AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 106:261–281 (1998)

Platyrrhine Systematics: A Simultaneous Analysis of Molecular and Morphological Data

INÉS HOROVITZ,* RAFAEL ZARDOYA, AND AXEL MEYER
Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook, New York 11794-5245.

KEY WORDS monkeys; total evidence; 12S ribosomal gene; homoplasy-correcting dynamic weighting

ABSTRACT Platyrrhine phylogeny has been investigated repeatedly with morphological characters and DNA nuclear gene sequences, with partially inconsistent results. Given the finding in the past decade that the mitochondrial genome is a potentially valuable source of phylogenetic information, we gathered DNA sequence data of a fragment of the 16S and the entire 12S mitochondrial genes. The objectives were to generate a cladistic phylogeny based on these data and to combine them in a simultaneous analysis with morphological characters and preexisting nuclear DNA sequences. Mitochondrial data analyzed on its own yielded a cladogram that was different from those generated with other data sets. The simultaneous analysis of mitochondrial, nuclear, and morphological data yielded a tree most congruent with that generated with nuclear data and to a lesser degree with the morphological one. It depicted a basal dichotomy that led to two major clades: one of them comprised [Atelinae (*Callicebus* + Pitheciini)] and the other major clade comprised [*Aotus* ((*Cebus*, *Saimiri*) (Callitrichinae))]. The weakest point of the phylogeny was the position of *Aotus* as basal within their clade as opposed to more closely linked with either the callitrichines or *Cebus-Saimiri*. Relationships within callitrichines and atelines were unstable as well. The simultaneous phylogenetic analysis of all data sets revealed congruent signal in all of them that was partially obscured in the separate analyses. Am J Phys Anthropol 106:261–281, 1998.

New World monkey or platyrrhine systematics has historically been a controversial subject. For decades, morphologists have addressed the issue with remarkably different results. In more recent years, phylogenetic analyses of DNA sequences of both nuclear and mitochondrial origin have yielded additional patterns of relationships, which differed from morphological trees proposed previously. There are a few features that they all share, however, particularly trees published since the 1970s. Most phylogenetic analyses agree on the existence of three groups—callitrichines, pitheciins, and atelines ("Linnaean" categories assigned vary among authors; we follow Schneider et al. [1993, 1996], Harada et al. [1995], and Horovitz and Meyer [1997]). Callitrichinae includes the marmosets (*Callithrix* and *Cebuella*), the tamarins (*Saguinus* and *Leontopithecus*), and Goeldi's monkeys (*Callimico*); Pitheciini includes the sakis (*Pithecia*), uakaris (*Cacajao*), and bearded sakis (*Chiropotes*); and Atelinae includes spider monkeys (*Ateles*), howler monkeys (*Al-*

Contract grant sponsor: NSF; contract grant numbers: SBR-9514173 and DEB-9615178.

Rafael Zardoya's present address is Museo Nacional de Ciencias Naturales, José Gutiérrez Abascal, 2, 28006 Madrid, Spain.

Axel Meyer's present address is Department of Biology, University of Konstanz, D-78457 Konstanz, Germany.

*Correspondence to: Inés Horovitz, Department of Vertebrate Paleontology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192. Tel: (212) 496-3481. Fax: (212) 769-5842. E-mail: horovitz@amnh.org

Received 30 September 1997; accepted 29 April 1998.

ouatta), woolly spider monkeys (*Brachyteles*), and woolly monkeys (*Lagothrix*). The position of four additional genera, the capuchin (*Cebus*), titi (*Callicebus*), owl (*Aotus*), and squirrel monkeys (*Saimiri*), has been very elusive. The three groups mentioned above are each supported by some unique morphological characters. Callitrichines have in absolute terms the smallest body size among anthropoids and display claws instead of nails in all manual and pedal digits except the hallux. Pitheciins display a gap in the dental series between the lower canine and the second incisor, a sharp lingual vertical edge on the lower canines, and crenulated molar enamel. Atelines have a prehensile tail covered ventrally by bare skin with friction ridges, a large body size, and very long forelimbs relative to hindlimbs. Hershkovitz (1977) considered Goeldi's monkey, *Callimico,* to be neither a "callitrichid" (including marmosets and tamarins) nor members of the "cebids," a family in which all "noncallitrichid" species have been included traditionally. He recognized characters of *Callimico* in common with callitrichines but considered them to be primitive or parallelisms correlated with body size. However, other morphologists found *Callimico* to be basal callitrichines; those characters that Hershkovitz considered primitive for callitrichines, others found to be derived (Rosenberger, 1979; Ford, 1986a; Kay, 1990).

There is no consensus about how callitrichines, atelines, and pitheciins are related to each other or to the remaining four genera, *Cebus, Saimiri, Aotus,* and *Callicebus,* or about the relationships within these three groups, with two exceptions: the sister group relationship between *Cacajao* and *Chiropotes* and that between *Callithrix* and *Cebuella* (the latter two are in fact considered congeneric by several authors; see Schneider and Rosenberger [1997]) is widely accepted (Fig. 1). If one compares the morphology of the platyrrhine genera, it becomes evident that they are easily distinguished from one another. For example, *Saimiri,* the squirrel monkeys, have a foramen in the interorbital septum; *Alouatta,* the howler monkeys, a remarkably hypertrophied hyoid bone; *Aotus,* enlarged orbits; and *Cebuella* are by far the smallest anthropoids (they weigh approximately 120 g). Most are generic autapomorphies, however, and it is not easy to find characters in common, except in the case of those uniting callitrichines, pitheciins, and atelines. This lack of indicators may be the result of a fast cladogenetic event that gave rise to the variety of monkeys that we see today (Fleagle, 1988).

Aotus and *Callicebus* (Fig. 1a, b) have been linked together repeatedly (Rosenberger, 1981, 1992; Ford, 1986b; Ford and Davis, 1992; Kinzey, 1992) based on behavioral and/or morphological characters, of which the most remarkable is that they are both monogamous. On the other hand, *Callicebus* share a few derived dental characters with pitheciins that *Aotus* lack (Rosenberger, 1979; Kinzey, 1992; Horovitz and Meyer, 1997).

Cebus and *Saimiri* (Fig. 1a) have also been linked by Rosenberger and collaborators based on craniodental characters (Rosenberger, 1979, 1981; Rosenberger et al., 1990). Ford (1986b) also considered this possibility and the alternative with *Cebus* basal to all platyrrhines and *Saimiri* sister to the *Aotus-Callicebus* dyad in a study that included postcranial and craniodental characters (Fig. 1b). Kay (1990) presented a tree based on craniodental characters, where *Saimiri* are the sister group of callitrichines and *Cebus* are sister group of most platyrrhines except *Callicebus,* which according to this phylogeny, are the most basal platyrrhines (Fig. 1c).

Rosenberger and coworkers (Rosenberger, 1984; Rosenberger et al., 1990) suggested that atelines and pitheciins plus *Aotus-Callicebus* are closely related (Fig. 1a), whereas Ford (1986b) found pitheciins to be the sister group of atelines, to the exclusion of *Aotus-Callicebus* (Fig. 1b). The former authors found callitrichines to be the sister group of the *Cebus-Saimiri* dyad, whereas Ford disagreed in that callitrichines were the sister-group of the pitheciins-atelines clade.

Molecular studies of the systematics of New World monkeys started in 1975 and at first were based on immunological distances (Cronin and Sarich, 1975, 1978; Sarich and Cronin, 1976, 1980; Baba et al., 1979, 1980). Most of these studies indicated that atelines,

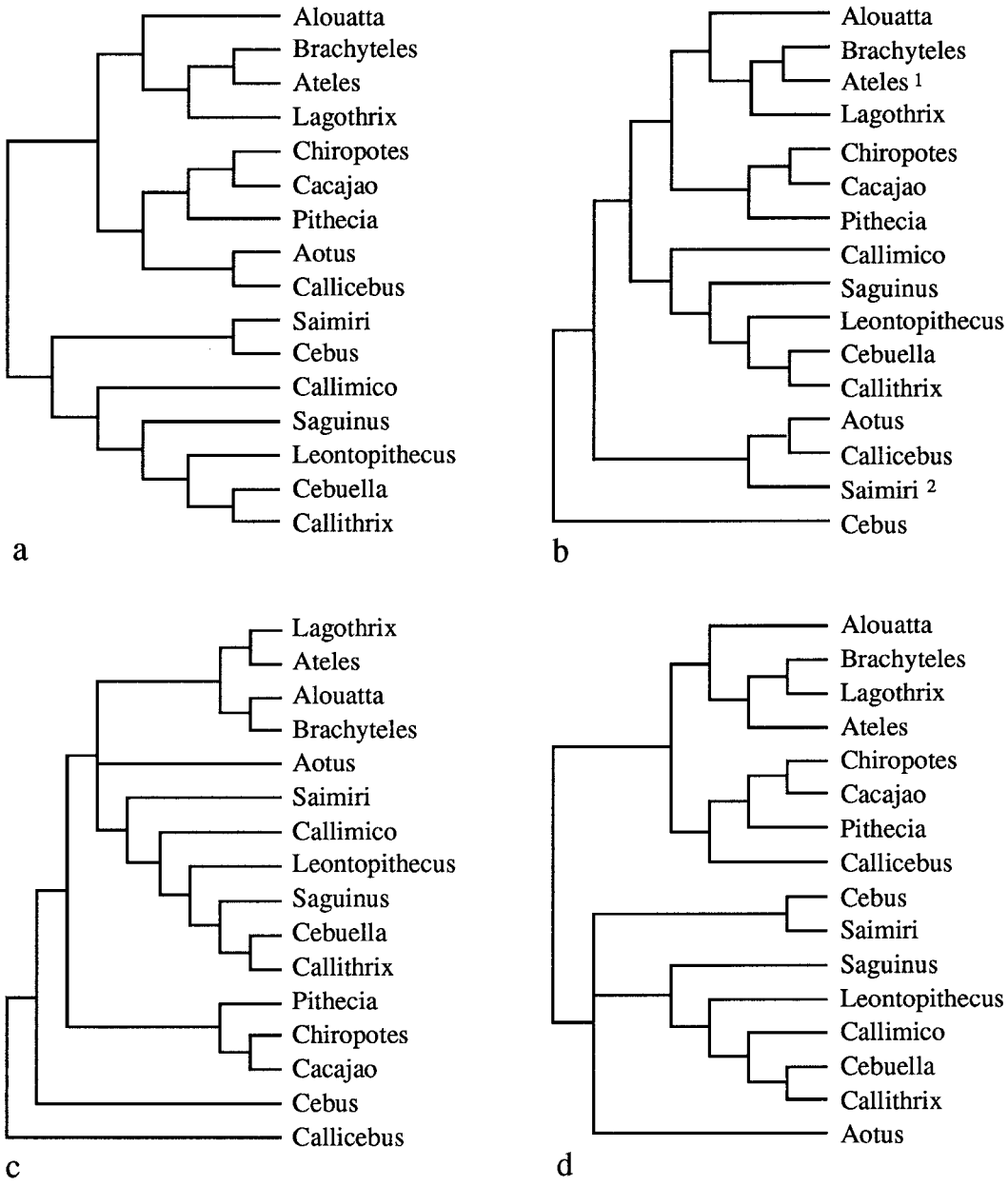

Fig. 1. Phylogenetic trees of New World monkeys according to **(a)** Rosenberger (1981, 1984), **(b)** Ford (1986) and Ford and Davis (1992) [*Ateles*[1] is placed alternatively as a sister group of *Lagothrix*, and *Saimiri*[2] as a sister group of *Cebus*], **(c)** Kay (1990), and **(d)** Schneider et al. (1996). (a), (b), and (c) are based on morphological characters, whereas (d) is based on DNA sequences for the ϵ-globin and IRBP nucleus-encoded genes.

pitheciins, and callitrichines were monophyletic. However, in the same way that morphological studies did, they failed to find consistent patterns of relationships among these clades and the remaining four genera, *Cebus*, *Saimiri*, *Callicebus*, and *Aotus*.

Molecular data amenable to cladistic analysis using the Wagner and Fitch parsi-

mony algorithms (Farris, 1970; Fitch, 1971) have been collected only since 1993. In the first published data set, sequences of the nucleus-encoded ϵ-globin gene produced highly consistent trees (Schneider et al., 1993) that yielded a mostly resolved consensus. The relationships among callitrichines, *Saimiri, Cebus,* and *Aotus* were unsettled in this analysis. This clade was the sister-group of atelines plus the *Callicebus*-pitheciin clade. Harada et al. (1995) and Schneider et al. (1996) published additional sequences of the same gene for *Cebus* and *Saimiri,* plus sequences of another nuclear gene, the interstitial retinol-binding protein (IRBP) gene, intron 1, for all New World monkey genera. Addition of the new sequences of the ϵ-globin gene to the previous more restricted data set resulted in a resolution of the polytomy among callitrichines, *Cebus, Saimiri,* and *Aotus: Aotus* were the sister-group of callitrichines, and the sister-genera *Saimiri-Cebus* were their closest relatives (Harada et al., 1995). Separate analyses of sequences of the IRBP gene for platyrrhine genera yielded a different overall topology: callitrichines were the sister group of the *Cebus-Saimiri* dyad, and next came *Aotus* (Harada et al., 1995; Schneider et al., 1996). The remarkable difference from the phylogenies based on the ϵ-globin was that the sister group to the callitrichines-*Aotus-Cebus-Saimiri* clade was the *Callicebus*-pitheciins clade, and the atelines were basal to all platyrrhines. When the sequences of the ϵ-globin and IRBP genes were combined (Fig. 1d), the topology was mostly the same as for the ϵ-globin gene alone, except that two most parsimonious trees were found. In one of them *Aotus* and callitrichines formed a clade, with the clade *Cebus-Saimiri* as their sister-group, whereas in the other the clade *Cebus-Saimiri* were the sister of callitrichines, and *Aotus* were basal to them all (Harada et al., 1995; Schneider et al., 1996).

Given the finding in the past decade that the mitochondrial genome is a potentially valuable source of phylogenetic information (e.g., Wilson et al., 1985; Avise, 1994), Horovitz and Meyer (1995) gathered preliminary data from a fragment of 542 sites of the 16S ribosomal gene. This data set had some power to resolve the relationships among genera, but the number of phylogenetically informative characters was not large and the degree of homoplasy was relatively high. Therefore, more mitochondrial data were gathered, which we are presenting in the current report: this is the DNA sequence of the complete 12S ribosomal gene.

Independently, Von Dornum and Ruvolo (1996) collected DNA sequences of the mitochondrial gene for cytochrome oxidase subunit II (COII) and introns of the nuclear gene for glucose-6-phosphate dehydrogenase (G6PD). According to their preliminary report and unpublished data (Von Dornum, 1997), they found support for a close relationship between *Cebus* and *Saimiri* and between *Callicebus* and the pitheciins.

Different data sets share a common history; therefore, the phylogenetic signal they contain should be the same in all of them, even if obscured by homoplasy in the resulting individual trees. On the other hand, the distribution of homoplasy is likely to be different in each data set, given that each one is subject to different constraints (e.g., those pertaining to function). If one conducts a simultaneous analysis of all data sets (Kluge, 1989; Kluge and Wolf, 1993; Nixon and Carpenter, 1996), the signal common to all of them is more likely to overwhelm the homoplasy than if each data set is analyzed separately. Horovitz and Meyer (1997) conducted a combined analysis of the ϵ-globin and IRBP sequences (Schneider et al., 1993, 1996; Harada et al., 1995), the fragment of the 16S ribosomal gene (Horovitz and Meyer, 1995), and morphological characters (Horovitz, 1997; Horovitz and Meyer, 1997, and references cited therein; Horovitz and MacPhee, in preparation). We present here a new combined phylogenetic analysis including the data just listed plus the new mitochondrial sequences of the 12S ribosomal gene.

MATERIALS AND METHODS

We present the phylogenetic analysis of mitochondrial sequences of the complete 12S ribosomal gene (951 sites after alignment; 324 phylogenetically informative characters) in the first section of this paper; the simultaneous analysis includes these se-

quences plus already published data including DNA sequences of the nucleus-encoded ϵ-globin gene (Schneider et al., 1993) (261 phylogenetically informative characters) and the IRBP gene intron 1 (Harada et al., 1995; Schneider et al., 1996) (332 phylogenetically informative characters), a fragment of the mitochondria-encoded 16S ribosomal gene (Horovitz and Meyer, 1995) (142 phylogenetically informative characters), and 76 morphological characters (Appendices A and B).

The morphological and simultaneous analyses additionally include one fossil ingroup taxon: this is *Cebupithecia sarmientoi*, from the late Miocene of La Venta, Colombia (Stirton, 1951; Stirton and Savage, 1951), and the fossil anthropoid outgroups *Aegyptopithecus, Apidium,* and *Parapithecus,* from the Oligocene deposits of Fayum (Simons, 1962, 1965; Kay et al., 1981; Fleagle and Kay, 1987). Molecular and morphological characters that we had no information about for certain taxa (mostly fossils) were recorded as "missing."

DNA source and extraction

Total cellular DNA was extracted from frozen or ethanol-preserved muscle (Kocher et al., 1989) or from frozen or Tris-SDS-EDTA-buffer-preserved blood from the following species: *Cebus apella, Saimiri sciureus, Aotus trivirgatus, Callithrix jacchus, Cebuella pygmaea, Saguinus geoffroyi, S. oedipus, Callimico goeldii, Leontopithecus rosalia, Ateles* sp., *Lagothrix lagothricha, Alouatta palliata, A. seniculus, Brachyteles arachnoides, Pithecia pithecia, Chiropotes satanas,* and *Callicebus moloch* as well as the outgroups *Hylobates lar, Nasalis larvatus,* and *Tarsius syrichta.* The sequence for another outgroup, *Homo sapiens,* was obtained from Anderson et al. (1981). The 12S ribosomal gene, consisting of 951 positions, was sequenced for all species. This length is that obtained after alignment.

PCR amplification, cloning, and DNA sequencing

A combination of four primers was designed to amplify contiguous and overlapping fragments (12S Pri F 5′-AGGTTTGGTCCTAGCCTTTCTATTA-3′, 12S Pri R 5′-AATTTCTATCGCCTATACTTT-3′, 12S Pri′F 5′-TGCCAGCCACCGCGGCCATACGATT-3′, 12S Pri′R 5′-GAGGGGATAAGTCGTTAACATGGTAAG-3′) of the 12S rRNA gene. These primers were designed based on highly conserved regions of an alignment of published sequences from hominoids and other mammals. Amplifications were done in 50 µl Tris (67 mM, pH 8.8) containing 1.5 mM $MgCl_2$, 0.3 mM of each dNTP, 150 ng of each primer, template DNA (10–1000 ng), and AmpliTaq DNA polymerase (2.5 U, Perkin-Elmer Cetus, Norwalk, CT). We used a Perkin-Elmer Cetus DNA Thermal Cycler to perform 30 cycles of PCR (denaturing at 94°C for 60 seconds, annealing at 50°C for 60 seconds, and extending at 72°C for 60 seconds) to generate double-stranded DNA fragments. An aliquot of the PCR product (5 µl) was cloned in pGEM-T vector (Promega, Madison, WI) following the manufacturer's instructions. Typically, two to four clones were sequenced for each PCR product. Recombinant plasmids were sequenced on an Applied Biosystems (Foster City, CA) 373A Stretch DNA sequencer using the Taq Dye Deoxy Terminator Cycle Sequencing Kit (Applied Biosystems) and M13 universal (−40) and reverse primers, following the manufacturer's instructions.

Sequence analysis

Multiple-sequence alignment was performed using Malign 1.89 (Wheeler and Gladstein, 1993), and the phylogenetic analyses were done with PAUP 3.1.1 (Swofford, 1993), with 100 replications of stepwise random addition of taxa using three bisection and reconnection on minimal trees only. Two weighting methods were applied: successive approximations character weighting (Farris, 1969) and homoplasy-correcting dynamic weighting (Horovitz and Meyer, 1995) with modifications to the original procedure. According to the original version of the latter method, data were weighted simultaneously in two ways: with a transformation-cost matrix T for changes and with a vector C of weights for each site (the latter being equivalent to a successive weighting). No weights were applied in the first run, and the tree(s) obtained were used as the starting point for the weighting. A vector C was built with the maximum value of the res-

caled consistency index for each character from the trees resulting from the previous iteration. The matrix T was built weighting different directions of changes separately (i.e., A ⇒ C and C ⇒ A may have different costs). Frequencies of changes were calculated from the tree(s) resulting from the previous iteration, and the minimum number of steps for all possible optimizations and trees was calculated with MacClade 3.0 (Maddison and Maddison, 1992). The function used to weight changes in the T matrix, suggested by Horovitz and Meyer (1995), was the following:

$$L_{ij} = -\ln (X_{ij}/2N_{ij})$$

where L_{ij} is the function for the cost of changing from state i to state j, X_{ij} is the same as defined above, and N_{ij} is the number of positions that show presence of character states i and j.

The corrections to homoplasy-correcting dynamic weighting we are introducing in this article follow the objective of reducing potential violations of two of the assumptions of metricity (Waterman et al., 1977; Farris, 1981, 1985; Swofford, 1981; Rogers, 1986; Wheeler, 1993). These corrections are (1) average the cost for changes in both directions, because distances between taxa should be symmetrical or $d_{ij} = d_{ji}$, and (2) correct these costs in such a way that the triangle inequality is not violated, namely that $d_{ik} \leq d_{ij} + d_{jk}$. This can be done in many different ways. One possibility is to calculate the difference between d_{ik} and $d_{ij} + d_{jk}$, divide this quantity by 3, round it up, add the result to d_{ij} and d_{jk}, and subtract it from d_{ik}; variations in this procedure caused no changes in topology in the trees we obtained, as long as the rules mentioned above are observed.

Matrices T and vectors C were calculated for the four gene data sets on the total evidence tree to compare rates of evolution within and between data sets on the tree that compromises between all of them. Fossils were excluded from the tree on which these calculations were done to reduce character optimization ambiguities.

Entire gaps were considered characters, not each position separately, and gaps with different lengths were coded in sections. For example, given the alignment in Table 1, we distinguish three different gaps on (a) positions 8–9, (b) positions 10–11, and (c) positions 12–13. There is a large number of possibilities in which these gaps could have evolved. Each position could represent a single deletion or insertion event, gaps b + c could have been a single deletion event in taxa B and C, etc. According to the auxiliary principle of Hennig (1966), we will consider gaps in the same positions across taxa as homologous; therefore, we consider gap "a" homologous in B through G; gap "b" homologous in B, C, F, and G; and gap "c" homologous in B and C. Distinguishing gaps "a," "b," and "c" allows us to capture all the information contained in these alignments and to postulate the smallest number of insertion-deletion events possible, which is the simplest hypothesis.

TABLE 1. Gap coding applied to DNA sequences

Taxon	Position
	1111111111222222
	12345678901234567890123 45
A	GGTAAACCGTGTCCCCTACAAGCTA
B	GGTAAAC– – –CCCTACAAGCTA
C	GGTAAAC– – –CCCTACAAGCTA
D	GGTAAAC–TGTCCCCTACAAGCTA
E	GGTAAAC–TGTCCCCTACAAGCTA
F	GGTAAAC– –TCCCCTACAAGCTA
G	GGTAAAC– –TCCCCTACAAGCTA

It has been suggested that secondary structure of ribosomal RNA molecules may be an important factor in estimating character weights for different regions of the genes coding for these molecules (Wheeler and Honeycutt, 1988; Vawter and Brown, 1993; Miyamoto et al., 1994). Examination of levels of homoplasy in the 16S gene, however, shows that there is considerable variation in rates of evolution within all kinds of secondary structures (i.e., stems, loops, bulges, and "other"); therefore, the site-specific weighting methods such as successive weighting and homoplasy-correcting dynamic weighting are a better correction for homoplasy (Horovitz and Meyer, 1995).

RESULTS

Mitochondrial data analysis

Two different weighting methods were applied to the 12S mitochondrial gene sequences. These were successive approxima-

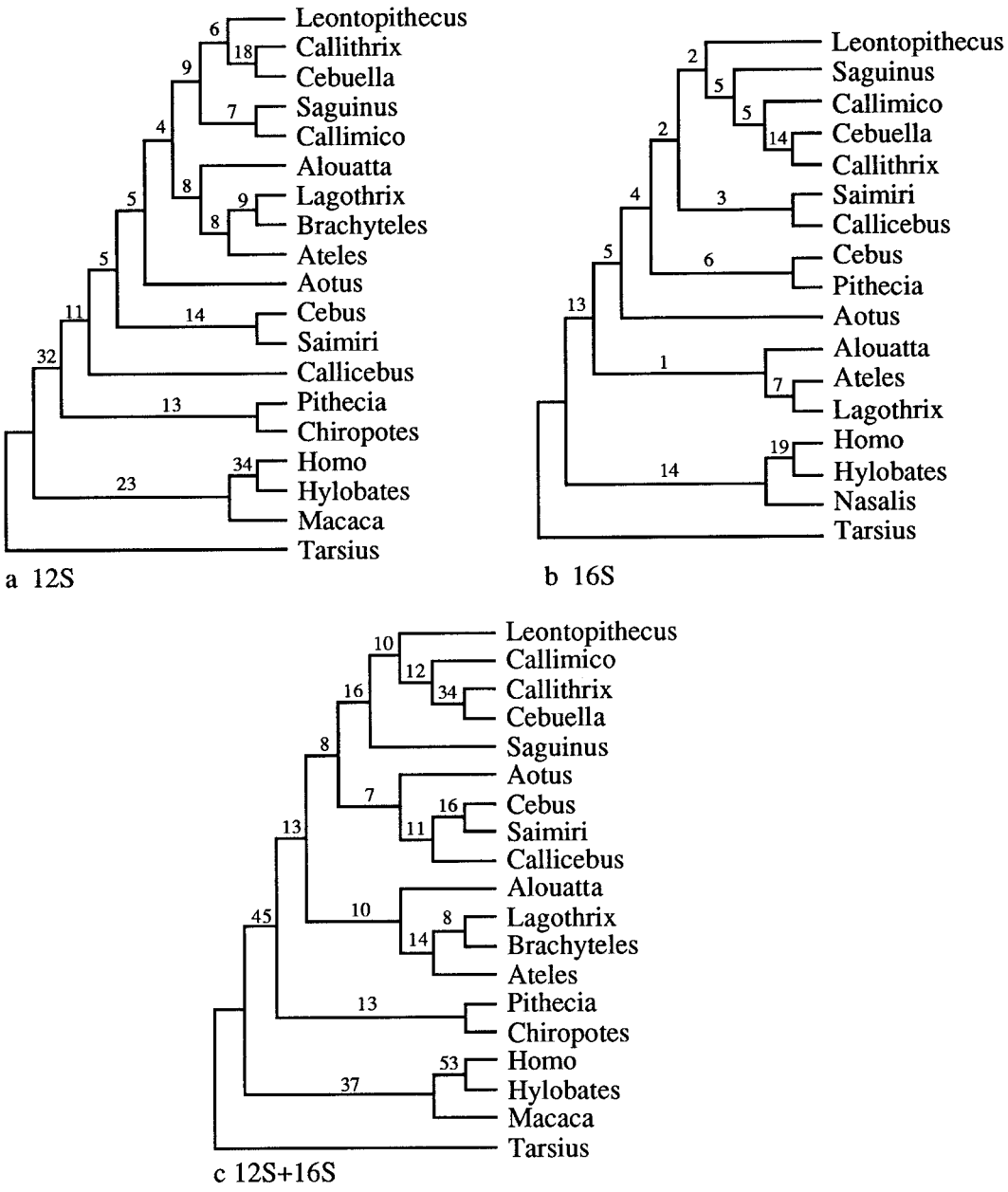

Fig. 2. **(a, b):** Cladograms obtained with successive weighting and gap coding specified in the text for (a) 12S and (b) 16S (Horovitz and Meyer, 1995) mitochondrial genes. **(c)** Single cladogram obtained when combining the 12S and 16S data sets (unchanged when subjected to successive approximations to character weighting). Numbers above branches indicate number of unambiguous characters supporting each node.

tions weighting (Farris, 1969) and homoplasy-correcting dynamic weighting (Horovitz and Meyer, 1995), with corrections explained in Materials and Methods. Application of these methods yielded the same tree (Fig. 2a), which was stable after the first successive weighting iteration (CI = 0.45 and RI = 0.44). In this tree callitrichi-

nes, atelines, and pitheciins are monophyletic; *Callimico* are sister group of *Saguinus*, and *Leontopithecus* of *Callithrix-Cebuella*; atelines are sister of callitrichines; and the next branch bears *Aotus*, then *Cebus-Saimiri*, *Callicebus*, and finally basal to all other platyrrhines are pitheciins.

A simultaneous analysis of the two mitochondrial data sets yielded a single tree (Fig. 2c; CI = 0.46, RI = 0.43) that was different from those obtained with the 12S or 16S genes analyzed separately (Fig. 2a, b). This tree was robust to either of the two weighting methods we applied previously. Sequences for both species of *Saguinus* and *Alouatta* were almost identical, and inclusion or exclusion of one species of each did not affect the topologies of the trees.

The transformation-cost weighting matrices T built as part of the homoplasy-correcting dynamic weighting method (Horovitz and Meyer, 1995) for the two mitochondrial genes analyzed separately were compared with each other before making the corrections necessary to pursue a tree search explained in Materials and Methods. The highest nucleotide-substitution costs were for changes G $\Leftrightarrow$ T and G $\Leftrightarrow$ C, and the lowest costs were for the changes A $\Rightarrow$ G and T $\Rightarrow$ C.

In both mitochondrial genes, C $\Leftrightarrow$ T changes (as an average of C $\Rightarrow$ T and T $\Rightarrow$ C) deserved less weight than A $\Leftrightarrow$ G changes (also as an average of both directions). Transitions deserved on average less weight than transversions. This pattern has been known for some time (Brown et al., 1982).

The tree obtained from simultaneous analysis of the 12S and 16S mitochondrial sequences (Fig. 2c) was compared with the trees obtained with the nuclear sequences (Fig. 3a; CI = 0.63, RI = 0.73) and morphological characters (Fig. 3b; CI = 0.48, RI = 0.70). Topologies of trees generated with individual data sets all differ from each other. A few features are common to all, however, which are the traditional groups known as callitrichines, pitheciins, and atelines. Relationships within these groups and with the remaining four genera—*Cebus*, *Saimiri*, *Callicebus*, and *Aotus*—differ among phylogenies.

The simultaneous analysis of the mitochondrial genes shows callitrichines most nested with *Cebus*, *Saimiri*, *Aotus*, and *Callicebus*. Next branches support atelines and further basally, pitheciins (Fig. 2c).

The two sets of nuclear sequences were combined and subjected to both weighting methods, and the tree was stable—it did not change with the different weighting procedures (Fig. 3a). The trees generated with nuclear sequences and morphological data (Fig. 3a, b) have additional features in common not shown by the trees generated with mitochondrial data. Namely, the existence of two basal clades of platyrrhines with the same composition. One of them includes atelines, pitheciins, and *Callicebus*, and the other includes callitrichines, *Aotus*, *Cebus*, and *Saimiri*.

Weighting matrices computed for the nuclear sequences showed similar patterns to those for the mitochondrial ones, although the bias was not as strong and there was a certain overlap in the cost of changes in one direction of some transitions and transversions: A $\Rightarrow$ C and A $\Rightarrow$ T had the highest costs for IRBP, and C $\Rightarrow$ G, A $\Rightarrow$ C, and A $\Rightarrow$ T for ϵ-globin. The lowest costs were assigned to G $\Rightarrow$ A and C $\Rightarrow$ T for IRBP and to T $\Rightarrow$ C and G $\Rightarrow$ A for ϵ-globin. As in the case of the mitochondrial genes, C $\Leftrightarrow$ T changes (as an average of C $\Rightarrow$ T and T $\Rightarrow$ C change costs) deserved less weight on average than A $\Leftrightarrow$ G changes in nuclear genes; transitions deserved on average less weight than transversions.

Simultaneous analysis of the morphological and molecular data sets

The simultaneous phylogenetic analysis of all data sets yielded the cladogram shown in Figure 4. The length is 3,198 steps (CI = 0.52, RI = 0.59). The topology is not perfectly congruent with any of the trees resulting from analyses of any of the separate data sets; however, it is closest to the tree generated with the nuclear data (Fig. 3a), which was the most consistent, followed in congruence by the tree based on morphological data (Fig. 3b). Combined analyses of the nuclear data with the mitochondrial 16S DNA sequences were conducted in a previous study (Horovitz and Meyer, 1997). The

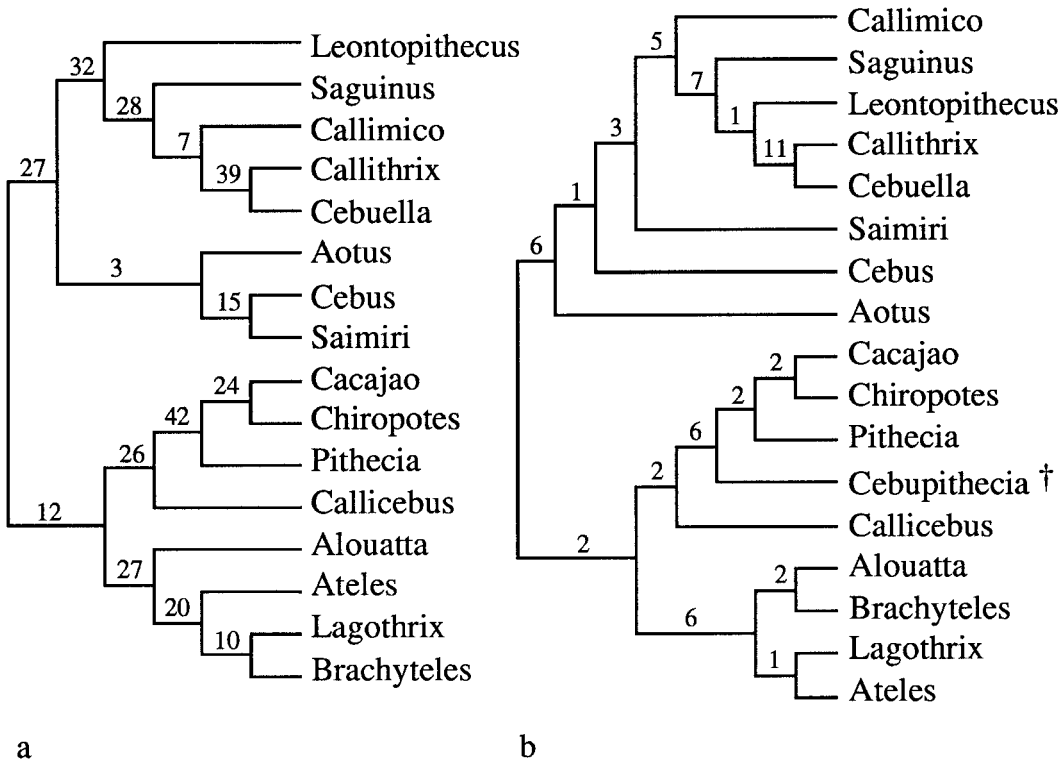

Fig. 3. Phylogenetic trees for **(a)** realigned nuclear genes ϵ-globin and IRBP combined (data from Schneider et al., 1993, 1996; Harada et al., 1995) and **(b)** morphological characters. Numbers above branches indicate number of unambiguous characters supporting each node. Dagger indicates fossil taxon.

topology obtained was tested and confirmed with the addition of morphological data (Horovitz and Meyer, 1997) and is now reconfirmed with the addition of the 12S data set. Support for different branches shows some common patterns in all data sets, yet some substantial differences are detected as well. The clade that includes atelines, *Callicebus*, and pitheciins is only weakly supported by the nuclear and morphological data when analyzed separately; however, combination of all data sets confirms this clade, with the additional support of the mitochondrial data sets (not revealed in the separate analysis).

Despite showing different topologies when analyzed separately, most branches of the tree obtained with the simultaneous analysis receive support from all data sets, except nodes 1, 2, and 3 (Fig. 4) that are not supported by any morphological data. Support for the position of the owl monkeys (*Aotus*) relative to the capuchin (*Cebus*) and squirrel monkeys (*Saimiri*) and the callitrichines is not strong. The completely resolved topology presented in Figure 4 is only three steps shorter than the grouping of the owl monkeys with the capuchin and squirrel monkeys and four steps shorter than the same genus grouped with callitrichines. Of the nodes unsupported by morphology, the monophyly of (*Callimico* (*Callithrix, Cebuella*)) and of (*Lagothrix, Brachyteles*) are among the least well supported by unambiguous molecular characters (Fig. 4). Nodes linked with fossil taxa are typically supported by fewer unambiguous characters because of missing entries.

Morphological synapomorphies. Morphological support for platyrrhini consists of a canal connecting the subarcuate fossa located in the caudal cranial cavity, and the sigmoid sinus which contains the sinus venosus, one of the major drainage vessels of the

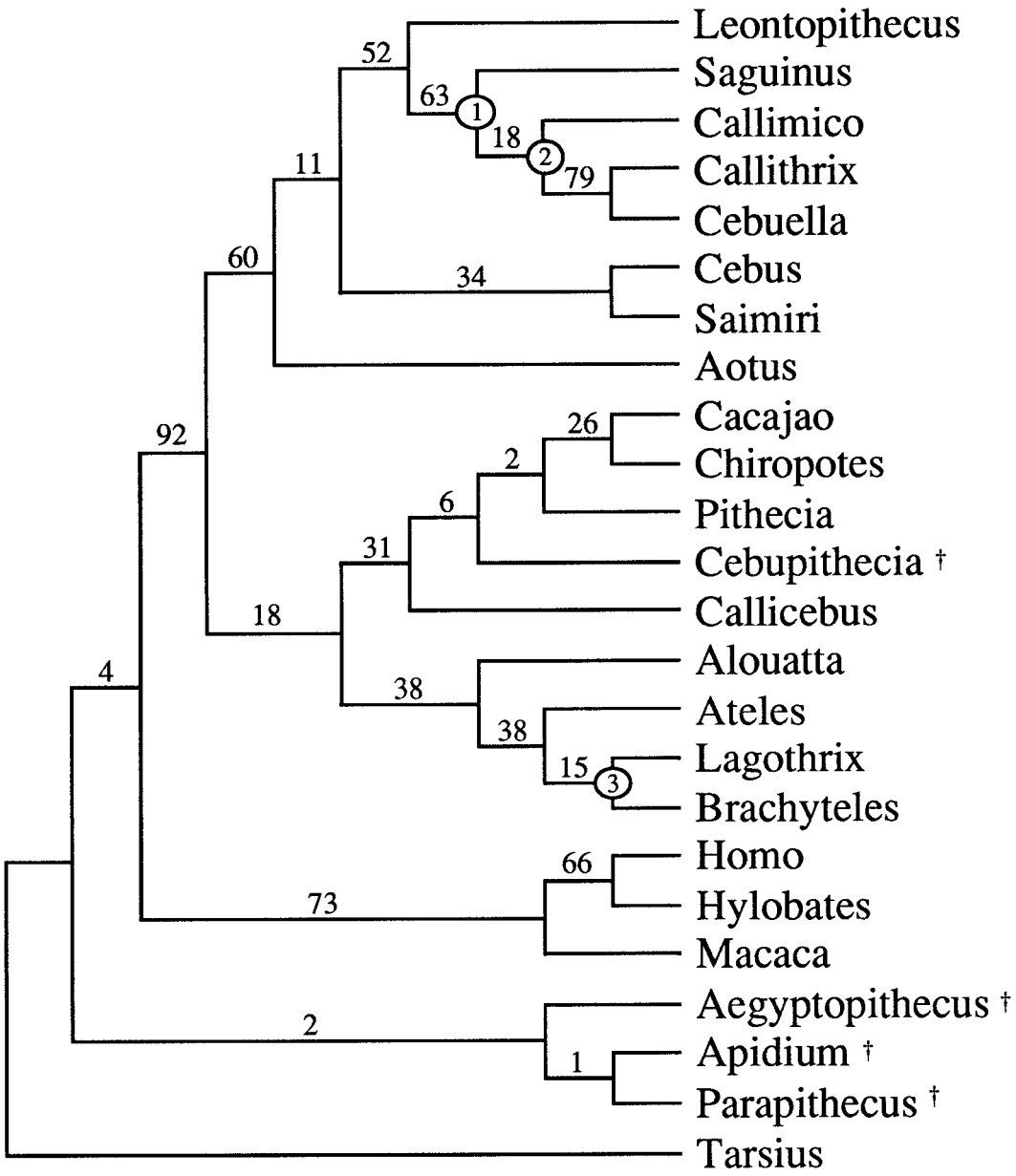

Fig. 4. Tree obtained from simultaneous analysis of mitochondrial genes 12S and 16S, nuclear genes ϵ-globin and IRBP, and morphological characters. Numbers above branches indicate number of unambiguous characters supporting each node. Daggers indicate fossil taxon. Nodes labeled 1 to 3 (circled numbers) are those unsupported by morphological characters.

brain. Another character that supports this node is the presence of ossification in the tentorium cerebelli, a membrane that separates the cerebrum from the cerebellum (Horovitz, 1995).

The grouping of *Aotus, Saimiri, Cebus,* and callitrichines is supported by the presence of two prominences on the promontorium, the reduction of the upper and lower molars to a length subequal to that of the

TABLE 2. Costs for each kind of change in the mitochondrial 12S and 16S genes and nuclear ϵ-globin and IRBP DNA sequences

	12S	16S	ϵ-globin	IRBP
A-C	1.88	1.71	2.23	1.71
A-G	1.17	1.21	1.32	1.20
A-T	1.95	2.00	2.06	1.98
C-G	3.04	3.18	2.27	1.32
C-T	0.94	0.88	1.20	1.14
G-T	3.16	3.09	1.77	1.47

fourth premolar, and loss of a heel on the lingual aspect of upper incisors. The grouping of these taxa to the exclusion of *Aotus* is in turn supported by further reduction of the last lower molar to be shorter than the fourth premolar (Rosenberger [1979] recognized a general reduction of the molars).

Characters supporting a *Saimiri-Cebus* relationship include exposure of the vomer in the orbit (Cartmill, 1978) and a widened fourth upper premolar, in such a way that it is either equal to or wider than the first molar.

Characters supporting the association of the atelines, *Callicebus,* and pitheciins include reduction of the pterygoid fossa and a deciduous lower second premolar with a rounded outline, derived from a mesiodistally elongated outline.

The fossil species *Cebupithecia sarmintoi* is most closely related to the pitheciin clade; therefore, we redefine the Pitheciini to include the fossil taxon in addition to the living *Pithecia, Chiropotes,* and *Cacajao. Callicebus* share a few derived characters with the pitheciins, such as trigonid and talonid of subequal height in the lower second molar and presence of prehypocrista on the first upper molar derived from a primitive condition of absence (subsequently reversed in living pitheciins).

Molecular change costs. Costs for different sorts of molecular changes were compared for the four genes. A matrix T was computed for each of the four data subsets on the tree resulting from the simultaneous analysis of all data sets (summarized in Table 2). The raw values (values not corrected for tree calculation; see Materials and Methods) were plotted, with each axis representing changes in one direction (Fig. 5). Mitochondrial data changes proved to deserve not only the lowest but also the highest cost values. These costs vary according to the optimization one applies to the ambiguous characters; it was reassuring, however, that we could replicate the pattern described above using only unambiguous characters and maximum and average number of steps of each sort for all data sets. The range for mitochondrial genes was always larger than for nuclear ones. In Table 2, we show the relative quality of each kind of change (averaged for both directions) in each data set calculated on the total evidence tree. This table shows that C ⇔ T changes have the lowest cost in all data sets, followed by A ⇔ G. The relative costs of transversions vary among data sets: the highest cost corresponds to changes C ⇔ G and G ⇔ T in both mitochondrial genes, A ⇔ C and C ⇔ G in the ϵ-globin gene, and A ⇔ T and A ⇔ C in IRBP.

When the weights of entire molecular characters were compared across data sets as measured by the C weighting vector, most of the characters with high rescaled consistency indices were nuclear. To make this assessment, we counted the number of characters (=sites) with a rescaled consistency index of one in the total evidence tree and divided these values by the total number of phylogenetically informative characters in each gene. The best fitting is the ϵ-globin gene, and in descending order are IRBP, 16S, and 12S.

DISCUSSION

To test the monophyly of Platyrrhini, we used living and fossil catarrhines and *Tarsius* as an outgroup of anthropoids (Platyrrhini + Catarrhini, plus basal fossil species). A preliminary morphological analysis including these taxa suggested that platyrrhines are in fact monophyletic (Horovitz, 1995). The morphological analysis and the simultaneous analysis of morphological and molecular data we conducted confirm this hypothesis. The position of *Aegyptopithecus* is not the traditional one as sister group of catarrhines; it appears as the sister of *Parapithecus* and *Apidium,* and this group as sister of all living anthropoids. This requires the loss of the second premolar to occur twice in the tree—in *Aegyptopithecus* and

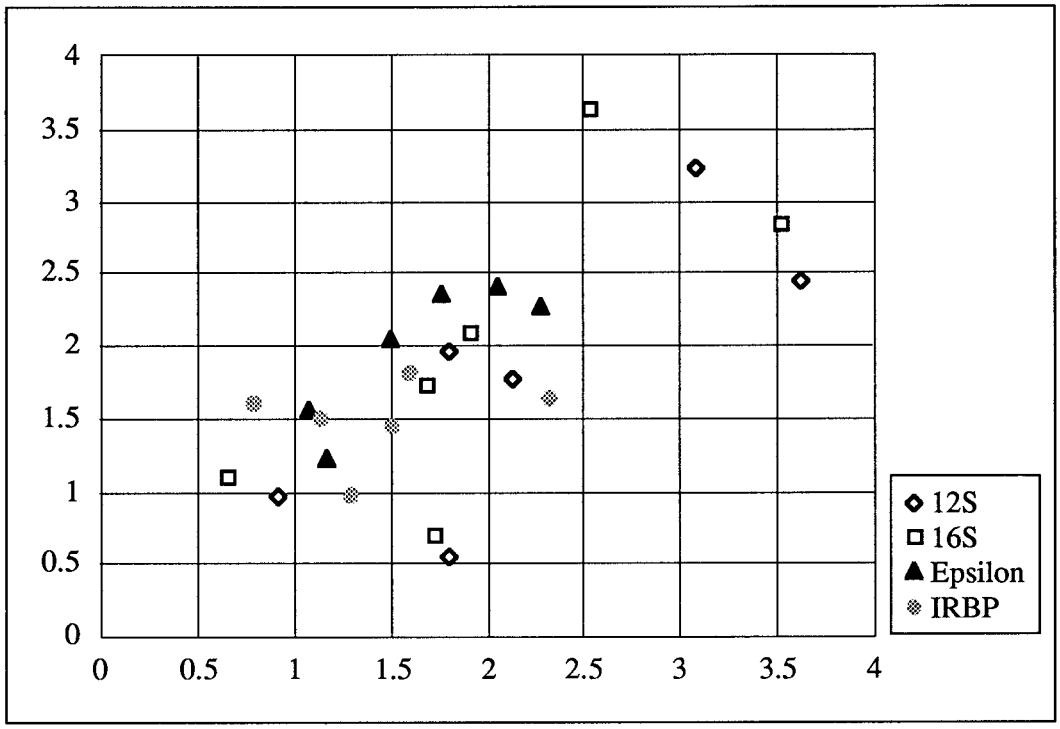

Fig. 5. Graph obtained with values from transformation-cost matrices T for the 12S and 16S mitochondrial genes as well as the ϵ-globin and IRBP nuclear genes (see summary in Table 2). Each axis is one direction of each change; therefore, the coordinates of each point or kind of change are the costs in each direction of that change. Values were calculated according to homoplasy-correcting dynamic weighting (Horovitz and Meyer, 1995). Frequencies of changes were calculated from the total evidence tree (Fig. 4), and the minimum number of steps for all possible optimizations and trees, as calculated by MacClade 3.0 (Maddison and Maddison, 1992), was used.

living catarrhines. This different topology may be an artifact due to an undersampling of basal anthropoids and outgroups of anthropoids, but this aspect of the tree is beyond the scope of this article.

The position of *Callimico* is also untraditional. No phylogenies based on morphology have ever suggested that *Callimico* are the sister group of *Callithrix* and *Cebuella*. The closest position to marmosets proposed by morphologists and accepted by most is basal within callitrichines. *Callimico* show several characteristics shared with other callitrichines. They are among the smallest and have in absolute terms the smallest cranial capacity among anthropoids (Appendix A, character 22). They also have claws in all manual and pedal digits except the hallux. At the same time, *Callimico* lack other characters present in *Callithrix, Cebuella, Leontopithecus,* and *Saguinus*. These are (1) reduction of the size of the pterygoid fossa from reaching the base of the skull to a shallow space between the lateral pterygoid process and the splinter-like medial process, (2) loss of the third molar, (3) loss of the hypocone on the first upper molar, and (4) birth of two offspring at a time (derived from a primitive condition of one). If *Callimico* are the sister group of *Callithrix* and *Cebuella,* all these characters are reversed in *Callimico.*

We evaluated the number of reversals that the sister group relationship of *Callimico* and the marmosets implies in the molecular data set. In other words, we examined how many of the synapomorphies of callitrichines were reversed in *Callimico* on the tree resulting from the simultaneous analysis of all data sets. Contrary to what

we observe in the morphological characters, few molecular reversals contradict this phylogenetic hypothesis. Of the 42 unambiguous molecular characters supporting Callitrichinae, only four are reversed in *Callimico.* Moreover, three of these characters are comparatively unreliable because they display individual CIs lower than 0.38 and RCs lower than 0.17. The one reliable character has CI = 0.67 and RC = 0.53.

Individual data set analyses show that this position for *Callimico* is supported by each one of the trees built with the molecular data sets analyzed separately, except for the 12S gene, that supports a sister group relationship between *Callimico* and *Saguinus.* Partially unpublished simultaneous analyses of molecular data, including the mitochondrial gene COII and the nuclear G6PD (Von Dornum, 1997), lend further support to the monophyly of marmosets and *Callimico.*

The *Callimico-Callithrix-Cebuella* clade is weakly supported in the cladogram resulting from the simultaneous analysis of all data sets, and we do not discard the possibility that it could be easily falsified by addition of more data. However, the molecular data available do not point to an alternative position of *Callimico* as basal to the remaining callitrichines.

The sister group relationship of *Lagothrix* and *Brachyteles* is supported by the three molecular data sets for which sequences of *Brachyeteles* were obtained—12S, ϵ-globin, and IRBP. As in the previous case, analyses including COII and G6PD lend further support to the results of our simultaneous analysis (Von Dornum, 1997).

The position of *Brachyteles* according to morphological data is controversial, but no one postulates a sister group relationship between *Brachyteles* and *Lagothrix.* Dental characters show an affinity of *Alouatta* and *Brachyteles* (Kay, 1990; MacPhee et al., 1995), whereas postcranial characters (and locomotory behavior) point at a close affinity between *Brachyteles* and *Ateles* (Rosenberger, 1979, 1981; Ford, 1986b; Rosenberger and Strier, 1989). The simultaneous analysis of all data sets points at *Lagothrix* and *Brachyteles* as sister taxa, followed by *Ateles;* therefore, the dental characters shared by *Brachyteles* and *Alouatta* are convergences, whereas those shared by *Ateles* and *Brachyteles* have an ambiguous optimization, and they have either been acquired by the ancestor of [*Ateles* (*Brachyteles, Lagothrix*)] and lost in *Lagothrix* or they have been acquired independently by *Ateles* and *Brachyteles.* There are only 7 molecular characters that have an ambiguous optimization with this same distribution, whereas 45 unambiguous characters support [*Ateles* (*Brachyteles, Lagothrix*)]. Of these seven characters, one has a CI = 0.67 and RC = 0.5, four have CI = 0.5 and RC = 0, and the remaining two CI = 0.33 and RC = 0, which is weak evidence for an *Ateles-Brachyteles* sister-group relationship. Likewise, *Brachyteles* and *Alouatta* show only two molecular convergences, one with CI = 0.33 and RC = 0 and the other with CI = 0.6 and RC = 0.33.

We evaluated the degree to which molecular characters in different data sets fit the total evidence tree and revealed contrasting properties between some mitochondrial and nuclear sites. Particularly interesting is our finding that changes in mitochondrial data have a wider range of change costs than nuclear data, including both lower and higher costs. Nuclear data, however, showed relatively more characters with high rescaled consistency indices, particularly the ϵ-globin. This is an empirical way of showing that successive weighting alone may not capture the whole picture of weights the data imply, as Horovitz and Meyer (1995) suggested. Although homoplasy-correcting dynamic weighting averages weights of kinds of changes across sites, and therefore it may not strictly reflect what each individual site deserves, it nonetheless seems to be a suitable correction for successive weighting when there are strong biases in the degree of homoplasy of certain kinds of changes.

The differences between mitochondrial and nuclear data shown in Figures 5 suggest that mitochondrial sites have, on average, a higher rate of mutation than nuclear ones but also that mitochondrial DNA shows a higher variety of rates among its sites than does nuclear DNA. This heterogeneity in rates is desirable in tree calculation to resolve cladogenetic events that occurred over

different periods. In some cases in which a certain radiation occurred over a short period, fast-evolving sites are more likely to document these branches, while slow-evolving sites are also necessary in preserving evidence unchanged about ancient branching events (Donoghue and Sanderson, 1992). Calculation of matrices T and vectors C for different data sets in a total evidence tree seems to be a useful tool in assessing the presence of heterogeneity within and between data sets in the rates of different sites and kinds of changes between data sets.

The mitochondrial genes analyzed separately yielded different topologies. This seems to be due to the presence of homoplasy and possibly to the shorter length of the 16S gene sampled, which on its own may not suffice to convey enough information about relationships. When combined, both genes showed support for the relationships suggested by the simultaneous analysis. This signal was not completely revealed in the separate analyses.

The nuclear genes made the strongest contribution to the total evidence topology. However, the contribution of the mitochondrial genes introduced a change in the position of *Aotus*, which despite not being strong, falsified what the nuclear genes indicated. In the resulting tree, *Cebus-Saimiri* were linked with callitrichines instead of *Aotus*.

In conclusion, the high congruence in topology between the nuclear and the combined tree seems to be due primarily to the high consistency of the nuclear data. Despite the low support that the nuclear data set lends to the clade that includes the atelines, *Callicebus*, and the pitheciins, the monophyly of this group seems to be confirmed with addition of the mitochondrial and morphological data. Addition of the mitochondrial to the nuclear data determines the position of *Aotus* to be basal to the other members of its clade. Addition of the morphological data confirms this position. The position of *Callimico* as basal to the *Callithrix-Cebuella* dyad is maintained despite its lack of support from morphological data, after combination of all data sets. The same is true regarding the position of *Brachyteles* as sister group of *Lagothrix*.

ACKNOWLEDGMENTS

This project was funded with an NSF Doctoral Dissertation Improvement Grant to IH (SBR-9514173) and an NSF grant to AM (DEB-9615178). The authors thank the following people who provided primate tissue samples: Horacio Schneider and Ira Sampaio (Universidad Federal do Para), Gabriel Aguado (Jardín Zoológico de Buenos Aires), George Amato (NY Zoological Society), Neal Clapp (Marmoset Research Center, University of Tennessee Medical Center), Virginia Crossett (Louisville Zoological Gardens), Mark Harrison (Primate Research Center, UC Davis), Guy Hoelzer (University of Nevada, Reno), Jeff Meldrum (Idaho State University, Pocatello), and Patricia Wright (SUNY, Stony Brook). The authors also thank Jim Carpenter and John Fleagle for comments and corrections to the manuscript.

LITERATURE CITED

Anderson S, Bankier AT, Barrell BG, de Bruijn MHL, Coulson AR, Drouin J, Eperon IC, Nierlich DP, Roe BA, Sanger F, Schreier PH, Smith AJH, Staden R, and Young IG (1981) Sequence and organization of the human mitochondrial genome. Nature *290:*457–465.

Ashley-Montagu MF (1933) The anthropological significance of the pterion in the primates. Am. J. Phys. Anthropol. *18:*158–336.

Avise JC (1994) Molecular Markers, Natural History and Evolution. New York: Chapman and Hall.

Baba ML, Darga LL, and Goodman M (1979) Immunodiffusion systematics of the primates. Part V. The platyrrhini. Folia Primatol. *32:*207–238.

Baba ML, Darga L, and Goodman M (1980) Biochemical evidence on the phylogeny of Anthropoidea. In R Ciochon and AB Chiarelli (eds.): Evolutionary Biology of the New World Monkeys and Continental Drift. New York: Plenum Press, pp. 423–443.

Brown W, Prager EM, Wang A, and Wilson AC (1982) Mitochondrial DNA sequences of primates: Tempo and mode of evolution. J. Mol. Evol. *18:*225–239.

Buffon GLL (1767) Histoire naturelle générale et particulière avec description du cabinet du roi [with supplement by M. Daubenton]. De l'Imprimerie Royale *15:*327.

Cartmill M (1978) The orbital mosaic in prosimians and the use of variable traits in systematics. Folia Primatol. *30:*89–114.

Cartmill M, MacPhee RDE, and Simons EL (1981) Anatomy of the temporal bone in early anthropoids, with remarks on the problem of anthropoid origins. Am. J. Phys. Anthopol. *56:*3–21.

Cronin JE and Sarich VM (1975) Molecular systematics of the New World monkeys. J. Hum. Evol. *4:*357–375.

Cronin JE and Sarich VM (1978) Marmoset evolution: The molecular evidence. Prim. Med. *10:*12–19.

Donoghue MJ and Sanderson MJ (1992) The suitability of molecular and morphological evidence in reconstructing plant phylogeny. In PS Soltis, DE Soltis, and

JJ Doyle (eds.): Molecular Systematics of Plants. New York: Chapman and Hall, pp. 340–367.
Erikson GE (1963) Brachiation in New World monkeys and in anthropoid apes. Symp. Zool. Soc. Lond. *10:*135–163.
Farris JS (1969) A successive approximations approach to character weighting. Syst. Zool. *18:*374–385.
Farris JS (1970) Methods for computing Wagner trees. Syst. Zool. *19:*83–92.
Farris JS (1981) Distance data in phylogenetic analysis. In VA Funk and DR Brooks (eds.): Advances in Cladistics: Proceedings of the First Meeting of the Willi Hennig Society. New York: Columbia University Press, pp. 3–22.
Farris JS (1985) Distance data revisited. Cladistics *1:*67–85.
Fick R (1911) Handbuch der Anatomie und Mechanik der Gelenke III. Jena: Gustav Fisher.
Fitch WM (1971) Toward defining the course of evolution: Minimum change for a specified tree topology. Syst. Zool. *20:*406–416.
Fleagle JG (1988) Primate Adaptation and Evolution. New York: Academic Press.
Fleagle JG and Kay RF (1987) The phyletic position of the Parapithecidae. J. Hum. Evol. *16:*483–531.
Ford SM (1986a) Comment on the evolution of claw-like nails in callitrichids (marmosets/tamarins). Am. J. Phys. Anthropol. *71:*1–11.
Ford SM (1986b) Systematics of the New World monkeys. In DR Swindler and J Erwin (eds.): Comparative Primate Biology. Vol. 1: Systematics, Evolution and Anatomy. New York: Alan R. Liss, pp. 73–135.
Ford SM and Davis LC (1992) Systematics and body size: Implications for feeding adaptations in New World monkeys. Am. J. Phys. Anthropol. *88:*415–468.
Harada ML, Schneider H, Schneider MPC, Sampaio I, Czeluzniak J, and Goodman M (1995) DNA evidence on the phylogenetic systematics of New World monkeys: Support for the sister-grouping of *Cebus* and *Saimiri* from two unlinked nuclear genes. Mol. Phylogenet. Evol. *4:*331–349.
Hennig W (1966) Phylogenetic Systematics. Urbana, IL: University of Illinois Press.
Hershkovitz P (1970) Notes of tertiary platyrrhine monkeys and description of a new genus from the late Miocene of Colombia. Folia Primatol. *12:*1–37.
Hershkovitz P (1977) Living New World Monkeys (Platyrrhini) with an Introduction to Primates. Chicago: Chicago University Press.
Hill JP (1926) Demonstration of the embryologia varia (development of *Hapale jacchus*). J. Anat. *60:*486–487.
Horovitz I (1995) A phylogenetic analysis of the basicranial morphology of New World monkeys. Am. J. Phys. Anthropol. Suppl. *20:*113.
Horovitz I (1997) Platyrrhine systematics and the origin of Greater Antilles monkeys. PhD Dissertation. State University of New York at Stony Brook.
Horovitz I and Meyer A (1995) Systematics of the New World monkeys (Platyrrhini, Primates) based on 16S mitochondrial DNA sequences: A comparative analysis of different weighting methods in cladistic analysis. Mol. Phylogenet. Evol. *4:*448–456.
Horovitz I and Meyer A (1997) Evolutionary trends in the ecology of New World monkeys inferred from a combined phylogenetic analysis of nuclear, mitochondrial, and morphological data. In TJ Givnish and KJ Sytsma (eds.): Molecular evolution and Adaptive Radiation. New York: Cambridge University Press, pp. 189–224.
Kay RF (1990) The phyletic relationships of extant and fossil Pitheciinae. J. Hum. Evol. *19:*175–208.
Kay RF and Meldrum DJ (1997) A new small platyrrhine and the phyletic position of Callitrichinae. In RF Kay, RH Madden, RL Cifelli, and JJ Flynn (eds.): Vertebrate paleontology in the Neotropics. Washington, DC: Smithsonian Institution Press, pp. 435–458.
Kay RF and Williams BA (1994) Dental evidence for anthropoid origins. In JG Fleagle and RF Kay (eds.): Anthropoid Origins. New York: Plenum, pp. 361–445.
Kay RF, Fleagle JG, and Simons EL (1981) A revision of the Oligocene apes from the Fayum Province, Egypt. Am. J. Phys. Anthropol. *55:*293–322.
Kinzey WG (1973) Reduction of the cingulum in the Ceboidea. In W Montagna (ed.): Symposium of the Fourth International Congress on Primatology. Vol. 3. Basel: Karger, pp. 101–127.
Kinzey WG (1992) Dietary and dental adaptations in the Pitheciinae. Am. J. Phys. Anthropol. *88:*499–514.
Kluge AG (1989) A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). Syst. Zool. *38:*7–25.
Kluge AG and Wolf AJ (1993) Cladistics: What's in a word? Cladistics *9:*183–199.
Kocher TD, Thomas WK, Meyer A, Edwards SV, Pääbo S, Villablanca FX, and Wilson AC (1989) Dynamics of mitochondrial DNA evolution in animals. Proc. Natl. Acad. Sci. USA *86:*6196–6200.
Lewis OJ (1974) The wrist articulation of the Anthropoidea. In FA Jenkins (eds.): Primate Locomotion. New York: Academic Press, pp. 143–169.
MacPhee RDE and Cartmill M (1986) Basicranial structures and primate systematics. In DR Swindler and J Erwin (eds.): Comparative Primate Biology. Vol. 1: Systematics, Evolution and Anatomy. New York: Alan R. Liss, pp. 219–275.
MacPhee RDE, Horovitz I, Arredondo O, and Jiménez Vázquez O (1995) A new genus for the extinct Hispaniolan monkey *Saimiri bernensis* Rimoli, 1977, with notes on its systematic position. Am. Mus. Novitates *3134:*1–21.
Maddison WP and Maddison DR (1992) MacClade. Analysis of Phylogeny and Character Evolution, Version 3.0. Program and documentation. Sunderland, MA: Sinauer Associates.
Martin RD (1992) Goeldi and the dwarfs: The evolutionary biology of the small New World monkeys. J. Hum. Evol. *22:*367–393.
Miyamoto MM, Allard MW, Adkins RM, Janecek LL, and Honeycutt RL (1994) A congruence test of reliability using linked mitochondrial DNA sequences. Syst. Biol. *43:*236–249.
Napier JR (1961) Prehensility and opposability in the hands of Primates. Symp. Zool. Soc. Lond. *10:*115–132.
Nixon KC and Carpenter JM (1996) On simultaneous analysis. Cladistics *12:*221–241.
Pocock RI (1925) Additional notes on the external characters of some platyrrhine monkeys. Proc. Zool. Soc. Lond. 27–47.
Rogers JS (1986) Deriving phylogenetic trees from allele frequencies: A comparison of nine genetic distances. Syst. Zool. *35:*297–310.
Rosenberger AL (1977) *Xenothrix* and Ceboid phylogeny. J. Hum. Evol. *6:*461–481.
Rosenberger AL (1979) Phylogeny, Evolution and Classification of New World Monkeys (Platyrrhini, Primates). PhD Dissertation. City University of New York.
Rosenberger AL (1981) Systematics: The higher taxa. In AF Coimbra-Filho and RA Mittermeier (eds.): Ecology and Behavior of Neotropical Primates. Vol. 1. Rio de Janeiro: Academia Brasileira de Ciencias, pp. 111–168.
Rosenberger AL (1984) Fossil New World monkeys dispute the molecular clock. J. Hum. Evol. *13:*737–742.

Rosenberger AL (1992) Evolution of feeding niches in New World monkeys. Am. J. Phys. Anthropol. *88:*525–562.
Rosenberger AL and Strier KB (1989) Adaptive radiation of the ateline primates. J. Hum. Evol. *18:*717–750.
Rosenberger AL, Setoguchi T, and Shigehara N (1990) The fossil record of callitrichine primates. J. Hum. Evol. *19:*209–236.
Sarich VM and Cronin JE (1976) Molecular systematics of the primates. In M Goodman and R Tashian (eds.): Molecular Anthropology. New York: Plenum Press, pp. 141–170.
Sarich VM and Cronin JE (1980) South American mammal molecular systems, evolutionary clocks, and continental drift. In RL Ciochon and AB Chiarelli (eds.): Evolutionary Biology of the New World Monkeys and Continental Drift. New York: Plenum Press, pp. 399–421.
Schneider H and Rosenberger AL (1997) Molecules, morphology, and platyrrhine systematics. In MA Norconk, AL Rosenberger, and PA Garber (eds.): Adaptive Radiations of Neotropical Primates. New York: Plenum Press, pp. 3–19.
Schneider H, Schneider MPC, Sampaio I, Harada ML, Stanhope M, Czelusniak J, and Goodman M (1993) Molecular phylogeny of the New World monkeys (Platyrrhini, Primates). Mol. Phylogenet. Evol. *2:*225–242.
Schneider H, Sampaio I, Harada ML, Barroso CML, Schneider MPC, Czelusniak J, and Goodman M (1996) Molecular phylogeny of the New World monkeys (Platyrrhini, Primates) based on two unlinked nuclear genes: IRBP Intron 1 and ϵ-globin sequences. Am. J. Phys. Anthrop. *100:*153–179.
Schultz AH (1930) The skeleton of the trunk and limbs of higher primates. Hum. Biol. *2:*303–438.
Schultz AH (1961) Vertebral column and thorax. Primatologia *4:*1–66.
Simons EL (1962) Two new primate species from the African Oligocene. Postilla *166:*1–12.
Simons EL (1965) New fossil apes from Egypt and the initial differentiation of Hominoidea. Nature *205:*135–139.
Stirton RA (1951) Ceboid monkeys from the Miocene of Colombia. Bull. Univ. Calif. Pub. Geol. Sci. *28:*315–356.
Stirton RA and Savage DE (1951) A New Monkey from the La Venta Late Miocene of Colombia. Bogotá: Compilación de los Estudios de Geología, Servicio Geológico Nacional, *7:*345–356.
Swofford DL (1981) On the utility of the distance Wagner procedure. In VA Funk and DR Brooks (eds.): Advances in Cladistics: Proceedings of the First Meeting of the Willi Hennig Society. New York: Columbia University Press, pp. 25–43.
Swofford DL (1993): PAUP: Phylogenetic analysis using parsimony. 3.1.1 Champaign.
Vawter L and Brown W (1993) Rates and patterns of base change in the small subunit ribosomal RNA gene. Genetics *134:*597–608.
Von Dornum MJ (1997) DNA sequence data from mitochondrial COII and nuclear g6PD loci and a molecular phylogeny of the New World monkeys (Primates, Platyrrhini). PhD Dissertation. Harvard.
Von Dornum M and Ruvolo M (1996) A nuclear and mitochondrial phylogeny for the New World monkeys (Primates, Platyrrhini). Am. J. Phys. Anthrop. Suppl. *22:*236.
Waterman MS, Smith TF, Singh M, and Beyer WA (1977) Additive evolutionary trees. J. Theor. Biol. *64:*199–213.
Wheeler WC (1993) The triangle inequality and character analysis. Mol. Biol. Evol. *10:*707–712.
Wheeler WC and Gladstein D (1993): Malign. 1.95. Program and documentation. New York.
Wheeler WC and Honeycutt RL (1988). Paired sequence differences in ribosomal RNAs: evolutionary and phylogenetic implications. Mol. Biol. Evol. *5:*90–96.
Wilson AC, Cann RL, Carr SM, George M, Gyllensten UB, Helm-Bychowski KM, Higuchi RG, Palumbi SR, Prager EM, Sage RD, and Stoneking M (1985) Mitochondrial DNA and two perspectives on evolutionary genetics. Biol. J. Linn. Soc. *26:*375–400.
Wislocki GB (1939) Observations on twinning in marmosets. Am. J. Anat. *64:*445–483.

APPENDIX A

Character list

(1) Number of offspring at a time (Hill, 1926; Wislocki, 1939): 0 = one, 1 = two.
(2) Number of lumbar vertebrae (Erikson, 1963): 0 = more than five, 1 = five or fewer.
(3) Thumb degree of development (Pocock, 1925): 0 = absent or reduced, 1 = present.
(4) Presence of external tail: 0 = absent, 1 = present.
(5) Tail ventral glabrous surface (Pocock, 1925): 0 = absent, 1 = present.
(6) Presence of claws on all manual and pedal digits except hallux (Buffon, 1767): 0 = absent, 1 = present.
(7) Carpometacarpal type of joint (Fick, 1911; Napier, 1961): 0 = nonsaddle, 1 = saddle.
(8) Rib cage shape (Schultz, 1961): 0 = larger dorsoventrally, 1 = larger laterally.
(9) Ulnar participation in wrist articulation (Lewis, 1974): 0 = absent, 1 = present.
(10) Sternal proportions (Schultz, 1930): 0 = manubrium shorter than 36% of the corpus length, 1 = manubrium longer than 46% the corpus length.
(11) Relative orbit size (orbital height/foramen magnum width) (character 4, MacPhee et al., 1995): 0 = smaller than 1.9, 1 = larger than 2.1.
(12) Development of postglenoid foramen (org.) (Horovitz, 1997; Horovitz and MacPhee, in preparation): 0 = absent, 1 = reduced, 2 = large.
(13) Ossification of tentorium cerebelli (Hershkovitz, 1977; Horovitz, 1995): 0 = absent, 1 = present.

(14) Pneumatization of anteroventral region of the middle ear (Horovitz, 1997; Horovitz and MacPhee, in preparation): 0 = absent, 1 = present.
(15) Paired prominences in the middle ear (Horovitz, 1997; Horovitz and MacPhee, in preparation): 0 = absent, 1 = present.
(16) Pterygoid fossa depth (Horovitz, 1997; Horovitz and MacPhee, in preparation): 0 = deep, 1 = shallow.
(17) Canal connecting sigmoid sinus and subarcuate fossa (Cartmill et al., 1981; Horovitz, 1995; character 6, MacPhee et al., 1995): 0 = absent, 1 = present.
(18) Vomer exposure in orbit (Cartmill, 1978; Rosenberger, 1979): 0 = absent, 1 = present.
(19) Ectotympanic shape (MacPhee and Cartmill, 1986): 0 = tube, 1 = ring, 2 = tube II.
(20) Temporal emissary foramen (character 7, MacPhee et al., 1995): 0 = present and large, 1 = small or absent.
(21) Eyeball physically enclosed (Martin, 1992): 0 = absent, 1 = present.
(22) Cranial capacity (Note: This character is used instead of the more traditionally used body size; the reason we do so is that there may be a slight overlap between *Saimiri* and the callitrichines in body size, whereas there is none in cranial capacity [Horovitz, 1997; Horovitz and MacPhee, in preparation): 0 = less than 15 cc, 1 = more than 15 cc.
(23) Ventral extent of zygomatic arch (Horovitz, 1997; Horovitz and MacPhee, in preparation): 0 = below alveoli level, 1 = above alveoli level.
(24) Pterion region contact (Ashley-Montagu, 1933): 0 = frontal-alisphenoid, 1 = zygomatic-parietal.
(25) Infraorbital foramen, vertical position relative to maxillary cheekteeth in Frankfurt plane (ord.) (character 5, MacPhee et al., 1995): 0 = above interval between M^1 and P^4 (or caudal to this position), 1 = above interval between P^4 and P^3, 2 = above anteriormost premolar (or rostral to this position).
(26) Zygomaticofacial foramen, size relative to M^1 breadth (character 1, MacPhee et al., 1995): 0 = small, 1 = large.
(27) Deciduous I_2 shape (Horovitz, 1997; Horovitz and MacPhee, in preparation): 0 = blade-like (lingual heel is absent), 1 = displays lingual heel, 2 = styliform (lingual heel is absent).
(28) Relative height of $I_{1,2}$ (ord.) (Rosenberger, 1979): 0 = I_1 absent, 1 = I_1 lower than I_2, 2 = I_1 and I_2 subequal.
(29) Alignment of I_1 and I_2 (Hershkovitz, 1970, 1977; Rosenberger, 1979): 0 = transversely arcuate, 1 = staggered.
(30) $I_{1,2}$ shape (Rosenberger, 1979): 0 = spatulate, 1 = styliform.
(31) Meso and distostyles on $I_{1,2}$ (Hershkovitz, 1977): 0 = absent, 1 = present.
(32) Diastema between C and I_2 (Rosenberger, 1979): 0 = absent, 1 = present.
(33) Mandibular C root shape (character 11, MacPhee et al., 1995): 0 = rounded/suboval, 1 = highly compressed.
(34) Lingual cingulum on mandibular C (Kinzey, 1973): 0 = complete, 1 = incomplete or absent.
(35) Lingual crest sharpness on mandibular C in worn and unworn teeth (Kay, 1990): 0 = rounded, 1 = sharp.
(36) Mandibular C lingual cingulum mesial elevation (Horovitz, 1997; Horovitz and MacPhee, in preparation): 0 = not elevated, 1 = elevated.
(37) Mandibular C lingual cingulum forming a spike on mesial edge of the tooth (Horovitz, 1997; Horovitz and MacPhee, in preparation): 0 = absent, 1 = present.
(38) Buccolingual breadth of mandibular C alveolus over mandibular P_4 equivalent (Horovitz, 1997; Horovitz and MacPhee, in preparation): 0 = canine larger than P_4, 1 = canine smaller than P_4.
(39) Deciduous P_2, angle subtended by distal portion of mesiodistal axis and postprotocristid (Horovitz, 1997; Horovitz and MacPhee, in preparation): 0 = smaller than 45°, 1 = larger than 45°.
(40) Cross-section shape of deciduous P_2 (Horovitz, 1997; Horovitz and MacPhee, in preparation): 0 = rounded, 1 = mesiodistally elongated.

(41) P_2 premolar size relative to P_3 and P_4 (Horovitz, 1997; Horovitz and MacPhee, in preparation): 0 = P_2 smallest premolar, 1 = P_4 largest premolar.
(42) Deciduous P_3 metaconid (Kay and Meldrum, 1997): 0 = absent, 1 = present.
(43) P_3 protoconid size relative to P_4 protoconid (Horovitz, 1997; Horovitz and MacPhee, in preparation): 0 = P_3 and P_4 protoconids are subequal, 1 = P_3 protoconid is the largest.
(44) P_3 talonid (Horovitz, 1997; Horovitz and MacPhee, in preparation): 0 = larger than P_2 talonid, 1 = subequal with P_3 talonid.
(45) P_3 metaconid height relative to protoconid height (ord.) (Rosenberger, 1979): 0 = metaconid absent, 1 = metaconid lower than protoconid, 2 = metaconid and protoconid subequal, 3 = metaconid taller than protoconid.
(46) P_4 metaconid height relative to protoconid height (ord.) (Rosenberger, 1979): 0 = metaconid lower than protoconid, 1 = metaconid and protoconid subequal, 2 = metaconid taller than protoconid.
(47) Hypoconid on P_4 (Kay and Williams, 1994): 0 = absent, 1 = present.
(48) Entoconid on P_4 (Kay and Williams, 1994): 0 = absent, 1 = present.
(49) Number of premolars: 0 = three, 1 = two.
(50) M_1, projection of distobuccal quadrant (DB complex) (character 14, MacPhee et al., 1995): 0 = not projecting, 1 = projecting (crown sidewall hidden).
(51) M_1, intersection of oblique cristid and protolophid (character 15, MacPhee et al., 1995): 0 = intersects protolophid buccally, directly distal to apex of protoconid (medial protocristid apparently longer than lateral protocristid), 1 = intersects protolophid more lingually, distilingual to apex of protoconid (medial and lateral protocristids are subequal).
(52) M_1 entoconid position (Rosenberger, 1977): 0 = on the talonid corner, 1 = mesially off the talonid corner.
(53) Buccal cingulum on $M_{1,2}$ (Kinzey, 1973): 0 = absent, 1 = present.
(54) M_2 trigonid/talonid relative height (Kay, 1990): 0 = trigonid taller than talonid, 1 = subequal.
(55) M_2 with mesoconid (Horovitz, 1997; Horovitz and MacPhee, in preparation): 0 = absent, 1 = present.
(56) M_3/P_4 relative length (ord.) (Horovitz, 1997; Horovitz and MacPhee, in preparation): 0 = M_3 absent, 1 = M_3 shorter, 2 = subequal, 3 = M_3 longer.
(57) Molar enamel surface (Rosenberger, 1977): 0 = smooth, 1 = crenulated.
(58) I^1 lingual heel (Rosenberger, 1979): 0 = absent, 1 = present.
(59) I^2 orientation (Rosenberger, 1979): 0 = vertical, 1 = proclivious.
(60) Maxillary C alveolus area relative to P^4 equivalent (character 21, MacPhee et al., 1995): 0 = C larger than P^4, 1 = C smaller or equal to P^4.
(61) Deciduous P^2 trigon (Horovitz, 1997; Horovitz and MacPhee, in preparation): 0 = absent, 1 = present.
(62) Deciduous P^3 hypocone (Horovitz, 1997; Horovitz and MacPhee, in preparation): 0 = absent, 1 = present.
(63) P^3 preparacrista (Horovitz, 1997; Horovitz and MacPhee, in preparation): 0 = absent or vestigious, 1 = high.
(64) P^4 protocone position (character 23, MacPhee et al., 1995): 0 = on widest point of trigon, 1 = mesial to widest point.
(65) P^4 ligual cingulum (Kinzey, 1973): 0 = absent, 1 = present but no mesial projection.
(66) P^4 hypocone (Kay, 1990; MacPhee et al., 1995): 0 = absent, 1 = present.
(67) P^4 and M^1 relative buccolingual breadth (MacPhee et al., 1995): 0 = P^4 smaller, 1 = P^4 subequal or bigger than M^1.
(68) M^1 mesostyle (Kinzey, 1973): 0 = absent, 1 = present, 2 = replaced by mesoloph.
(69) M^1 hypocone/prehypocrista presence (ord.) (Rosenberger, 1979; character 30, MacPhee et al., 1995): 0 = hypocone and prehypocrista present, 1 = hypocone present and prehycrista absent, 2 = hypocone and prehypocrista absent.
(70) M^1 postmetacrista slope (character 26, MacPhee et al., 1995): 0 = distobuccal

slope, 1 = distal or distolingual slope, 2 = absent.

(71) M^1 alignment of protocone and hypocone (character 27, MacPhee et al., 1995): 0 = parallel, 1 = hypocone lingual.

(72) M^1, pericone/lingual cingulum (ord.) (character 29, MacPhee et al., 1995): 0 = absent, 1 = lingual cingulum only, 2 = distinct pericone on lingual cingulum.

(73) M^2 hypocone (Rosenberger 1979; character 32, MacPhee et al., 1995): 0 = absent, 1 = present.

(74) M^2 cristae on distal margin of trigon (character 31, MacPhee et al., 1995): 0 = cristae form distinct, continuous wall between protocone and metacone, 1 = cristae interrupted by a fossette or do not form a distinct wall, 2 = cristae absent or differently organized.

(75) M^3 length (ord.) (Rosenberger 1979; Horovitz, 1997; Horovitz and MacPhee, in preparation): 0 = M^3 absent, 1 = M^3 shorter than P^4, 2 = M^3 and P^4 subequal, 3 = M^3 longer than P^4.

(76) Maxillary M's parastyles (Horovitz, 1997; Horovitz and MacPhee, in preparation): 0 = absent, 1 = present.

Molecular characters[1]

Sequence	Authors	Accession numbers
ϵ-globin gene	Schneider et al., 1993	L25354-L25371
IRBP intron 1	Harada et al., 1995; Schneider et al., 1996	U18601-U18609 U18611-U18619 U19748-U19753
16S rDNA fragment	Horovitz and Meyer, 1995	U38997-U39012
12S rDNA gene	Current report	AF069964-AF069983

[1] These sequences were aligned and used in the phylogenetic analysis. They are deposited in GenBank Data Libraries under the corresponding accession numbers.

APPENDIX B. Matrix for morphological characters listed in Appendix A

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
1 Tarsius	0	0	1	1	0	0	0	0	0	0	1	2	0	0	0	0	0	0	2	0	0	0	1	1	1	0
2 Leontopithecus	1	0	1	1	0	1	0	0	0	0	0	2	1	1	1	1	1	0	1	1	1	0	1	0	2	0
3 Saguinus	1	0	1	1	0	1	0	0	0	0	0	2	1	0	1	1	1	0	1	1	1	0	1	0	2	0
4 Callimico	0	0	1	1	0	1	0	0	0	0	0	0 & 1	1	0	1	0	1	0	1	1	1	0	1	0	2	1
5 Callithrix	1	0	1	1	0	1	0	0	0	0	0	2	1	1	1	1	1	0	1	1	1	0	1	0	2	0
6 Cebuella	1	0	1	1	0	1	0	0	0	0	0	2	1	1	1	1	1	0	1	1	1	0	1	0	2	0
7 Aotus	0	0	1	1	0	0	0	0	0	0	1	2	1	0	1	0	1	0	1	1	1	1	0	0	2	0
8 Cebus	0	0	1	1	0	0	0	0	0	0	0	2	1	0	1	0	1	1	1	1	0	1	1	0	2	0
9 Cacajao	0	0	1	1	0	0	0	0	0	0	0	0 & 1	1	0	0	1	1	0	1	1	0	1	1	0	2	0
10 Pithecia	0	0	1	1	0	0	0	0	0	0	0	1	1	0	1	1	1	0	1	1	0	1	1	0	2	0
11 Chiropotes	0	0	1	1	0	0	0	0	0	0	0	0 & 1	1	0	0	0 & 1	1	0	1	1	0	1	1	0	2	0
12 Saimiri	0	0	1	1	0	0	0	0	0	0	0	2	0 & 1	0	1	0	1	1	1	0	0	1	1	0	2	0
13 Alouatta	0	1	1	1	1	0	0	0	0	0	0	1	1	0	0	1	1	0	1	0	0	1	1	0	0	1
14 Lagothrix	0	1	1	1	1	0	0	0	0	0	0	0 & 1	1	0	0	1	1	0	1	0	0	1	1	0	1	1
15 Brachyteles	0	1	0	1	1	0	0	0	0	0	0	1	1	0	0	1	1	0	1	0	0	1	1	0	1	1
16 Callicebus	0	0	1	1	0	0	0	0	0	0	0	0	1	0	1	1	1	0	1	1	1	1	0	0	2	1
17 Cebupithecia	?	?	?	?	?	?	?	?	?	?	?	0	1	0	0	?	1	?	1	?	?	?	?	?	2	0
18 Ateles	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0 & 1	0	1	0	0	1	1	0	1	1
19 Homo	0	0	1	0	?	0	1	1	1	1	0	0	0	1	0	0	0	0	0	1	0	1	1	1	0	0
20 Hylobates	0	1	0	0	?	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	0
21 Cercopithecoids	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0
22 Aegyptopithecus	?	?	?	1	?	?	0	?	?	?	0	2	?	0	0	0	0	?	1	?	0	1	1	1	0	0
23 Apidium	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	?	0	?	?	?	?	?	?	?	1	?
24 Parapithecus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52
1 Tarsius	1	0	?	1	0	0	0	1	0	1	0	1	0	1	0	0	0	1	1	0	0	0	1	0	0	0
2 Leontopithecus	1	2	0	0	0	0	0	1	0	1	1	0	0	1	1	?	1	0	1	1	0	0	1	0	0	0
3 Saguinus	1	2	0	0	0	0	0	1	0	1	1	0	0	1	1	0	1	0	1 & 2	1	0	0	1	0	1	0
4 Callimico	1	2	0	0	0	0	0	1	0	1	1	0	0	1	1	?	0	0	2	1	0	0	1	1	1	0
5 Callithrix	0	1	1	1	1	0	1	0	0	1	0	0	0	1	1	0	1	1	1	0	0	0	1	0	0	0
6 Cebuella	0	1	1	1	1	0	1	0	0	1	0	0	0	1	1	0	1	1	1	0	0	0	1	0	0	0
7 Aotus	1	2	0	0	0	0	0	1	0	0 & 1	0 & 1	0	1	1	1	1	0	0	2	1 & 2	0 & 1	1	1	0	0	0
8 Cebus	1	2	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	3	2	1	1	1	0	0	0
9 Cacajao	2	2	0	1	0	1	0	1	1	0	0	0	1	0	0	1	0	0	1	1	1	1	1	0	0	1
10 Pithecia	2	2	0	1	0	1	0	1	1	0	0	0	1	0	0 & 1	1	0	0	1	1 & 2	1	1	1	0	0	1
11 Chiropotes	2	2	0	1	0	1	0	1	1	0	0	0	1	0	0 & 1	1	0	0	2	1	1	1	1	0	0	1
12 Saimiri	1	2	0	0	0	0	0	1	0	0 & 1	1	0	0	0 & 1	1	1	0	0	2	1	1	1	1	0	0 & 1	0
13 Alouatta	1	1	0	0	0	0	0	1	0	1	0	0	1	0	1	1	0	0	1	0	1	1	1	1	1	1
14 Lagothrix	1	2	0	0	0	0	0	1	0	0 & 1	0	0	1	0	1	1	0	0	2	1	0 & 1	1	1	0	0	1
15 Brachyteles	?	?	0	0	0	0	0	1	0	1	0	0	?	?	0	?	0	0	1	1	0 & 1	1	1	1	0	?
16 Callicebus	1	2	0	0	0	0	1	1	0	1	0	0	1	0	0	1	0	0	1	1	1	1	1	0	0	1
17 Cebupithecia	?	?	0	?	?	1	0	1	1	0	?	0	?	?	?	?	?	?	?	?	1	0	1	0	0	1
18 Ateles	1	2	0	0	0	0	0	1	0	1	0	0	1	0	1	1	0	0	2	1	0 & 1	0	1	0	0	1
19 Homo	1	2	0	0	0	0	1	0	0	?	?	1	?	?	?	?	?	?	1	0	0 & 1	1	0	0	0	1
20 Hylobates	1	2	0	0	0	0	0	1	0	1	0	0	?	?	?	1	?	?	0	1	1	1	0	0	0	1
21 Cercopithecoids	1	2	0	0	0	0	0	1	0	1	1	0	?	?	?	1	?	?	0	1	1	1	0	1	0	1
22 Aegyptopithecus	?	2	0	0	0	0	1	1	0	1	0	0	?	?	?	?	?	?	0	0	0	0	0	0	0	1
23 Apidium	?	2	0	0	0	0	1	1	0	1	0	0 & 1	?	?	0	?	0	0	1	0	0	0	1	0	1	1
24 Parapithecus	?	?	?	?	?	0	1	1	0	1	0	?	?	?	0	?	1	0	1	0	0	0	1	0	0	?

APPENDIX B (continued)

	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76
1 Tarsius	1	0	0	3	0	0	0	1	0	0	0	?	1	0	0	0	2	0	?	1	0	0	3	1
2 Leontopithecus	1	0	0	0	0	0	0	0	1	?	0	0	1	0	0	0 & 1	2	1	?	1	0	0	0	1
3 Saguinus	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0 & 1	2	0	?	1	0	0	0	1
4 Callimico	0	0	0	1	0	0	0	0	1	?	0	1	1	0	0	1	0	1	1	1	1	0	1	1
5 Callithrix	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0 & 1	2	0	?	1	0	0	0	1
6 Cebuella	1	0	0	0	0	0	0	0	0	0	0	1	0 & 1	0	0	1	2	1	?	1	0	0	0	1
7 Aotus	0	0	0	2	0	0	0	0	1	0	0	1	1	0	0	0	0	1	0	0 & 1	1	0	1	0
8 Cebus	0	1	0	1	0	0	0	0	1	0	1	1	1	0	1	0	1	1	0	0	1	1	1	0
9 Cacajao	0	1	1	2	1	1	1	0	1	0	1	1	0	0 & 1	1	0	1	1	0	1	1	1	2	0
10 Pithecia	0	1	1	1	1	1	1	0	1	0	1	1	0	0 & 1	0	0	0	1	0	1	1	1	3	0
11 Chiropotes	0	1	1	2	1	1	1	0	1	1	1	1	0	0 & 1	1	0	1	1	0	1	1	1	2	0
12 Saimiri	1	0	0	1	0	0	0	0	1	1	0	1	1	0	1	0 & 1	1	0	0	2	1	0	1	1
13 Alouatta	0	0	0	3	0	1	0	0	1	0	0	0	0	0 & 1	0	2	1	0	0	0 & 1	1	1	3	0
14 Lagothrix	0	0	0	3	0	1	0	0	1	0	0	0	0	1	0	0	1	1	0	0	1	0	3	0
15 Brachyteles	0	0	0	3	0	?	0	0	?	?	0	0	0	0	0	2	1	1	0	0	1	?	2	?
16 Callicebus	0	1	0	3	0	1	0	1	1	0	0	1	1	1	0	0	0	1	0	1	1	1	2	0
17 Cebupithecia	0	?	?	2	0	?	1	0	?	?	1	1	1	?	0	0	0	1	0	1	1	?	1	1
18 Ateles	0	0	0	3	0	1	0	0	1	0	0	0	0	1	0	0	1	1	0	0	1	0	2	0
19 Homo	0	1	0	3	0	0 & 1	0	0	?	?	0	1	0	0	0	0	1	1	0	0 & 1	1	0	3	0
20 Hylobates	0	0	0	3	0	1	0	0	?	0	0	1	0	0	0	0	1	1	0	0 & 1	1	0	3	0
21 Cercopithecoids	0	0	0	3	0	1	1	0	?	1	0	1	0	0	0	0	1	1	0	0 & 1	1	2	3	1
22 Aegyptopithecus	1	0	0	3	0	1	0	0	?	?	0	1	1	1	0	0 & 1	1	0	0	1	1	0 & 1	3	1
23 Apidium	1	0	0	3	0	?	?	1	?	?	0	1	0	1	0	0 & 1	1	1	1	2	1	2	3	1
24 Parapithecus	1	0	0	3	0	?	?	?	?	?	0	0	?	?	?	0	1	?	?	?	1	2	3	1