontopithecina
                  - *Leontopithecus:* lion tamarins
                - Subtribe Callimiconina
                  - *Callimico:* goeldi's monkey
                - Subtribe Callitrichina
                  - *Callithrix* (5 Ma)
                    - *C. (Callithrix): m*armosets (jacchus group)
                      - *C. (Cebuella):* pygmy marmosets
                      - *C. (Mico):* marmosets (argentata group)
          - Plesion Tremacebidae: *Tremacebus*
          - Family Pitheciidae
            - Subfamily Pitheciinae (17 Ma)
              - Tribe Callicebini
                - *Callicebus* (6 Ma)
                  - *C. (Callicebus):* titi monkeys (moloch group)
                  - *C. (Torquatus):* titi monkeys (torquatus group)

TABLE 5a—*Continued*

- Tribe Pitheciini
  - Plesion Cebupitheciina: *Cebupithecia*
  - Subtribe Pitheciina (10 Ma)
    - *Pithecia:* saki monkeys
    - *Chiropotes* (6 Ma)
      - *C. (Cacajao):* uacari monkeys
      - *C. (Chiropotes):* bearded saki monkeys
- Family Atelidae
  - Subfamily Atelinae (16 Ma)
    - Tribe Alouattini
      - *Alouatta:* howler monkeys
    - Tribe Atelini (13 Ma)
      - Subtribe Atelina
        - *Ateles:* spider monkeys
      - Subtribe Brachytelina (11 Ma)
        - *Lagothrix:* woolly monkeys
        - *Brachyteles:* woolly spider monkeys
- Infraorder Catarrhini
  - Plesion Propliopithecoidea: *Catopithecus, Aegyptopithecus*
  - Superfamily Cercopithecidae (25 Ma)
    - Family Cercopithecidae
      - Plesion Victoriapithecinae: *Victoriapithecus*
      - Subfamily Cercopithecinae (14 Ma)
        - Tribe Colobini (10 Ma)
          - Subtribe Colobina
            - *Colobus:* Colobus monkeys
          - Subtribe Presbytina
            - *Presbytis:* langurs
        - Tribe Cercopithecini (10 Ma)
          - Subtribe Cercopithecina
            - *Cercopithecus:* guenons
          - Subtribe Papionina (7 Ma)
            - *Macaca:* macaques
            - *Cercocebus* (4 Ma)
              - *C. (Mandrillus):* mandrills, drills
              - *C. (Cercocebus):* mangabeys
            - *Papio* (4 Ma)
              - *P. (Theropithecus):* gelada baboons
              - *P. (Papio):* baboons (hamadryas group)
    - Family Hominidae
      - Plesion Proconsulinae: *Proconsul*
      - Subfamily Homininae (18 Ma)
        - Tribe Hylobatini
          - Subtribe Hylobatina (8 Ma)
            - *Symphalangus:* siamangs
            - *Hylobates:* gibbons
        - Tribe Hominini (14 Ma)
          - Subtribe Pongina
            - *Pongo:* orangutans
          - Subtribe Hominina (7 Ma)
            - *Gorilla:* gorillas
            - *Homo* (6 Ma)
              - *H. (Pan):* chimpanzees, bonobos
              - *H. (Homo):* humans

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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* (see text). For example, the age of 63 Ma placed after order Primates is the estimated age of Primates, treated as a *crown group,* but also of Adapiformes, Strepsirhini, Omomyiformes, and Haplorhini, treated as *total groups* (see text); similarly the age of 50 Ma placed after Strepsirhini is the estimated age of this semiorder, now treated as a *crown group,* but also of suborders Lemuriformes and Loriformes, treated as *total groups,* etc. Plesion designates an extinct taxon.

clock calculations applied to the DNA hybridization data of Benveniste (1985), Sibley and Ahlquist (1987), and Caccone and Powell (1985) yield similar dates to those found by Bailey *et al.* (1992) for hominid clades, when 25 Ma is the reference date for the cercopithecid–hominid divergence node and the degree of DNA divergence between cercopithecid and hominid taxa is equated to this reference date. Thus we used the DNA hybridization data to estimate divergence times (LCA ages) of the hylobatan and cercopithecid clades represented in this data but not in the γ and $\psi\eta$ datasets of Bailey *et al.* (1992). Orthologous noncoding sequences from our ϵ and cercopithecid γ data sets also contributed information for estimating the LCA ages shown in Table 5 for the hylobatan and cercopithecid clades, respectively.

The Taxonomic Arrangement of Primate Clades

The provisional classification presented in Table 5 differs in several respects not only from the traditional primate classifications with their paraphyletic Pongidae, Cebidae, and Prosimii (Simpson, 1945; Martin, 1990) but also from the widely accepted phylogenetic classification of Groves (1993). Aside from replacing the paraphyletic taxa of traditional classifications with strictly monophyletic taxa, our provisional age related classification (Table 5) eliminates the superfamily Hominoidae, places Hominidae within Cercopithecoidae, and reduces the taxonomic ranks of most cercopithecid and hominid clades.

In constructing this classification, two main guidelines were followed. The first guideline was that each taxon with extant members should represent a monophyletic group or clade and that the sister-group relationships of the clades should be made evident by the hierarchical groupings of lower ranked taxa into higher ranked taxa. The second guideline was that taxa at the same hierarchical level or rank should represent clades that are equally old, i.e., at an equivalent evolutionary age. Thus, if permitted by the first guideline, taxa at a higher rank (e.g., families) should not only be older than taxa at a lower rank (e.g., subfamilies) but also taxa at the same rank (e.g., different families even if in superfamilies of different primate suborders) should be roughly at about the same age. Furthermore, we wanted a system of equating rank to estimated absolute age that could be extended from Primates to other mammalian orders as phylogenetic classifications with strictly monophyletic taxa are developed for these orders. In this regard, Romer (1962) placed the rise of modern orders and suborders of mammals in the Eocene, the rise of modern families of mammals in the Oligocene, and the rise of modern subfamilies of mammals in the Miocene. Similarly, our age-related classification (Table 5) places the primate suborders, families, and subfamilies, when treated as *total groups,* in the Eocene, Oligocene, and Miocene geological periods, respectively (Table 6).

TABLE 6

Ages of Origins of Euprimate Taxa

Taxa treated as			
Crown groups	*Total groups*	Ma[a]	Geological period
Order	Semiorders	63	Paleocene
Semiorders	Suborders	58–50	Late Paleocene to early Eocene
Suborders	Infraorders	45–40	Middle Eocene
Infraorders	Superfamilies	39–29[b]	Middle Eocene to middle Oligocene
Superfamilies	Families	28–25	Middle to late Oligocene
Families	Subfamilies	23–22	Early Miocene
Subfamilies	Tribes	20–14	Early to middle Miocene
Tribes	Subtribes	14–10	Middle to late Miocene
Subtribes	Genera	11–7	Late Miocene
Genera	Subgenera	6–4	Late Miocene to early Pliocene

[a] Ages are taken from those listed in the Provisional Age Related Primate Classification (Table 5); each pair of ages brackets the range of LCA ages for clades included under that rank. Because the ordinal *crown group* Primates has only one LCA for its descendant clades (the semiorders treated as *total groups*), only one age (the reference date of 63 Ma, see text) is listed for the *crown group* rank of order.

[b] The Provisional Classification (Table 5) shows no examples of more than one superfamily per infraorder. However, the origins of the superfamilies in an age related system would be placed between the origins of infraorders and the origins of families, when the taxa at these three ranks are treated as *total groups.*

Each age placed in parentheses alongside a taxon in Table 5 represents the estimated age for the LCA of all subordinate taxa within that higher taxon. Thus, e.g., the age of 45 Ma placed alongside Lemuriformes is the estimated age for the two infraorders (as *total groups*) placed within that suborder. The lemuriform infraorder called Chiromyiformes (Groves, 1989) has *Daubentonia* as its only living genus, and to save space, the classification does not show taxa at intermediate ranks between infraorder and genus that *Daubentonia* could be placed in. However, conceptually if extinct members of Chiromyiformes in the succession of geological periods between 45 Ma and the present were to be discovered, then it would be apparent that *Daubentonia* belonged not only to an infraorder but also to each taxon at a subordinate rank between infraorder and genus.

An age-related phylogenetic classification, such as attempted here for primates (Table 5), in theory is well suited to accommodate extinct as well as extant taxa. To do so the all purpose category Plesion for extinct taxa can be used as advocated by Patterson and Rosen (1977). Because our morphological analysis could not confirm that adapiforms are cladistically closest to the strepsirhine clade of Lemuriformes and Loriformes but could weakly confirm that adapiforms belonged within the order Primates, we indented plesion Adapiformes as if it were a primate semiorder. Similarly, plesion

Omomyiformes is treated as a primate semiorder. The plesions Homunculidae (for 20 Ma *Homunculus*) and Tremacebidae (for 24 Ma *Tremacebus*) are treated as ceboid families, whereas plesion Cebupitheciina (for 13 Ma *Cebupithecia*) is treated as a subtribe within tribe Pitheciini in agreement with the morphological analyses of others (Ford, 1986; Kay, 1990; Rosenberger *et al.*, 1990) and ourselves. Plesion Propliopithecoidea (for 35 Ma *Catopithecus* and 31 Ma *Aegytopithecus*) is treated as a catarrhine superfamily, while plesions Victoriapithecinae (for 22 Ma *Victoriapithecus*) and Proconsulinae (for 22 Ma *Proconsul*) are treated as cercopithecid and hominid subfamilies, respectively.

The lemuroid families Cheirogaleidae, Indridae, and Lemuridae are the same as the families with these names in other current primate taxonomies (Groves, 1993; Rowe, 1996; Shoshani *et al.*, 1996). The estimated age of origin (or LCA) of these families is 28 Ma (Fig. 5). As yet the lemuroid Megaladopidae (for *Lepilemur*) is not represented by DNA sequences. Also, as yet there is not sufficient sequence data to establish the sequential order of dichotomous branchings among the lemuroid families. This is also the case for the three clades to extant loriforms, which on the basis of the estimated age of 23 Ma for their LCA are treated as subfamilies Galagoninae, Lorinae, and Perodicticinae of family Loridae.

Within Platyrrhini, the estimated ages of origin of the ceboid families, subfamilies, tribes, subtribes, and genera as *total groups* are 25, 22, 20 to 16, 13, and 11 to 10 Ma, respectively (Table 5). Ranking the monophyletic taxa according to their estimated absolute ages places the origins of subgenera, as *total groups* (or genera as *crown groups*), at 6 to 4 Ma. By this yardstick *Callicebus moloch* and *Callicebus torquatus* with an estimated LCA age of 6 Ma should be treated as members of different subgenera, i.e., *Callicebus (Callicebus) moloch* and *Callicebus (Torquatus) torquatus. Cacajao* and *Chiropotes* also have an estimated LCA age of 6 Ma; thus they are treated as subgenera of *Chiropotes*, i.e. *C.* (*Cacajao*) and *C. (Chiropotes). Callithrix*, with an estimated LCA age of 5 Ma for its species groups, divides into three subgenera, *C.* (*Callithrix*) for the jacchus group, *C.* (*Cebuella*), and *C.* (*Mico*) for the argentata group. To represent the finding that the latter two are sister groups, they are listed at a more indented position under *Callithrix* than is *C.* (*Callithrix*).

The yardstick of estimated absolute age of origin applied to the monophyletic taxa within the catarrhine family Cercopithecidae places all extant members of the family in the single subfamily Cercopithecinae which then divides into tribes Colobini and Cercopithecini, each in turn dividing into two subtribes. Within Papionina, the sister groups *Cercocebus* and *Mandrillus* with an estimated LCA age of 4 Ma are treated as subgenera of *Cercocebus*, i.e., *C.* (*Cercocebus*) and *C.* (Mandillus). Similarly, *Papio* and *Theropithecus* as sister groups with an estimated LCA age of 4 Ma are treated as subgenera of *Papio*. Thus we designate the two *Papio* subgenera as *P.* (*Theropithecus*) and *P.* (*Papio*), the latter for the hamadryas group of baboons.

The yardstick of estimated absolute age applied to the taxa within Hominidae places all extant members of the family within subfamily Homininae which then divides into Hylobatini and Hominini, the latter in turn dividing into subtribes Pongina and Hominina, the latter for *Gorilla, Pan,* and *Homo*. However *Pan* and *Homo* are sister groups with an estimated LCA age of 6 Ma. Thus, by the principle of rank equivalence with other primate clades of the same age, *Pan* and *Homo* should be treated as subgenera of *Homo*, i.e., *H.* (*Pan*) and *H.* (*Homo*). *Hylobates (Hylobates) lar* and *Hylobates (Symphalangus) syndactylus* provide an exception to these reductions of ranks of taxa within Hominidae. Because their estimated LCA age is 8 Ma, our age-related classification treats them as species in separate genera, i.e., *Hylobates lar* and *Symphalangus syndactylus*, within subtribe Hylobatina. We still have to determine if the other two recognized subgenera of *Hylobates, H.* (*Bunopithecus*) and *H.* (*Nomascus*) (Groves, 1993), should also be treated as separate genera. It is clear, however, that relative to the great apes, the gibbons have been grossly undersplit.

Closing Comments

The provisional nature of the classification shown in Table 5 needs to be emphasized. The cladistic relationships among the taxa in the classification are likely to be further resolved as DNA sequence evidence becomes more extensive and includes not only the taxa presently represented in the classification but also the primate species and genera not yet represented. Similarly, more extensive morphological evidence including that on fossils is likely to be gathered. The local molecular clock approach coupled to better evidence from fossils should then yield a more accurate series of estimated LCA ages, possibly requiring changes in the hierarchical ranks of the taxa representing clades. Finally, the concept itself of an age-related classification is not widely accepted. Indeed, even though Hennig (1966) presented very cogent arguments for a rank equals age system of classification, later he (Hennig, 1981) initiated a trend among cladists to abandon the use of ranks altogether (de Queiroz and Gauthier, 1992). Since most systematists still use ranks in their taxonomies, there may well be merit to an age-related phylogenetic classification, at least for those groups such as primates and other mammals, where a crude correlation already exists between rank and age in existing classifications. As paraphyletic taxa are converted into strictly monophyletic taxa, the correlation between age of origin of a taxon and its rank is likely to increase.

An extra word of caution is called for. As Hennig

(1966) noted, if you try to rank taxa across phyla according to times of origin, you get into difficulties. Indeed, the genera *Drosophila* and *Eucalyptus* have time depths comparable to virtually the entire Mammalia! Thus it is not possible to extend any age/ranking equivalences beyond a certain level (probably classes) without disrupting the entire classificatory system and causing great confusion. Nevertheless, even if confined only to individual orders, the exercise of ranking according to time of origin can produce a more meaningful phylogenetic classification. The important conclusion from this exercise is that there is widespread inconsistency of ranking among primate taxa: some are much oversplit compared to others of equivalent time depth. However, as we have attempted to show, this inconsistency can be lessened in an age-related phylogenetic classification of primates.

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