INFERRING LARGE PHYLOGENIES: THE BIG TREE PROBLEM

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RH: PRIMATE SUPERTREE

A Dated MRP Supertree for the Order Primates

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ABSTRACT

Supertrees are phylogenetic trees whose topologies are derived from a set of partially overlapping, smaller trees. Here we present a supertree for the order Primates, constructed by analyzing source trees we binary-coded using Matrix Representation using Parsimony analysis (MRP). The source trees are derived from previously published studies, and are based on a variety of data types, reconstructed using a variety of methods. In terms of the number of species included in the analysis, the composite estimate presented here is the largest phylogeny of the Primates available to date; it is well-resolved and generally fits with our understanding of the systematics of this order. Areas with few or incongruent data are identified using strength-of-grouping and rQS values. In addition to this updated topology, we present divergence dates estimated using a new method that utilizes overlapping fossil-calibrated clock-like DNA sequence data. For the nodes for which no molecular estimates are available we provide expected ages under a pure birth model. We analyze the divergence date estimates and find that, overall, the Order Primates has diversified at a constant rate of cladogenesis, though looked at in more detail we note, in agreement with earlier studies, a significantly elevated rate in the cercopithecines.

Keywords: MRP; Maximum Parsimony; Phylogeny; Divergence Dates; Primates; Supertrees.

The phylogeny of the order Primates, the order to which we belong, encompasses some of the most intensively studied problems in systematics. Many novel techniques (e.g. modeling of substitution rate heterogeneity) have first been applied to parts of the primate tree, for example to the 'hominid trichotomy', that is, the topology of the set of *Homo*, *Pan* and *Gorilla* (Adachi and Hasegawa, 1995; Arnason et al., 1998; Penny et al., 1995; Rogers, 1993; Suzuki et al., 1994). It is therefore perhaps surprising that only one species-level phylogeny of the whole order has been available, in a study that was published over a decade ago (Purvis, 1995, see also Purvis and Webster, 1999). The scope and methodological sophistication of phylogenetics has grown in the years since, and a new estimate that incorporates the subsequent accumulation of phylogenetic knowledge is timely. Here we present such a study, in the form of a supertree analysis of previously published phylogenies of the order Primates. In addition, we present divergence dates estimated from calibrated, clock-like DNA sequences, and expected node ages under a pure birth model for those nodes for which no molecular data are available.

Supertrees

A sobering fact in phylogenetics is that few estimates of large trees, regardless of methodology, accurately represents the branching order or divergence times of the part of the true tree of life it intends to approximate (though see Rokas et al., 2003). The reasons for this are many, ranging from the fact that sometimes the pattern of evolution of the underlying comparative data is different from that of the divergence of the taxa under study (e.g., the 'gene tree' versus 'species tree' problem sensu Maddison, 1997) to methodological issues such as inconsistency in some of the most commonly used

methods of inference (Gaut and Lewis, 1995; Huelsenbeck, 1995; Huelsenbeck and Lander, 2003).

Supertrees are phylogenetic trees whose topologies are derived from a set of usually smaller, overlapping trees - here referred to as 'source trees'. The accuracy of the estimates obtained using supertree methods is therefore sensitive to all the methodological issues associated with the source trees, even if the supertree method itself were without methodological problems of its own. Supertree methods have received criticism on this potential 'garbage in, garbage out' problem (Gatesy et al., 2002; Springer and De Jong, 2001). Careful selection of source trees and of the method of analysis should however address most of the issues raised (Bininda-Emonds et al., 2002; Bininda-Emonds et al., 2003). We therefore contend that supertrees can be usefully applied to a number of different issues in phylogenetics and evolutionary biology that require large phylogenies, at least while other methods of combined data analysis (such as the 'supermatrix' approach) are in their infancy or are unable to achieve the same level of taxon coverage with the presently available data. For example, a supertree based on reasonably congruent source trees that sufficiently cover the groups under study can be used for comparative studies (e.g. in Nunn, 1999; Thierry et al., 2000) or macro-evolutionary studies (e.g. in Gittleman and Purvis, 1998; Purvis et al., 1995) of a broader taxonomic scope than any single presently available phylogeny. Also, a supertree can be interpreted as a summary of what is currently known about the phylogeny of a given group – and so might steer research priorities, or might serve as a 'snapshot' of the data currently contained in a phylogenetic database (Page, 2004). The supertree that we present here is intended to serve these purposes: to be a useful tool for primatologists and

evolutionary biologists while indicating which parts of the primate tree need further investigation.

Matrix Representation using Parsimony analysis

Different methods for the amalgamation of source trees are available; these can be classified into those that i) directly combine source tree topologies, such as the MinCut algorithm (Page, 2002; Semple and Steel, 2000); or ii) two-step methods that combine source trees through some form of matrix representation (Baum, 1992; Ragan, 1992; Ronquist et al., 2004) of their shape, where the set of representations is analyzed under an optimality criterion and conventional search strategies, or, as more recently proposed, using Metropolis-Hastings coupled Monte Carlo Markov chains (Ronquist et al., 2004).

The most commonly used supertree method, Matrix Representation using Parsimony analysis, or MRP (Baum, 1992; Ragan, 1992), follows a two-step approach. MRP is in essence a method by which tree shapes can be coded into binary matrices that can be interpreted as 'pseudo-character state matrices' and thus can be analyzed using the methods available for such data – in practice usually heuristic searching under Maximum Parsimony (e.g. in Bininda-Emonds et al., 1999; Jones et al., 2002; Liu et al., 2001; Purvis, 1995).

MRP, and by extension the supertrees built using this method, have met with considerable skepticism (Gatesy et al., 2002; Gatesy and Springer, 2004; Springer and De Jong, 2001), and defense (Bininda-Emonds et al., 2004; Bininda-Emonds et al., 2003). Our rationale for choosing MRP is as follows:

i) Combined MRP matrices can be analyzed using fairly well characterized methods such as heuristic searching under Maximum Parsimony; that is,

the properties of the inferential techniques employed in supertree reconstruction using MRP are well characterized;

ii) The methods available for the analysis of MRP matrices have been implemented in commonly used software packages for phylogenetic inference such as PAUP*4b10 (Swofford, 2003) or MrBayes (Huelsenbeck and Ronquist, 2003);

iii) Additional methods have been developed to calculate support on MRP supertrees, such as the rQS method (Bininda-Emonds et al., 2005), employed here.

Divergence date estimates on supertrees

For some robust types of comparative analyses, setting all branch lengths to the same arbitrary non-zero value (or no value at all) serves as sufficient correction for shared ancestry (Maddison, 1990). However, for some other types of analyses (such as those of speciation and extinction rates) trees must be ultrametric and the relative node depths must be proportional to the ages of the clades they subtend. As the purpose of this study is to present an estimate that is of use for these kinds of studies we present divergence dates estimated using a novel method based on overlapping clock-like genes (Vos and Mooers, 2004), combined with estimates of clade growth that are discussed below.

METHODS

R.V. collected 200 source trees from 130 references dating from 1993 onwards covering 219 species. Source trees were located through Web of Science database

searches using “phylogen* AND primates” or “taxonom* AND primates” as search terms. Subsequently, R.V. scanned through the references of the articles as well as through all issues of the *American Journal of Primatology*, the *American Journal of Physical Anthropology*, *Evolutionary Anthropology*, *Folia Primatologia*, the *International Journal of Primatology*, the *Journal of Human Evolution*, the *Journal of Molecular Evolution*, *Molecular Biology and Evolution*, *Molecular Phylogenetics and Evolution*, *Primates* and *Systematic Biology*.

A criticism that has been leveled at supertrees is the potential for data duplication: multiple, published trees might be based on the same data set, thus biasing the supertree topology toward that of overrepresented source topologies (Gatesy et al., 2002; Springer and De Jong, 2001). A tree selection protocol should therefore be employed. We followed the recommendations made by Bininda-Emonds *et al*. (Bininda-Emonds et al., 2004), in summary:

- Within publications, source trees may be accepted that:
  - Are based on independent data sources; or, if multiple trees are presented where one is based on a superset of the other (e.g. all changes versus transversions only) the tree based on more inclusive data is used. As a second best, the tree explicitly preferred by the authors is used (usually this is the case where different optimality criteria are used, such as maximum parsimony and maximum likelihood, and the authors prefer the ‘more sophisticated’ maximum likelihood), or, as a last resort, a consensus over trees based on non-independent data sources.

- Analyze non-overlapping taxon sets. If there is overlap, the most comprehensive tree is used.

- Between publications, source trees may be accepted that:
  - In addition to the conditions for within-publication source trees, are the result of the more recent analysis. Research groups sometimes publish a series of articles based on a growing set of sequences. In cases like this, the most recent source is preferred.

In addition to this tree selection process, candidate trees must be modified in several ways to prepare them for the supertree analysis. In many phylogenetic analyses, multiple outgroups are used, which are constrained to be monophyletic with respect to the ingroup. Since this constraint is somewhat subjectively imposed, we pruned all outgroup taxa from the source trees. Lastly, we collapsed all clades consisting of below species-level OTUs (e.g. subspecies, haplotypes). In many cases, this is straightforward: in a source tree (((A1,A2),B),C) where A1 and A2 are two below species-level instances of taxon A, the resulting tree is ((A,B),C). Where haplotypes or subspecies do not form monophyletic groups, the source tree is collapsed in a conservative, agnostic manner: if the source tree's topology is (((A1,B),C),A2), the result is the polytomy (A,B,C). Synonymous taxa were identified using the Primates section of the *Mammal Species of the World* taxonomy (Groves, 1993); the names we use here follow the conventions therein. The choice for this taxonomy, and its online database version (http://www.nmnh.si.edu/msw/), which we used for disambiguation, was made in order to retain compatibility with the consortium producing a supertree of all Mammals, to which we have contributed our data.

All source trees we collected were taken from articles published after 1993 to avoid overlap with an additional 174 source trees (counting the Purvis's compartmentalization of the Order) included in this study from a previously published primate supertree (Purvis, 1995). We converted this pooled collection of 374 source trees into MRP (Baum, 1992; Ragan, 1992) matrices using RadCon (Thorley and Page, 2000). No formal attempt was made to correct for non-independence between the two sets of source trees (e.g due to recycling of data: some of the trees in the post-1993 dataset used similar data from the studies published pre 1993). The data sets, commented to indicate where and why changes (of the types described above, i.e. collapsing of haplotype trees and taxonomic disambiguation) were made, are available from this journal's website.

[overlap between our trees and Purvis' trees]

Phylogenetic inference

To infer the supertree topology we ran Parsimony Ratchet (Nixon, 1999) searches on the pooled data set. This approach is different from that taken by Purvis (1995), who analyzed the 'major' clades separately due to computing power constraints. The 'traditional' approach to heuristic searching consists of performing one or more independent searches, starting from a topology obtained through the stepwise addition of taxa in a randomized order. Rather than perform independent heuristic searches, the Parsimony Ratchet performs a single long search comprised of a series of short bouts of optimization, alternating with searches on a perturbed tree landscape to escape from local optima (Nixon, 1999). Using this strategy, some of the true phylogenetic signal is retained during reweighted hill-climbing cycles, while greatly reducing the time spent in stepwise addition. Ratcheting techniques have been used with success in supertree

192 construction (Jones et al., 2002), and phylogenetic inference using morphological data
193 sets (Faivovich, 2002; Fontal-Cazalla et al., 2002; Quicke et al., 2001), molecular data
194 sets (Malia et al., 2002; Simmons et al., 2002) and combined molecular and
195 morphological data sets (Giribet et al., 2002).
196 We used the Parsimony Ratchet strategy as implemented in PAUPRat (Sikes and
197 Lewis, 2001). PAUPRat constructs a script file that is executed in PAUP* (Swofford,
198 2003) in combination with the MRP data set in NEXUS (Maddison et al., 1997) format.
199 The weighting scheme used in this study is the default 'uniform' setting of PAUPRat
200 (Sikes and Lewis, 2001). Under this scheme, the initial weight of all characters is set to 1
201 (other options are 'additive' and 'multiply', both of which preserve *a priori* defined
202 weighting schemes though they differ in the way the predefined weights under these
203 schemes are altered). A user-defined percentage of characters is sampled with
204 replacement from the data and the weight of these characters is incremented by one.
205 Because characters are sampled with replacement, some characters may have their
206 weights adjusted multiple times.
207 In our study, experimentation with different reweighting schemes showed no
208 improvement in the length of the shortest retrieved tree anywhere above 15% upweighted
209 characters, which is the percentage used to obtain the results we report here.
210 Each search consisted of 200 iterations. In a previous supertree study (Salamin et
211 al., 2002) it was shown that treating MRP character states as irreversible could increase
212 the resolution of the resulting phylogeny, and irreversible MRP appears to be as accurate
213 as standard MRP (Bininda-Emonds and Sanderson, 2001). We therefore ran the searches
214 using this modification of maximum parsimony. We constructed majority rule and strict

consensus trees over the resulting set of unique optimal trees. The majority rule consensus tree and MRP matrix have been submitted to TreeBASE under accession number "SN2421".

Inference of Bremer values and rQS values.

A Bremer value (Bremer, 1994) on a clade is the difference in the number of steps between the most parsimonious tree and the shortest tree that does not include that clade and can be interpreted as the net support for the most parsimonious grouping of a set of taxa compared to the second most parsimonious grouping. In a supertree context, Bremer values are difficult to interpret because of the non-independence of the MRP pseudocharacters. Nevertheless, we calculated Bremer values using a script we wrote that traverses through the supertree's topology, and for each node writes the Parsimony Ratchet (Nixon, 1999) commands modified to include an 'inverse constraint' requirement for the taxa the focal node subtends (an 'inverse constraint' on a heuristic search is a rule to reject all proposed topologies that include a predefined taxon bipartition or constraint tree shape). The script is available in the Bio::Phylo package at http://search.cpan.org/~rvosa/. As an alternative, perhaps more suitable measure of source tree support for supertree topology we also calculated the reduced qualitative support (rQS) index (Bininda-Emonds et al., 2005) using a script kindly provided by Olaf Bininda-Emonds.

Divergence date estimation

Although several approaches now exist to combine branch lengths on source trees in a supertree analysis (Bryant et al., 2004; Semple et al., 2004), most of our source trees have

no time-based branch lengths, and our aim in this study is to present a supertree based on previously published sources. Hence, although we could have pooled additional, unpublished, molecular phylogenies into the supertree analysis, we chose instead to estimate divergence dates in a separate procedure. The protocol we followed is discussed in more detail in Vos & Mooers (2004). In short, we collected sequence data from the GenBank flat file release 132.0. We parsed the sequence meta data for the Primates to collect suitable candidate genes, focusing on loci with high taxon coverage for the Order, which we aligned using ClustalW (Thompson et al., 1994) and subsequently by hand using Se-Al v2.0a11 (http://evolve.zoo.ox.ac.uk/software.html?id=seal).

For each of the alignments we selected the appropriate substitution model - constrained to the supertree's topology - using MODELTEST (Posada and Crandall, 1998). We then tested, using a likelihood ratio test with a liberal alpha-level of 0.001 whether the gene's evolution on the primate supertree was consistent with a molecular clock. The liberal alpha dealt with possible Type II error due to multiple genes and the known illiberality of likelihood-based molecular clock tests (Norman and Ashley, 2000; Yang et al., 1995; Zhang, 1999).

For candidate loci that did not conform to the molecular clock we tested whether removing some deviating taxa from the alignment would create a subset that did conform to a clock. We did this by iteratively pruning the tips that most deviate from the average root-to-tip path length, performing the likelihood ratio test after each iteration (though retaining the original model of evolution; this may offer a slight bias, if lineages evolving at different rates also evolve under different molecular processes). A script that automates this procedure is available from the authors. This yielded, in total, 55 datasets containing

on average 17 sequences (median = 12, range 4-59) after pruning on average three to four sequences (median = 0, range 0-63) (see Table 2). For each of these loci we estimated the branch lengths under the appropriate substitution model. An alternative approach that disregards the molecular clock entirely would be to obtain ultrametric trees by non-parametric rate smoothing (Sanderson, 1997) or penalized likelihood (Sanderson, 2002) – however, NPRS seems to produce biased estimates, with nodes concentrated nearer the root (Ruber and Zardoya, 2005): penalized likelihood could have been used on a locus-by-locus approach, but we would still have had to combine the resulting subtrees.

In order to combine the dates from these 55 ultrametricized trees, we did the following:

1. Nine nodes were chosen that were both present in a large number of the subtrees and that could be dated from the literature. These nodes were: i) calibrated on the split between the apes and the Old World monkeys; ii) on the split between *Homo* and *Pan*; iii) on the split between *Homo* and *Pan*, and *Gorilla*; iv) the basal split of the great apes; v) the split between the great apes and the gibbons; vi) the split between the Old World monkeys apes, and the New World monkeys; vii) the split between the lemurs and the lorisiforms; viii) the split between the colobines and the cercopithecines; ix) and the root. We dated each of these nodes using several (partially overlapping but widely-cited) estimates from the recent literature (Adachi and Hasegawa, 1995; Adachi and Hasegawa, 1996; Arnason et al., 2000; Arnason et al., 1998; Arnason et al., 1996; Arnason et al., 1996; Easteal and Herbert, 1997; Gingerich and Uhen, 1994; Goodman et al., 1998; Kumar and Hedges, 1998; Nei and Glazko, 2002; Porter et al., 1997; Purvis, 1995; Stauffer et

al., 2001; Yoder, 1997). Where multiple estimates for the age of a particular split (node) were available from the literature, the median was used (see Table 2).

2. Each of the 55 ultrametric trees was then scaled using these anchor points: some trees will have only a single anchor, while others may have several – in the latter case, separate trees were constructed, one for each anchor. This gives us a large set (252) of dated trees.
3. We constructed subsets of trees, grouped according to the anchor used. Within each, the anchors were fixed, and the other nodes adjusted accordingly: for any node with more than one estimate (i.e. found in more than one tree in the subset), we took the median, an approach also taken in earlier studies that combine different divergence date estimates for the same node (e.g. in Purvis, 1995).
4. Finally, because the node ages were well-behaved, we took the mean (and Standard Error) of the age of each node across the nine subsets corresponding to the nine different anchors. This entire procedure is designed to weight the dates from the literature equally.

However , as this approach combines estimates from different loci (each with their own rates and models of evolution) there is no obvious way in which the robustness of the composite dates can be quantified.

For a large number of clades (corresponding to 116 out of 210 or 55% of the nodes in the final tree) no molecular estimates were available. The most common method for inferring such unknown ages is to assume a model of diversification (Purvis, 1995, who applied this method to 70 of 160 or 44% of the nodes). We approximated the expected age of the nodes in these clades by randomly drawing, with replacement, 10^6

labeled histories (that is, phylogenies with a chronological ordering of internal nodes). For each of these histories we considered the set of expected time intervals between speciation events ($1/n$ where n is the number of accumulated lineages), and thus node ages, if speciation had proceeded under a pure birth model since the age of the most recent common ancestor for which a molecular estimate was available (this method now has an analytical solution, Gernhard and Steel, personal communication; Gernhard, 2006). As an aside, this approach could be modified to generate more sophisticated waiting times expectations, for example considering extinction. We subsequently averaged over the set of histories to arrive at the approximations presented here.

We performed the calculations using a module we wrote for the *Mesquite* program (Maddison and Maddison, 2001) that is available from the authors on request. This method avoids an unrecognized property of a simpler one used for previous supertrees (Purvis et al., 1995; and Bininda-Emonds et al., 1999), where clade age was made proportional to the natural logarithm of clade size relative to that of an ancestral, dated clade: even on a fully pectinate tree, the simpler method, applied iteratively, produces node ages that actually model a slow-down in diversification rate (i.e. progressively longer waiting times) whereas waiting times are understood to shorten as cladogenesis proceeds under constant speciation, and even more so if extinction is taken into consideration. The method used here incorporates a constant diversification rate that is identical for all tree shapes (see Fig. 1).

RESULTS AND DISCUSSION

The MRP data set we analyzed consisted of 218 taxa (excluding the hypothetical outgroup) and 2368 binary pseudo-characters. For all reweighting fractions of at least

10% the shortest trees found had a length of 3214. 200 ratchet iterations (15% reweighted) yielded 187 distinct most parsimonious trees. However, constructing a majority rule consensus tree yields a result with very little conflict: on average, every node in the majority rule consensus tree (which we present here) is present in 96.55% of the 187 most parsimonious trees. The supertree is generally well resolved with a resolution (expressed as the number of internal branches the tree contains divided by the number of maximum possible (n-2 for binary trees, Colless, 1980) of 96.77%. (The corresponding resolution of the strict consensus tree is 85.32%). The deepest splits in the topology are shown in Figure 2, and the triangular tips it subtends are expanded in the subsequent Figures 3-13. The numbers on the nodes correspond with those in Table 3, which shows the estimated and interpolated divergence dates and the support values.

Resolution and support

In the context of supertrees, Bremer support values may be interpreted as indicative of the net number of source trees that unequivocally support a node. Low values may indicate either a low total number of source trees that include at least two taxa on either side of the focal node in the supertree or incongruence among studies. However, the groupings of taxa, the nodes that are reconstructed in an MRP supertree, are not only determined by the groupings proposed by the source trees and their support but also by the relative support for neighboring nodes. The source trees may suggest a certain grouping unequivocally, yet the topology of the supertree may not include that grouping because of the stronger support for a surrounding topology that precludes it. Conversely, a grouping may be reconstructed in the supertree that has no support from source trees yet is necessitated by the surrounding reconstructed topology. This explains why MRP

supertrees sometimes include nodes that have no support from source trees or are even contradicted by them. In our study, ten nodes were introduced in the majority rule supertree for which no supporting source trees exist in our data set (see Table 3), and three such nodes appear in the strict supertree.

For most of the topology, the genera identified in the taxonomy (Groves, 1993) are reconstructed as monophyletic. The only exceptions are *Trachypithecus* (Fig. 5) and *Galago* (Fig. 13). Bremer support values for these clades are low, most notably for nodes 149-156 in Figure 5 (*Trachypithecus*) and Table 3 and nodes 201, 203, 205 and 206 in Figure 13 (*Galago*). The largest polytomy in the tree (node 148 in Fig. 5, a split of four taxa) indicates another weakly supported area of the Primate phylogeny. Other areas in the tree however are quite strongly supported: the 'Hominid trichotomy' (nodes 88, 89 and 90) as it is shown in Figure 6 has Bremer support values of 79 for the root of the subtree, and 49 and 47 for the subsequent splits, the highest values in the tree. Average support over the whole tree was 5.77, with a standard deviation of 2.06.

Comparison with the Purvis Supertreee

Both the present study and that undertaken by Purvis (1995) set out to infer a composite tree using previously published phylogenetic information. Hence, although the intention is to cover as many species as possible, not all known Primate species are included in either of these studies. The disparity in taxon coverage between the two (Purvis 1995: 203 taxa, present study: 218 taxa) is caused by the fact that many phylogenies have been published in the meantime, some of which included data on species for which Purvis had no data available. Conversely, Purvis distinguished some

taxa that are considered to belong to the same species, or are subspecies, in the taxonomy we followed (Wilson & Reeder, 1993).

Methodologically, the two studies differ in that the Purvis study analyzed subsets of the primate supertree (putative clades) which he then attached to a backbone, while the advances in computer power, as well as the introduction of the Parsimony Ratchet algorithm (Nixon, 1999), allowed us to analyze the complete dataset at once, freeing us from having to make *a priori* assumptions about monophyletic subdivisions in the primate supertree.

Another difference lies in the estimation of divergence dates: Purvis incorporated disparate data on divergence timing such as rescaled source tree topologies and karyological clocks; the present study uses molecular data directly. Where no data on divergence timing were available, Purvis used a different method to interpolate dates (clade age was made proportional to the natural logarithm of clade size), while here we choose a technique that more closely approximates the clade growth curve that is expected under a pure birth model.

In order to compare the two studies, we first disambiguated classification conflicts using the Mammal Species of the World online database (http://nmnhgoph.si.edu/msw/, accessed 12/16/2003) and pruned the two strict consensus trees to the same set of 191 taxa.

We compared the two trees on a node-by-node basis, identifying the nodes that subtend the same set of terminal taxa as a match (the subtree topology may still differ), and the nodes in the present tree that subtend a set absent in the Purvis (1995) tree as a conflict (see Table 4). The most notable conflicts are nodes 76 and 42 in the New World

Monkeys, and node 194 in the strepsirrhines (see Table 3). The former two nodes indicate a rearrangement in the placement of *Callicebus* - Purvis (1995) places these as the sister group of *Aotus* (see Fig. 7, 8, 9). The latter conflict is caused by the placement of *Daubentonia madagascariensis,* which the present study places as basal to all Malagasy Strepsirrhines, while Purvis (1995) places it as basal to the Indridae. Nevertheless, the number of matching clades is 112 (out of 150 nodes in the Purvis (1995) tree), with the remaining conflicts confined to shallow nodes.

Finally, we asked whether there was a difference in the support of source trees for the different topologies. We calculated, for each source tree, its fit to the supertrees using c.i. (the compatibility index; Rodrigo, 1992). We would expect that pre-1993 trees should fit the Purvis tree better than the present tree, and that post-1993 trees should fit the present tree better. This is true: the mean c.i. of the pre-1993 source trees on the present supertree is 0.72, that of the post-1993 source trees is 0.85; conversely, the mean c.i. of the pre-1993 trees on the Purvis supertree is 0.74, and that of the post-1993 trees is 0.73. However, comparisons that also differentiate between molecular and non-molecular datasets did not offer decidedly better predictive value: the present supertree is not overly influenced by congruent molecular datasets. In no case were interactions between these three variables (e.g. age of study and whether the dataset was molecular or not) significant partial predictors of agreement (Wald chi-square tests, $p>0.05$).

Implications for systematics

In our tree, Cercopithecidae divides into the monophyletic traditional subfamilies Colobinae (i.e. the genera *Trachypithecus*, *Presbytis*, *Semnopithecus*, *Pygathrix*, *Nasalis*, *Colobus* and *Procolobus*) and Cercopithecinae (the genera *Macaca*, *Cercocebus*,

Mandrillus, *Papio*, *Theropithecus*, *Lophocebus*, *Cercopithecus*, *Chlorocebus*, *Erythrocebus*, *Miopithecus* and *Allenopithecus*). Within the family, all but the genus *Trachypithecus* are reconstructed as monophyletic clades.

The results that we present here with respect to the Great Apes (fig. 2, fig. 6) conform to the overwhelming consensus of recent years; that is, the 'hominid trichotomy' is rooted on *Gorilla*, and *Pongo* is the most basal of the great apes.

The New World monkeys, the platyrrhines (fig. 7, 8, 9 and 10), are a group whose deeper, intergeneric, relationships are still uncertain. In our results all genera are monophyletic, and can be grouped into three clades: Cebidae (*Cebus*, *Saimiri*, *Aotus* and the callitrichines); Atelidae (the atelines) and Pitheciidae (the pithecines).

The phylogenetic position of tarsiers (*Tarsius*, fig. 2, fig. 11) has long been controversial (Martin, 1990; Shoshani et al., 1996). Some authors have grouped tarsiers with the strepsirhines in the suborder Prosimii (Fleagle, 1988; Schwartz, 1986; Simpson, 1945), or as basal to the entire primate tree (Gingerich, 1973; Gingerich, 1975). Recently, the prevailing view is to group the tarsiers with the anthropoids (Groves, 1993; Nowak, 1991), and most molecular studies support this (but see (Jaworski, 1995). As a result of these new studies, the tree presented here includes this grouping, with a relatively strong Bremer support of 9 (Table 3).

All the Malagasy strepsirhines form a strongly supported (Table 3, fig. 2, fig. 12) monophyletic group, congruent with the hypothesis of a single colonization of the island (e.g. Yoder et al., 1996). Within the Malagasy strepsirhines the tree is well resolved, and all genera (*sensu* Groves, 1993) are monophyletic. In our results, *Lemur catta* is

reconstructed as basal to the genus *Hapalemur,* and *Daubentonia* is basal to the whole clade.

Recent findings suggest that the species diversity is perhaps far greater among the mouse lemurs *Microcebus* than previously thought (Rasoloarison et al., 2000; Yoder et al., 2000). As well, the subspecies diversity among *Eulemur* is large and complex (Djelati et al., 1997; Pastorini et al., 2000; Tattersall and Sussman, 1998; Wyner et al., 1999). In this study we have taken the conservative approach of only including those taxa recognized by Groves (1993), noting however that there may be more Lemurs than are presented here.

The other members of the strepsirhines, the lorisoids (fig. 2, fig. 13) are members of weakly supported groupings (Table 3). For example, the genus *Galago* forms a polyphyletic group (fig. 13). More data need to be brought to bear on the phylogenetic affinities within this group.

Rates of cladogenesis

The molecular estimates of divergence time were calculated under the molecular clock. Several alternative approaches to derive divergence dates from DNA sequences are possible, such as a two-step approach where branch lengths obtained without the assumption of rate constancy are 'linearized' using one of several available approaches such as penalized likelihood, (Sanderson, 2002) or non-parametric rate smoothing, (Sanderson, 1997). However, these techniques yield transformed estimates that, at best (for PL), are similar to estimates using a molecular clock, and at worst (for NPRS) are biased towards a clustering of nodes near the root (Ruber and Zardoya, 2005). Here, we report estimates based on data that are consistent with a molecular clock, combined with

expected dates under a pure-birth model. The age of many of the nodes near the tips of the supertree are based solely on pure-birth modeling, as homologous clock-like sequences for sister species, given the sparse sampling in the database, are rarer in GenBank than those for more distantly related species that speak to deeper nodes on the supertree. However, the estimates based on molecular data are not concentrated in any one clade, and are found distributed over all depths in the tree (see Fig. 14).

The slope of the lineage-through-time plot for the combined molecular and interpolated divergence dates (the gray curve in Fig. 15) suggests constant growth ($p<0.05$ under a one-tailed test of the gamma statistic; Pybus and Harvey, 2000, implemented in Paradis *et al.*, 2003). Many of the recent nodes are inferred using this same model, which might favor the selection of the constant growth model. By pruning those nodes (terminal or internal) for which no sequence data (and so no molecular estimate of divergence time) is available we obtain a subtree of molecular estimates. If we confine ourselves to this subset of lineages the same clade growth model is selected ($p<0.05$), though consequently with a lower estimated net growth rate – see the black curve in Fig 15 – hence the constant growth model is in any case not favored due to the pure birth interpolation.

Rutger Vos 12.8.06 1:21
Comment: Gamma full supertree: 2.476600, gamma pruned supertree: 3.51723. N full: 218, N pruned: 108. I calculated the p-values using the ape gammaStat method, which, AFAIK, also works on incomplete phylogenies (and maybe even does the same thing you were planning to do?)

A look in more detail at the major clades broadly confirms earlier analyses (Chan and Moore, 2002; Moore et al., 2004; Paradis, 1998; Purvis et al., 1995) suggesting a significantly elevated rate of cladogenesis in Cercopithecinae (Table 5) compared to all others (when fit by maximum likelihood using the method of Nee et al., 1994). Whether this increased rate is due to key innovations, ecological opportunity, or some combination of factors remains an open question.

CONCLUSIONS

The supertree presented here is the largest supertree estimate of phylogeny for the order Primates to date (though see Purvis et al., 1999, where a composite tree of 233 species is presented). The findings presented here agree to a large extent with earlier findings – as well they should, considering that this study essentially summarizes prior research. In that context the present study also exposes a dearth of phylogenetic and molecular data for some groups. Notable among these are Galaginae (Fig 13), for which some paraphyletic genera were reconstructed. Another problematic area of the Primate supertree is that of the deep nodes in the New World monkeys (e.g. Fig. 7, 8), where contradictory source trees contribute to the phylogenetic instability. Indeed, this ability to highlight areas that need more work may be one of the main uses of the supertree method to systematists. Supertree results can also be viewed in this light as indicators of where molecular data collection should be directed.

Our study also illustrates an approach to combining divergence dates derived from disparate molecular data under the assumption of rate constancy. The assumption of a molecular clock is a contentious issue in phylogenetics. It is possible that rate smoothing approaches (Sanderson, 1997; Sanderson, 2002) may serve as an alternative means of deriving composite molecular estimates of divergence dates, and we call for more work here. Any approach must deal with the robustness and the quantitative measure of robustness of composite estimates (see, eg., Magallon and Sanderson, 2001), and the ability to include partially overlapping data.

To interpolate divergence dates for splits for which no molecular estimates were available we employed a simulation technique whereby large sets of labeled histories and

their expected waiting times under a pure birth model were sampled. As we know very little about the actual time course of macroevolution, we have little evidence for this being a reasonable general model for waiting times (e.g. compared with adaptive radiation or saturated community models; see Mooers et al., in press). More work is desperately needed here.

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TABLE 1. Recently published estimates of dates for major primate splits. 1. Apes-Old World monkeys; 2. *Homo-Pan*; 3. (*Homo*, *Pan*)-*Gorilla*; 4. ((*Homo*,*Pan*),*Gorilla*)-*Pongo*; 5. Great apes-Gibbons; 6. Old World Monkeys-New World Monkeys; 7. Root; 8. Lemurs-Lorisiforms; 9. Colobinae-Cercopithecinae.
All ages are in millions of years ago. Adapted from Vos & Mooers (2004).

	1	2	3	4	5	6	7	8	9
Nei and Glazko (2002)	23	6	7			33			
Stauffer *et al*. (2001)	23	5.4	6.4	11	15				
Gingerich and Uhen (1994)							63		
Yoder (1997)								54	
Arnason *et al*. (1998)	50					60	80		30
Porter *et al*. (1997)	25								
Goodman *et al*. (1998)						38			
Adachi and Hasegawa (1995)		4		16					
Easteal and Herbert (1997)				8.5					
Kumar and Hedges (1998)	23.3	5.5	6.7	8.2	14.6	47.6			
Arnason *et al*. (1996b)		6.1							
Adachi and Hasegawa (1996)		4.3							
Arnason *et al*. (2000)		13	16	30	35	70			
Arnason *et al*. (1996a)		10.4	14.2	19.2	32.4				
Purvis (1995)	27.5	7.0	8.3	14.5	18.2	40.5	57.5	45.1	14.4
Median of published studies	24.1	6	7.6	14.5	18.2	44.0	63	49.5	22.2

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TABLE 2. Genes used for dating the tree. See text for details.

Locus	Number of sequences	Pruned
alpha13galacto	18	0
ATP7A	7	0

BRCA1	7	0
calmodulin	6	0
CCR5	59	3
CD4	17	0
COII	44	5
CXCR4	38	3
cytba	17	63
cytbb	8	47
DRD4	14	0
fut1	26	6
G6PD	22	0
gamma1globin	13	0
IL10	9	0
IL16	7	0
IL2	10	1
IL3	4	0
IL4	8	0
interferongamma	13	0
IRBP.intron1	23	12
IRBP.partial	23	0
LZM	16	1
ND1	12	0
ND2	12	1
ND3	34	0
ND4b	32	1
ND4L	14	26
ND5	26	1
ND6	12	0
NRAMP1	14	0
PLCB4	7	0
PNOC	7	0
SRY	56	1
trnaala	10	0
trnaarg	35	0
trnaasn	10	0
trnaasp	10	0
trnacys	10	0
trnagln	9	0
trnaglu	10	0
trnagly	29	0
trnaile	10	0
trnalys	10	0
trnaphe	6	0
trnapro	11	0
trnathr	12	0
trnatrp	10	0
trnatyr	10	0
trnaval	26	0
TSPY	38	0
vwf	17	0
ZFXa	9	0
ZFXb	13	0

ZFY 10 3

TABLE 3. Divergence dates and support for nodes. Ages labeled "a" are interpolated from a pure birth model, and those labeled "b" are estimated from molecular data.

Node	Age	Stderr	Clade size	Bremer support	Mean rQS index	Number of sources with hard matches	Number of sources with hard mismatches	Number of sources with equivocal trees
1	3.314008a	n/a	2	4	0.013	5	0	369
2	3.272367a	n/a	2	6	0.008	6	3	365
3	7.881723a	n/a	4	1	0.003	6	5	363
4	1.377923a	n/a	2	1	0.003	1	0	373
5	3.033345a	n/a	3	1	0.016	7	1	366
6	5.071805a	n/a	4	0	0.013	7	2	365
7	1.960615a	n/a	2	0	0	2	2	370
8	4.383235a	n/a	3	0	0	3	3	368
9	7.676796a	n/a	7	0	-0.019	1	8	365
10	9.818911a	n/a	8	0	-0.021	1	9	364
11	12.68218a	1.235	12	5	0.051	19	0	355
12	1.43E-14b	0.000	2	1	0.003	1	0	373
13	7.682266a	n/a	3	7	0.013	5	0	369
14	15.65228a	3.930	15	7	-0.011	23	27	324
15	1.43E-14b	0.000	2	1	0	1	1	372
16	1.43E-14b	0.000	2	1	0	1	1	372
17	0.511943b	0.338	4	2	0.027	11	1	362
18	3.429579a	n/a	2	1	0.003	1	0	373
19	11.20397b	1.729	6	2	0.029	12	1	361
20	2.071066b	0.366	2	9	0.019	7	0	367
21	3.713118b	0.657	3	3	0.045	19	2	353
22	11.3592a	1.758	9	35	0.112	44	2	328
23	18.37584b	2.947	10	3	0.045	33	16	325
24	18.99167a	5.096	25	14	0.16	62	2	310
25	1.231955a	n/a	2	0	0	0	0	374
26	2.62541a	0.070	3	0	0	1	1	372
27	4.155122a	n/a	4	0	0.003	1	0	373
28	6.283654a	n/a	5	0	0.003	1	0	373
29	8.675736a	1.124	6	0	0.019	8	1	365
30	4.522607a	n/a	2	1	0.003	1	0	373
31	11.75498a	1.124	8	0	0.016	7	1	366
32	15.78918a	0.400	9	8	0.029	11	0	363
33	22.03249b	3.357	34	9	0.07	51	25	298
34	1.758327a	n/a	2	0	0	1	1	372
35	3.946727a	n/a	3	0	0.013	9	4	361
36	6.829616a	n/a	4	0	0.013	9	4	361
37	8.429973b	3.031	5	6	0.07	26	0	348
38	0.138835b	0.138	2	6	0.013	5	0	369
39	3.9671a	n/a	2	3	0.008	4	1	369
40	7.267568b	n/a	4	10	0.04	15	0	359
41	23.1875b	3.104	9	25	0.086	43	11	320
42	25.68486a	5.942	43	11	0.187	91	21	262
43	2.913174a	n/a	2	2	0.003	1	0	373
44	9.031937b	0.756	3	2	0.045	24	7	343
45	1.209202b	0.317	2	5	0.005	3	1	370
46	2.046641b	0.139	3	1	0.019	9	2	363

TABLE 3. Divergence dates and support for nodes. Ages labeled "a" are interpolated from a pure birth model, and those labeled "b" are estimated from molecular data.

47	2.890899a	n/a	2	2	0	1	1	372
48	4.700399b	0.319	6	5	0.043	16	0	358
49	11.29623b	1.060	9	11	0.102	40	2	332
50	1.611309a	n/a	2	0	0.029	11	0	363
51	3.417882a	n/a	3	0	0.029	11	0	363
52	5.710881a	n/a	4	0	0.029	11	0	363
53	6.920234b	1.338	5	0	0.037	14	0	360
54	12.73689a	0.267	6	4	0.043	16	0	358
55	20.68827b	2.723	15	27	0.12	46	1	327
56	2.327182a	n/a	2	2	0.005	2	0	372
57	2.357248a	n/a	2	1	0.003	1	0	373
58	5.330026a	n/a	4	2	0.008	3	0	371
59	1.991047a	n/a	2	2	0.003	1	0	373
60	4.727224a	n/a	3	0	0	1	1	372
61	7.993336a	n/a	7	0	0	1	1	372
62	10.29525a	n/a	8	0	0	1	1	372
63	3.080813a	n/a	3	0	0	1	1	372
64	7.327279a	n/a	4	0	0	1	1	372
65	13.3041a	n/a	12	1	0.003	2	1	371
66	16.47941a	n/a	13	6	0.051	19	0	355
67	1.764904a	n/a	2	0	0.003	1	0	373
68	3.780603a	n/a	3	0	0.003	1	0	373
69	6.551048a	n/a	4	1	0.005	2	0	372
70	10.24107a	n/a	5	2	0.011	4	0	370
71	3.709371a	n/a	2	3	0.005	2	0	372
72	3.679223a	n/a	2	1	0.003	1	0	373
73	8.124424b	n/a	4	8	0.056	22	1	351
74	11.8862b	n/a	9	20	0.094	35	0	339
75	20.96835a	3.493	22	10	0.061	33	10	331
76	25.31997a	6.891	37	12	0.048	39	21	314
77	30.15532b	4.441	80	45	0.369	138	0	236
78	0.792181b	0.085	2	1	0.003	2	1	371
79	1.804391a	n/a	3	8	0.016	6	0	368
80	4.016289a	0.941	4	4	-0.016	1	7	366
81	3.105567b	0.569	2	1	0	3	3	368
82	3.520138b	0.349	3	3	-0.003	3	4	367
83	0.888868a	n/a	2	2	-0.013	0	5	369
84	3.548143b	0.681	5	3	0.011	6	2	366
85	3.548143b	0.681	6	8	0.019	8	1	365
86	4.016289a	1.950	7	3	0.008	7	4	363
87	5.878584b	0.542	11	7	0.051	19	0	355
88	1.961341b	0.144	2	47	0.11	44	3	327
89	5.069091b	0.415	3	49	0.139	65	13	296
90	6.413876b	0.321	4	79	0.238	92	3	279
91	15.84305b	0.960	5	9	0.259	104	7	263
92	19.63822b	1.300	16	16	0.369	138	0	236
93	5.179923b	1.068	2	1	-0.008	5	8	361
94	0.96245a	1.106	2	6	0.013	5	0	369
95	0.760628a	n/a	2	1	0.003	1	0	373
96	0.490956a	1.106	2	0	0.008	3	0	371
97	1.040339a	n/a	3	1	0.011	4	0	370
98	1.704561a	n/a	5	2	0.011	5	1	368
99	2.332285a	0.716	7	1	0.008	4	1	369

TABLE 3. Divergence dates and support for nodes. Ages labeled "a" are interpolated from a pure birth model, and those labeled "b" are estimated from molecular data.

100	1.23689a	n/a	2	1	0.003	1	0	373
101	2.956938a	1.216	9	1	-0.011	1	5	368
102	0.769316a	n/a	2	3	0.008	3	0	371
103	0.789489a	n/a	2	4	0.011	4	0	370
104	1.24921b	0.296	4	5	0.008	3	0	371
105	2.564199a	0.790	5	1	-0.008	1	4	369
106	3.637249a	0.840	14	0	-0.003	2	3	369
107	4.22004a	n/a	15	2	-0.003	2	3	369
108	8.59E-05b	0.000	2	1	0.003	2	1	371
109	0.839612b	0.091	3	5	0.003	2	1	371
110	4.920964a	0.938	18	2	0.008	5	2	367
111	5.724032a	0.888	20	1	0.019	14	7	353
112	6.751236a	1.021	21	4	0.024	14	5	355
113	8.292042b	1.498	22	2	0.045	20	3	351
114	0.27622b	0.179	2	4	0.003	3	2	369
115	0.908084b	0.154	3	5	0.016	8	2	364
116	2.221603b	0.443	4	5	0.016	9	3	362
117	1.047513b	0.128	2	0	-0.003	1	2	371
118	0.70926a	0.324	2	0	-0.005	1	3	370
119	1.709499a	0.499	4	2	0	2	2	370
120	2.800668b	0.486	5	4	0.008	5	2	367
121	4.433933b	0.342	9	4	0.016	8	2	364
122	2.250415b	0.919	2	2	0	2	2	370
123	1.645312b	0.320	2	1	0.003	1	0	373
124	0.13504b	0.069	2	1	0.003	1	0	373
125	2.654026b	0.458	4	5	0.011	4	0	370
126	3.582641b	0.564	6	5	0.008	5	2	367
127	6.259739a	0.491	15	1	0.035	16	3	355
128	7.483745a	5.047	16	8	0.056	22	1	351
129	1.547503b	0.176	2	0	0.008	9	6	359
130	2.233375b	0.299	3	7	0.027	15	5	354
131	2.313178b	0.471	2	0	0	3	3	368
132	1.958261b	0.245	2	8	0.032	12	0	362
133	5.443154b	0.969	4	13	0.035	14	1	359
134	6.714332b	0.914	7	11	0.032	17	5	352
135	9.23115a	0.564	23	7	0.118	46	2	326
136	11.25912b	1.145	45	6	0.176	67	1	306
137	0.800086b	0.086	2	2	0.005	2	0	372
138	3.486339a	1.296	3	1	0.008	3	0	371
139	6.030347a	n/a	4	2	0.011	4	0	370
140	2.237741a	n/a	2	1	0.003	1	0	373
141	5.256468a	n/a	3	2	0.005	2	0	372
142	11.95993b	2.295	7	3	0.013	5	0	369
143	3.48278a	n/a	2	4	0.011	4	0	370
144	1.035514a	n/a	2	1	0.003	1	0	373
145	2.604488b	0.192	3	1	0.008	3	0	371
146	3.873409b	0.510	4	5	0.016	6	0	368
147	8.001457b	0.708	5	2	0.011	6	2	366
148	1.595359a	n/a	4	1	0.003	1	0	373
149	3.804516a	n/a	5	0	0.003	2	1	371
150	6.932486a	0.869	2	0	0	1	1	372
151	6.932486a	0.577	3	0	0	3	3	368
152	0.696042a	n/a	2	0	0.003	1	0	373

TABLE 3. Divergence dates and support for nodes. Ages labeled "a" are interpolated from a pure birth model, and those labeled "b" are estimated from molecular data.

153	0.801338b	0.124	4	0	0.003	1	0	373
154	2.900798b	0.243	5	0	0.019	7	0	367
155	3.735895a	n/a	6	0	0.021	8	0	366
156	5.132287a	0.000	7	0	0.021	8	0	366
157	6.932486a	0.803	15	1	0.024	10	1	363
158	8.877896a	0.922	20	2	0.037	15	1	358
159	8.896662b	2.159	22	6	0.056	21	0	353
160	13.60246b	1.113	29	10	0.072	27	0	347
161	18.33012b	1.085	74	27	0.243	92	1	281
162	32.41041b	1.507	90	18	0.529	200	2	172
163	51.23347b	3.875	170	11	0.794	297	0	77
164	16.07951b	1.456	2	1	0.013	5	0	369
165	15.98969a	n/a	2	1	0.003	1	0	373
166	38.21588a	n/a	4	3	0.016	6	0	368
167	62.609b	3.352	174	9	0.781	297	5	72
168	9.407427b	0.464	2	2	0.005	2	0	372
169	2.729257a	0.264	2	1	0.005	2	0	372
170	4.093885a	0.674	3	2	0.013	7	2	365
171	7.061984a	0.748	4	2	0.013	7	2	365
172	11.46329a	0.860	6	1	0.043	16	0	358
173	17.02967a	n/a	7	7	0.048	18	0	356
174	1.534145b	0.417	2	1	0.003	2	1	371
175	5.872105b	0.230	3	3	0.005	4	2	368
176	7.439765a	n/a	4	3	0.003	6	5	363
177	13.61071b	0.562	5	13	0.027	13	3	358
178	3.677795b	0.156	2	5	-0.019	5	12	357
179	3.754391b	0.185	3	3	-0.035	2	15	357
180	3.066328b	0.151	2	5	-0.016	4	10	360
181	6.369492a	0.156	5	25	0.048	18	0	356
182	11.89144b	1.176	6	3	-0.019	8	15	351
183	5.667141b	0.530	2	1	0	1	1	372
184	5.667141b	0.530	3	4	0.013	6	1	367
185	6.232139b	0.640	4	7	0.016	14	8	352
186	13.05581a	0.443	10	10	0.07	29	3	342
187	1.366414a	n/a	2	1	0.003	1	0	373
188	3.002269a	n/a	3	1	0.003	1	0	373
189	5.022715a	n/a	4	1	0.003	1	0	373
190	7.591075a	n/a	5	1	0.003	1	0	373
191	11.20404a	n/a	6	2	0.008	3	0	371
192	17.1708a	n/a	16	2	0.053	27	7	340
193	22.04095b	0.884	21	6	0.045	28	11	335
194	27.51953b	1.122	28	14	0.115	52	9	313
195	39.47811b	1.720	29	26	0.131	56	7	311
196	2.672337a	n/a	2	3	0.003	1	0	373
197	9.194181b	1.217	3	4	0.021	11	3	360
198	4.698149a	n/a	2	2	0	4	4	366
199	16.34787b	2.164	5	4	0.037	18	4	352
200	2.371579a	n/a	3	2	0.016	7	1	366
201	5.397494a	n/a	4	1	-0.019	0	7	367
202	4.240976b	0.561	2	3	0.008	5	2	367
203	8.517026b	1.127	6	1	0.005	6	4	364
204	3.574516a	n/a	2	2	-0.005	2	4	368
205	3.6487a	n/a	2	1	0	1	1	372

TABLE 3. Divergence dates and support for nodes. Ages labeled “a” are interpolated from a pure birth model, and those labeled “b” are estimated from molecular data.

206	8.517089b	1.127	4	1	-0.013	1	6	367
207	8.517089b	1.127	10	2	0.035	13	0	361
208	20.91996b	1.286	15	18	0.102	42	4	328
209	51.86696b	4.207	44	9	0.249	96	3	275
210	65.09789b	4.324	218	n/a	1	374	0	0

TABLE 4. Comparison between Primate supertree analysis results

	Purvis (1995)	Present study
Number of taxa	203	218
Resolution	79.21	85.32
Resolution of common taxon subset	78.95	86.84
Matching clades	112/150	112/165

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TABLE 5. Rates of cladogenesis for major clades, all nodes

clade	b-d (s.e.)
Apes	0.076 (0.061)
Atelidae	0.10 (0.058)
Cebidae	0.12 (0.013)
Cercopithecinae	0.29 (0.032)
Colobinae	0.19 (0.026)
Galaginae	0.11 (0.021)
Lemurinae	0.086 (0.012)
New world monkeys	0.12 (0.0098)
Old world monkeys	0.24 (0.020)
Pithecidae	0.12 (0.019)
Strepsirhini	0.076 (0.021)

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FIGURES

Figure 1. Comparison of expected divergence dates calculated using the natural log of clade sizes (diamonds) and divergence dates calculated using a pure birth model (boxes). The approach based on the natural log of clade sizes results in *increasing* waiting times as cladogenesis proceeds and in differing slopes of lineage-through-time plots depending on the tree shape (solid diamonds: ladder shaped tree; open diamonds: fully balanced trees), whereas the pure birth approach does neither.

Figure 2. Backbone topology. The triangular tips are expanded in the subsequent figures. The node labels are unique identifiers over the whole tree, and correspond with the entries in Table 3. See text for details.

Figure 3. Topology for *Macaca*, *Cercocebus*, *Mandrillus*, *Papio*, *Theropithecus* and *Lophocebus*. The node labels are unique identifiers over the whole tree, and correspond with the entries in Table 3. See text for details.

Figure 4. Topology for *Cercopithecus*, *Chlorocebus*, *Erythrocebus*, *Miopithecus*, *Allenopithecus*. The node labels are unique identifiers over the whole tree, and correspond with the entries in Table 3. See text for details.

Figure 5. Topology for *Trachypithecus*, *Presbytis*, *Semnopithecus*, *Pygathrix*, *Nasalis*, *Colobus*, *Procolobus*. The node labels are unique identifiers over the whole tree, and correspond with the entries in Table 3. See text for details.

Figure 6. Topology for *Hylobates*, *Pan*, *Homo*, *Gorilla* and *Pongo*. The node labels are unique identifiers over the whole tree, and correspond with the entries in Table 3. See text for details.

Figure 7. Topology for *Saguinus*, *Leontopithecus*, *Callithrix*, *Callimico* and *Aotus*. The node labels are unique identifiers over the whole tree, and correspond with the entries in Table 3. See text for details.

Figure 8. Topology for *Saimiri* and *Cebus*. The node labels are unique identifiers over the whole tree, and correspond with the entries in Table 3. See text for details.

Figure 9. Topology for *Callicebus*, *Pithecia*, *Cacajao* and *Chiropotes*. The node labels are unique identifiers over the whole tree, and correspond with the entries in Table 3. See text for details.

Figure 10. Topology for *Ateles*, *Lagothrix*, *Brachyteles*, *Alouatta*. The node labels are unique identifiers over the whole tree, and correspond with the entries in Table 3. See text for details.

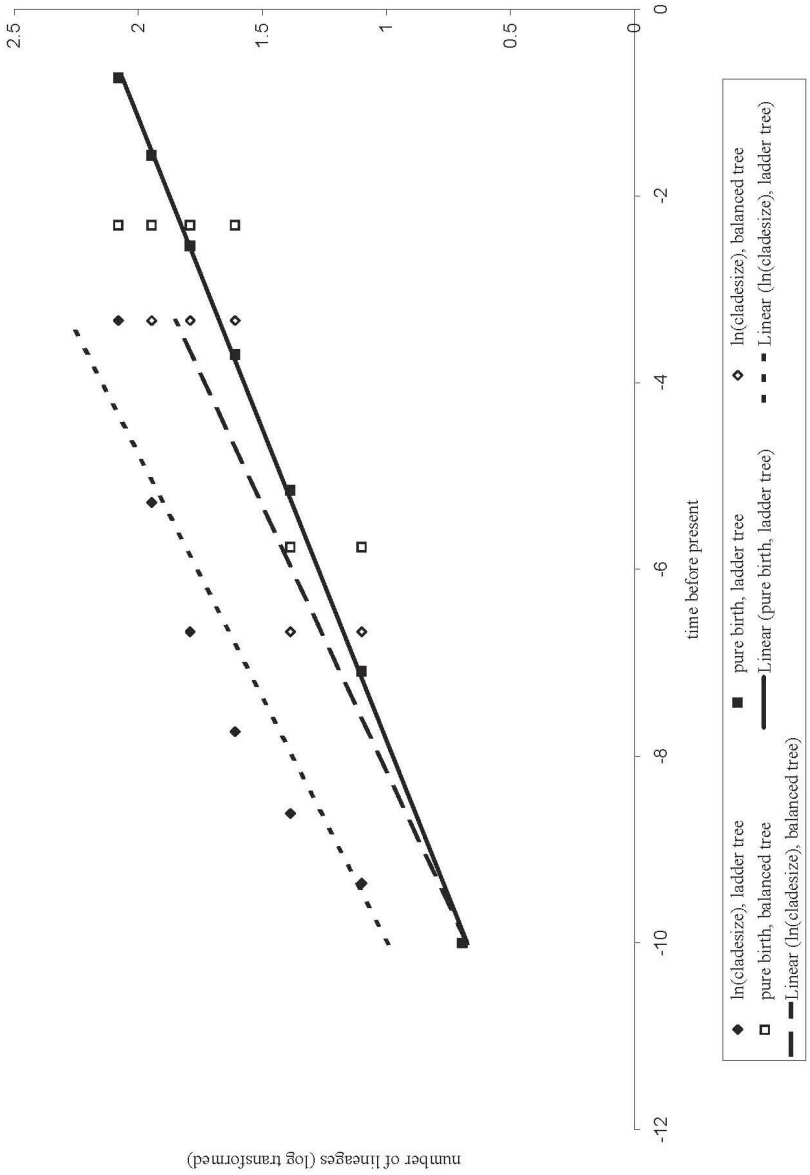
Figure 11. Topology for *Tarsius*. The node labels are unique identifiers over the whole tree, and correspond with the entries in Table 3. See text for details.

Figure 12. Topology for *Eulemur*, *Varecia*, *Hapalemur*, *Lemur*, *Lepilemur*, *Propithecus*, *Indri*, *Avahi*, *Microcebus*, *Allocebus*, *Cheirogaleus*, *Phaner* and *Daubentonia*. The node labels are unique identifiers over the whole tree, and correspond with the entries in Table 3. See text for details.

Figure 13. Topology for *Galago*, *Otolemur*, *Galagoides*, *Euoticus*, *Nycticebus*, *Loris*, *Arctocebus* and *Perodicticus*. The node labels are unique identifiers over the whole tree, and correspond with the entries in Table 3. See text for details.

Figure 14. Distribution of modeled node depths versus depths estimated from calibrated near-clocklike sequences. Diamond boxes indicate mean and 95% confidence interval. See text for details.

Figure 15. Lineage through time plots for the order Primates (log transformed number of lineages). The gray curve shows lineage through time growth when both molecular estimates of divergence dates, as well as interpolated (pure birth) based divergence dates are considered. The black curve shows lineage through time curve only considering lineages for which molecular estimates are available. See text for details.



1225
1226

1227 Figure 1.

FIGURE V-2. SUPERTREE BACKBONE TOPOLOGY

The triangular tips are expanded in the subsequent figures. The node labels are unique identifiers over the whole tree, and correspond with the entries in Table 2. See text for details.

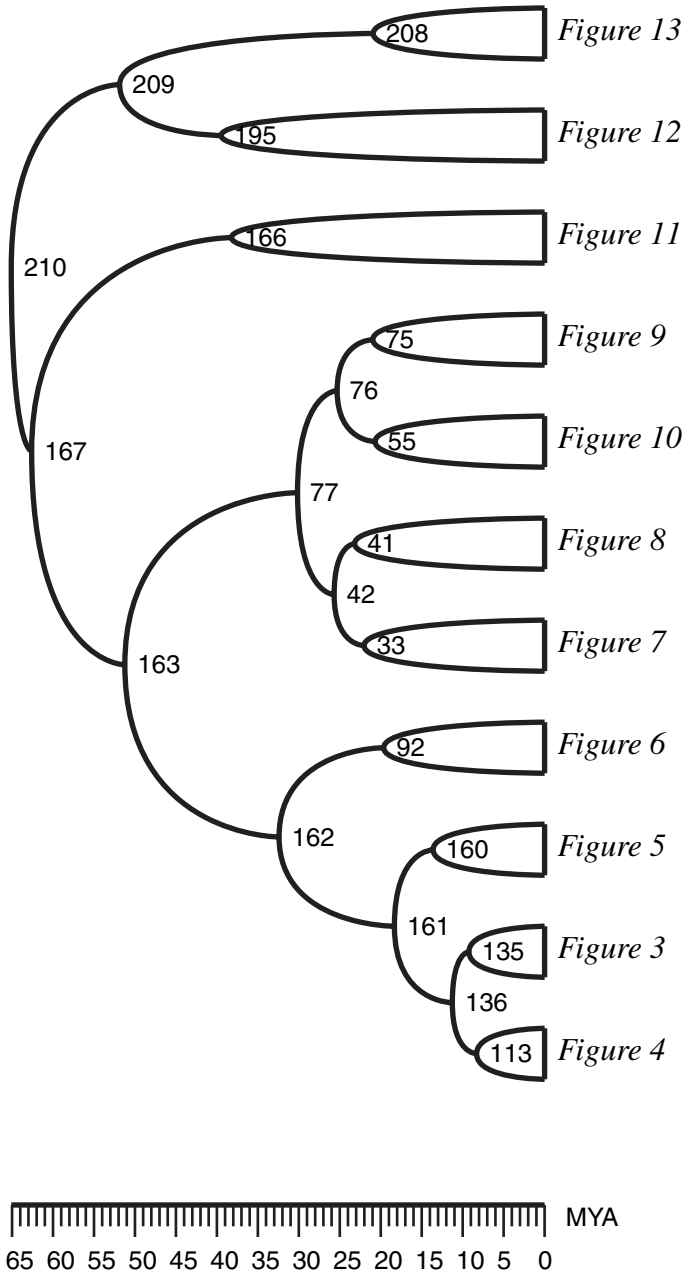


FIGURE V-3. MACACA, CERCOCEBUS, MANDRILLUS, PAPIO, THEROPITHECUS, LOPHOCEBUS

The node labels are unique identifiers over the whole tree, and correspond with the entries in Table 2. See text for details.

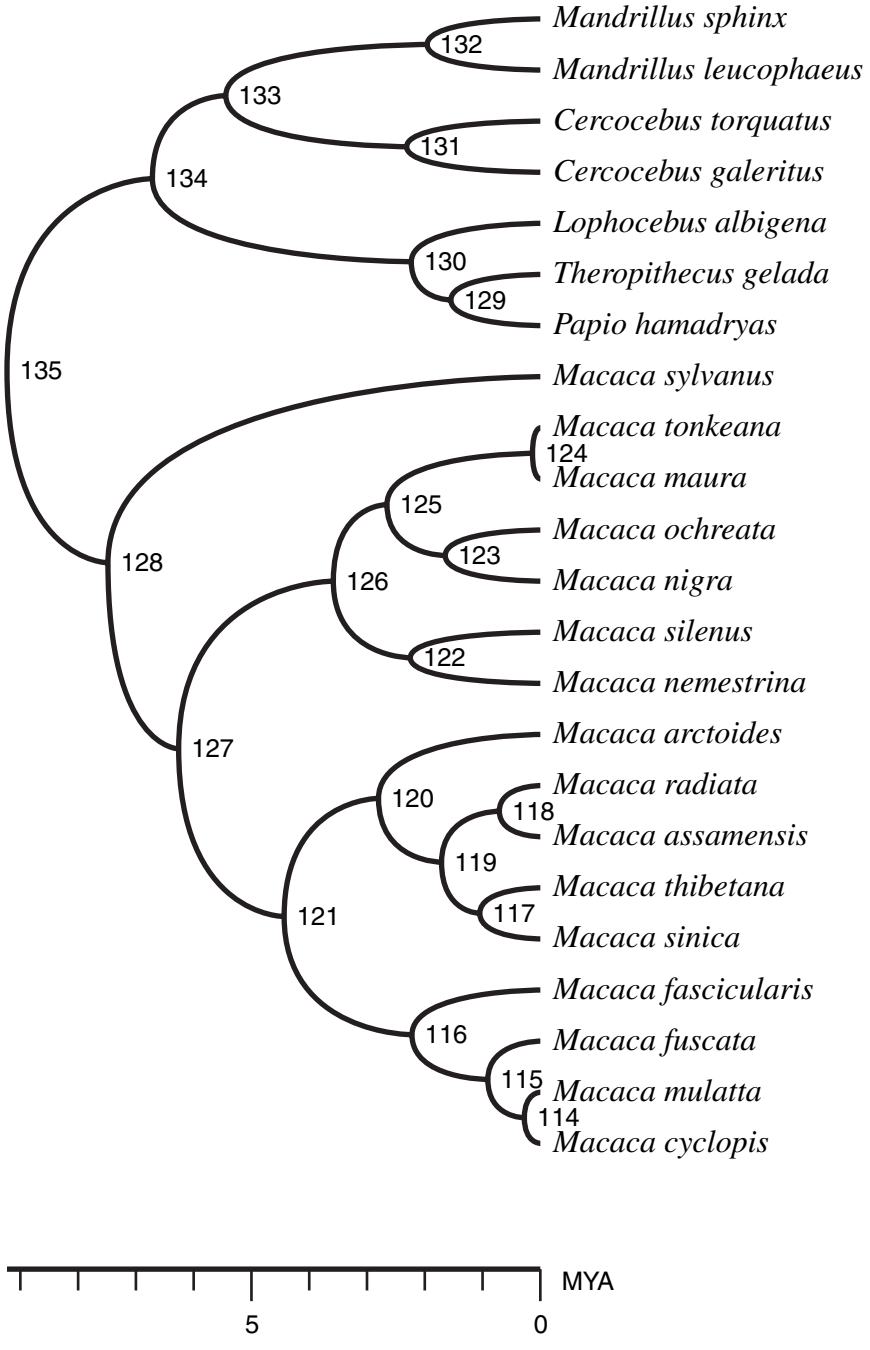


FIGURE V-4. CERCOPITHECUS, CHLOROCEBUS, ERYTHROCEBUS, MIOPITHECUS, ALLENOPITHECUS

The node labels are unique identifiers over the whole tree, and correspond with the entries in Table 2. See text for details.

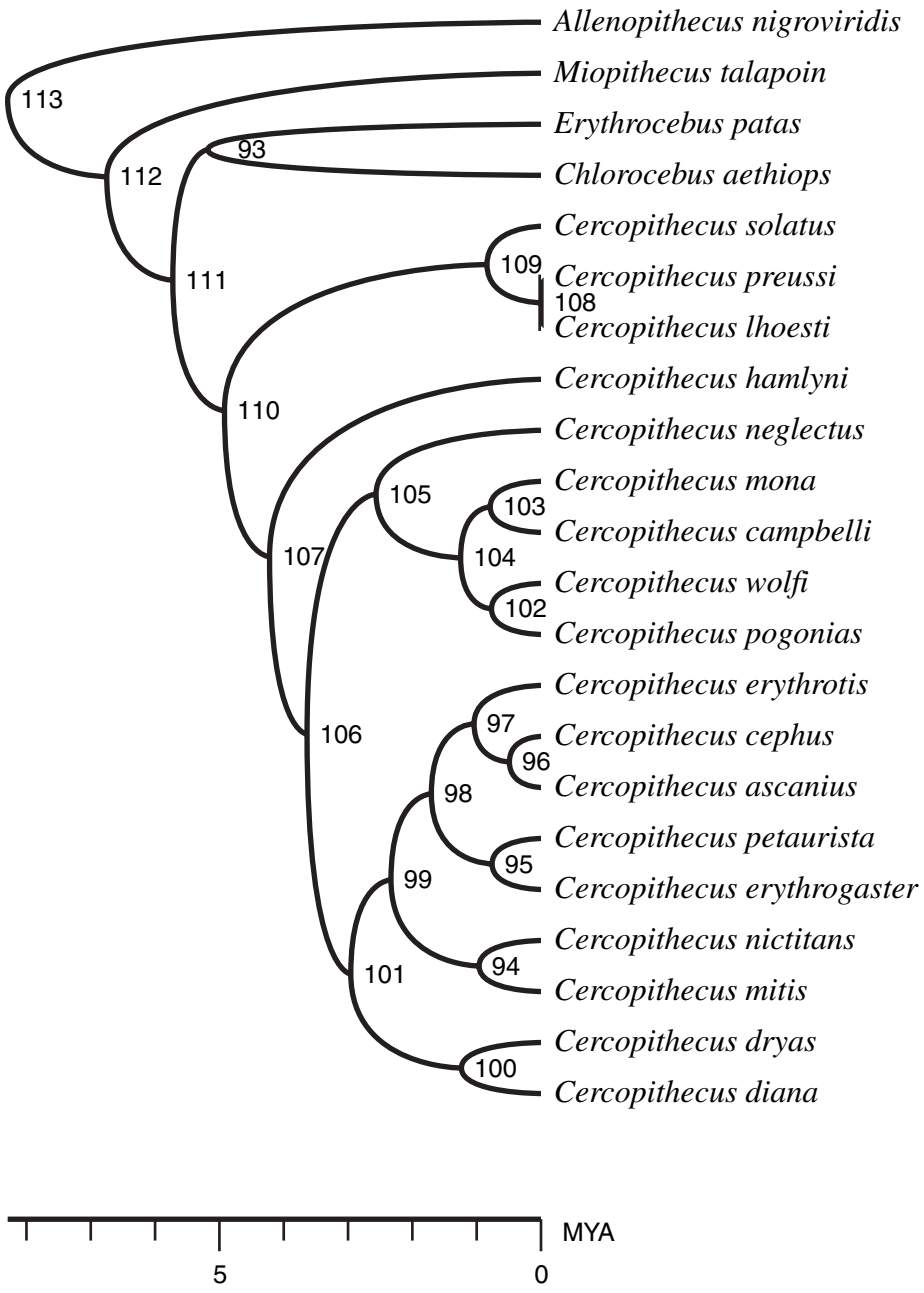


FIGURE V-5. TRACHYPITHECUS, PRESBYTIS, SEMNOPITHECUS, PYGATHRIX, NASALIS, COLOBUS, PROCOLOBUS

The node labels are unique identifiers over the whole tree, and correspond with the entries in Table 2. See text for details.

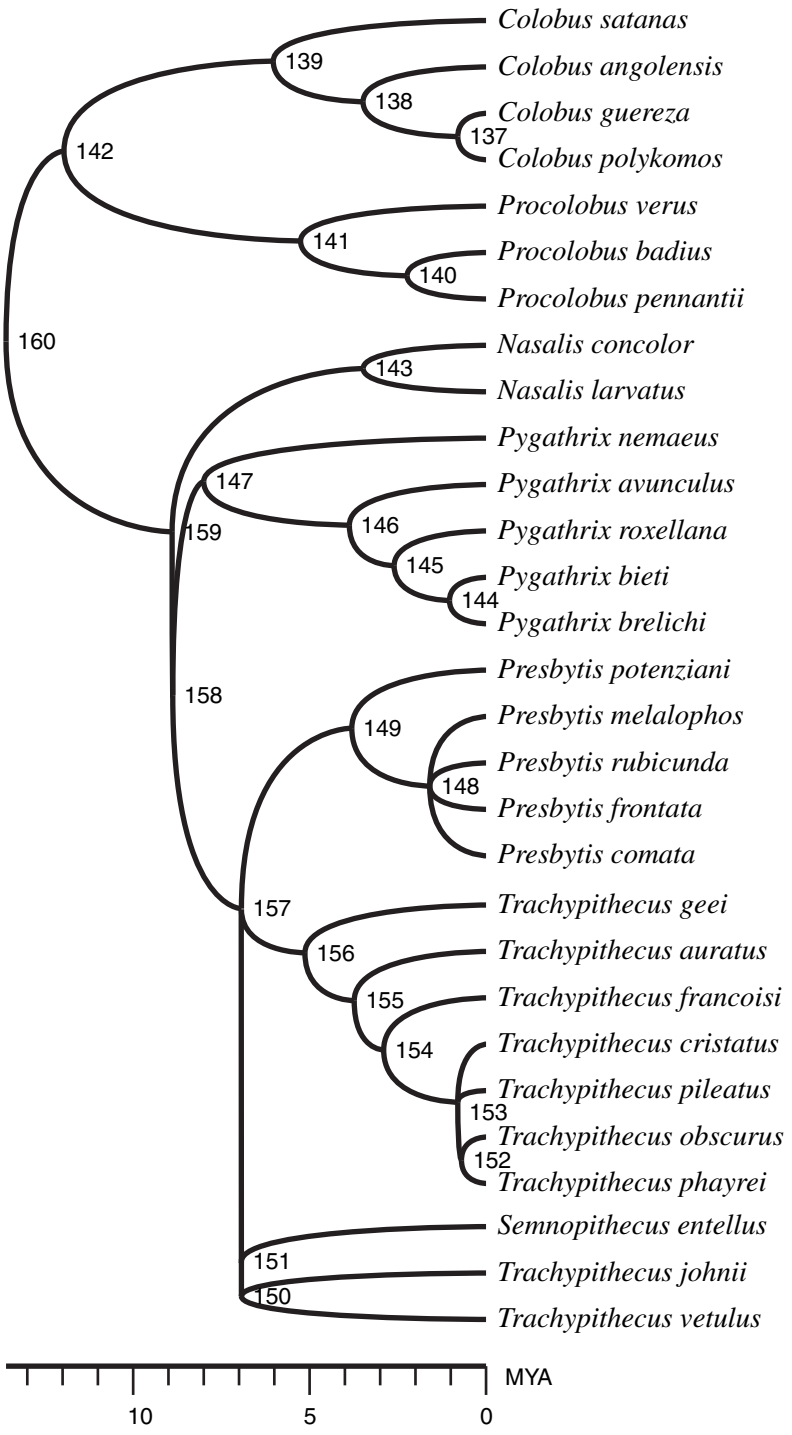


FIGURE V-6. HYLOBATES, PAN, HOMO, GORILLA, PONGO

The node labels are unique identifiers over the whole tree, and correspond with the entries in Table 2. See text for details.

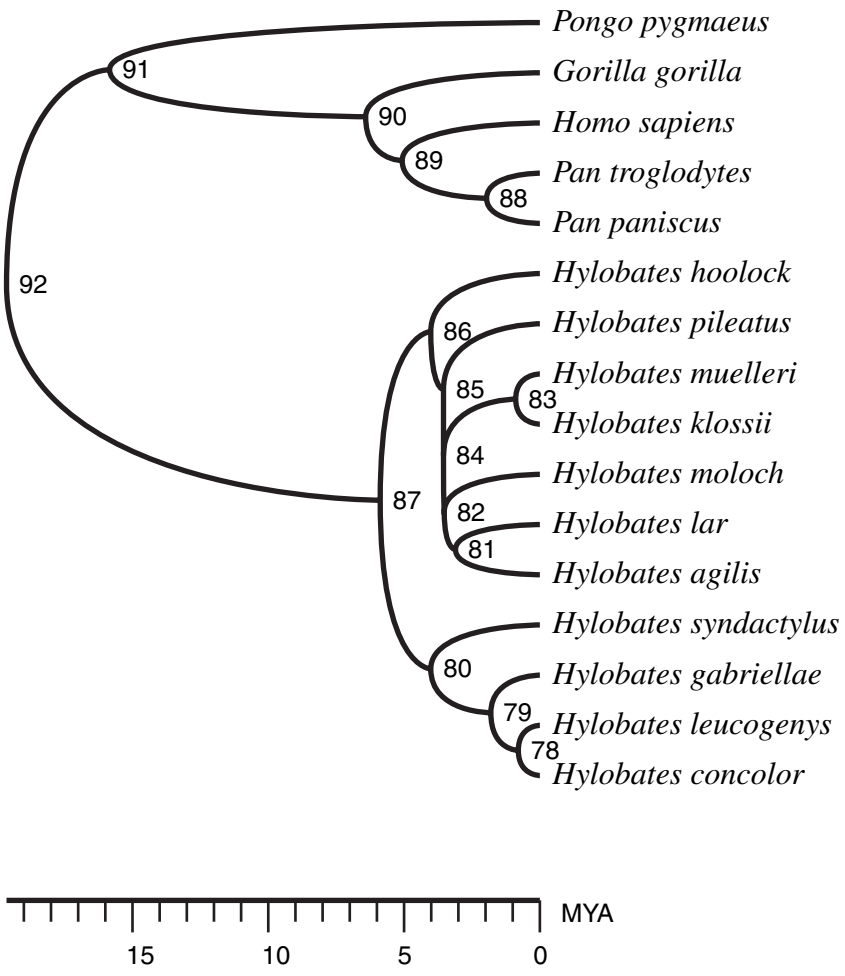


FIGURE V-7. SAGUINUS, LEONTOPITHECUS, CALLITHRIX, CALLIMICO, AOTUS

The node labels are unique identifiers over the whole tree, and correspond with the entries in Table 2. See text for details.

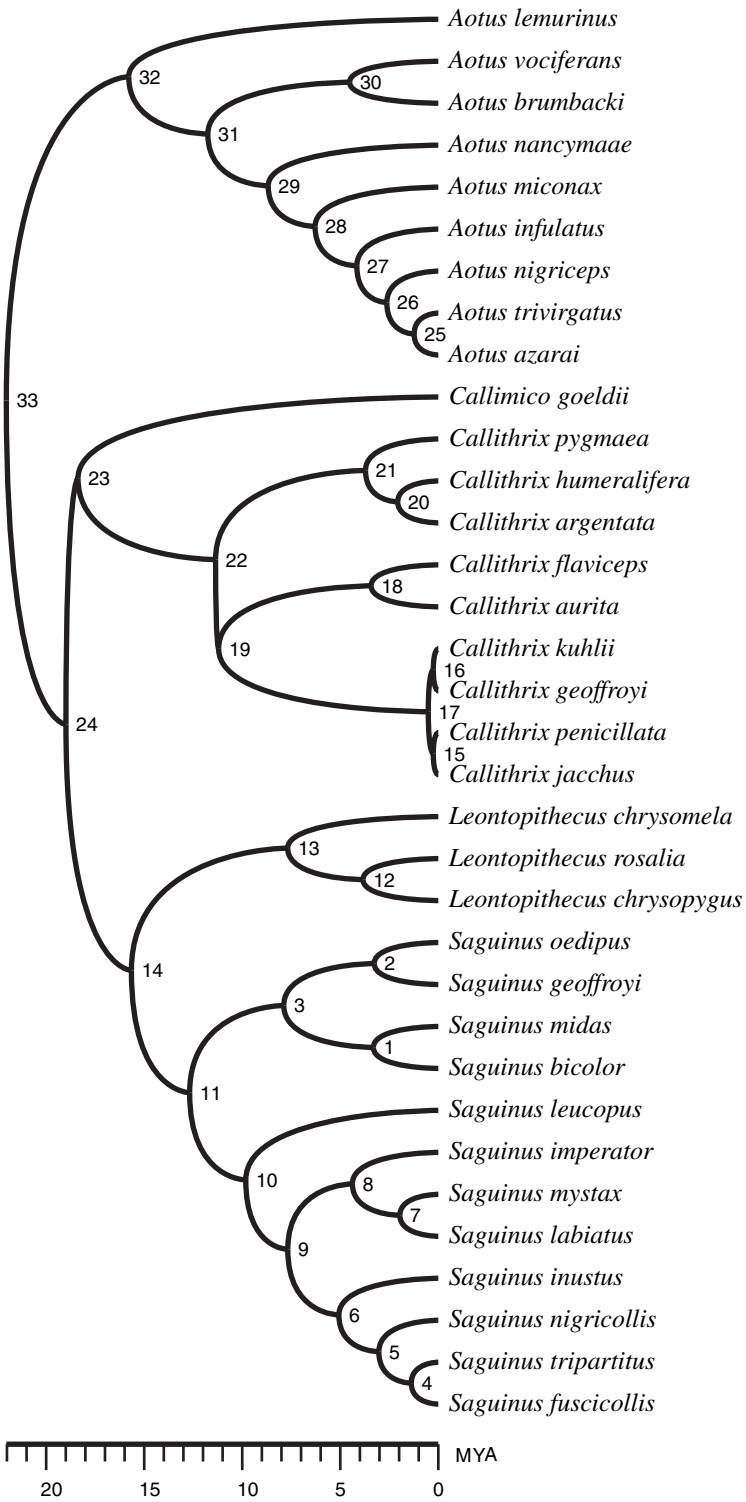


FIGURE V-8. SAIMIRI AND CEBUS

The node labels are unique identifiers over the whole tree, and correspond with the entries in Table 2. See text for details.

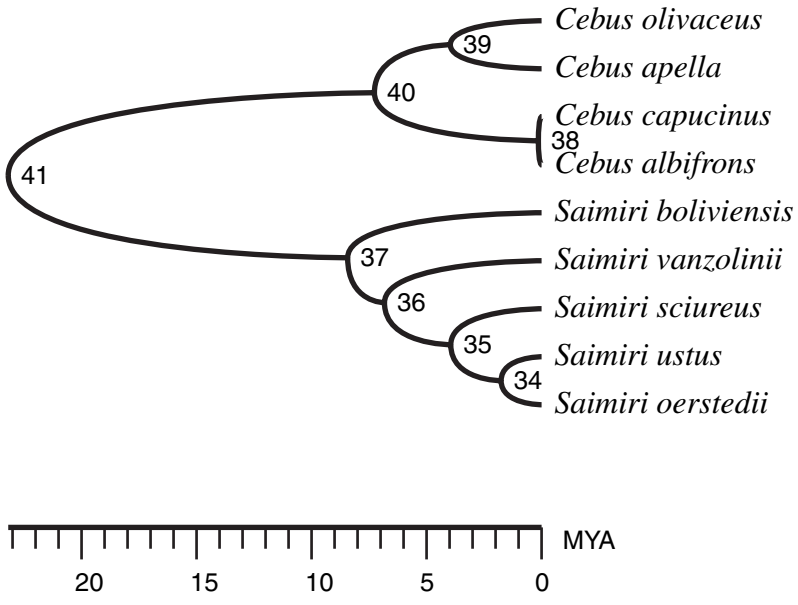


FIGURE V-9. CALLICEBUS, PITHECIA, CACAJAO, CHIROPOTES

The node labels are unique identifiers over the whole tree, and correspond with the entries in Table 2. See text for details.

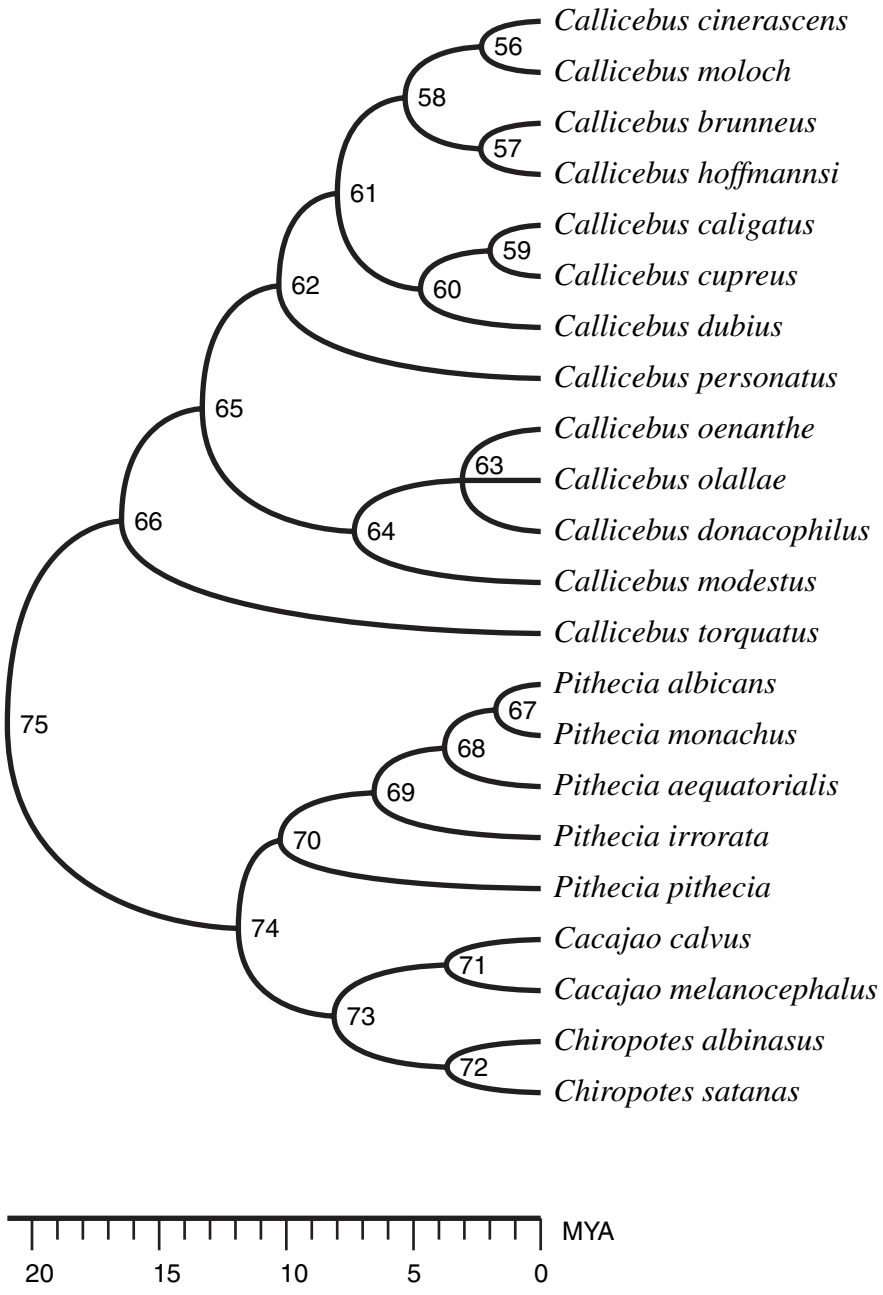


FIGURE V-10. ATELES, LAGOTHRIX, BRACHYTELES, ALOUATTA

The node labels are unique identifiers over the whole tree, and correspond with the entries in Table 2. See text for details.

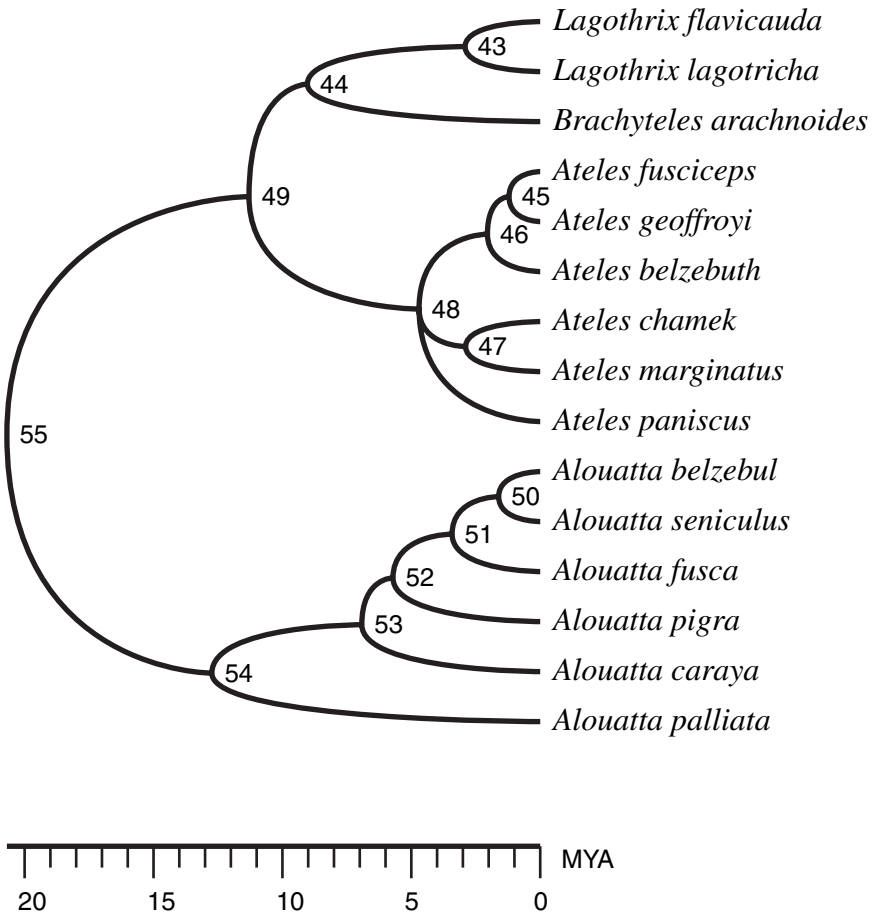


FIGURE V-11. TARSIUS

The node labels are unique identifiers over the whole tree, and correspond with the entries in Table 2. See text for details.

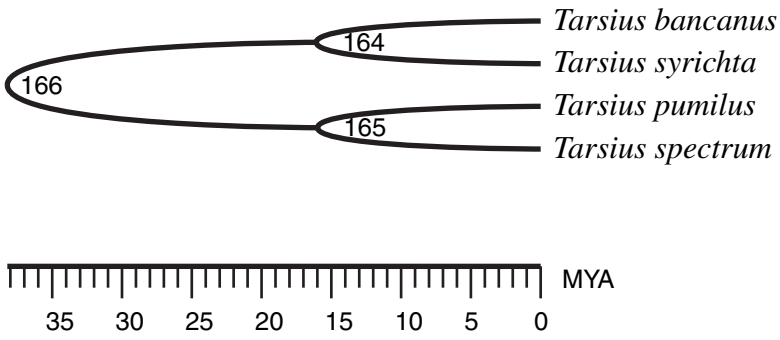


FIGURE V-12. EULEMUR, VARECIA, HAPALEMUR, LEMUR, LEPILEMUR, PROPITHECUS, INDRI, AVAHI, MICROCEBUS, ALLOCEBUS, CHEIROGALEUS, PHANER, DAUBENTONIA

The node labels are unique identifiers over the whole tree, and correspond with the entries in Table 2. See text for details.

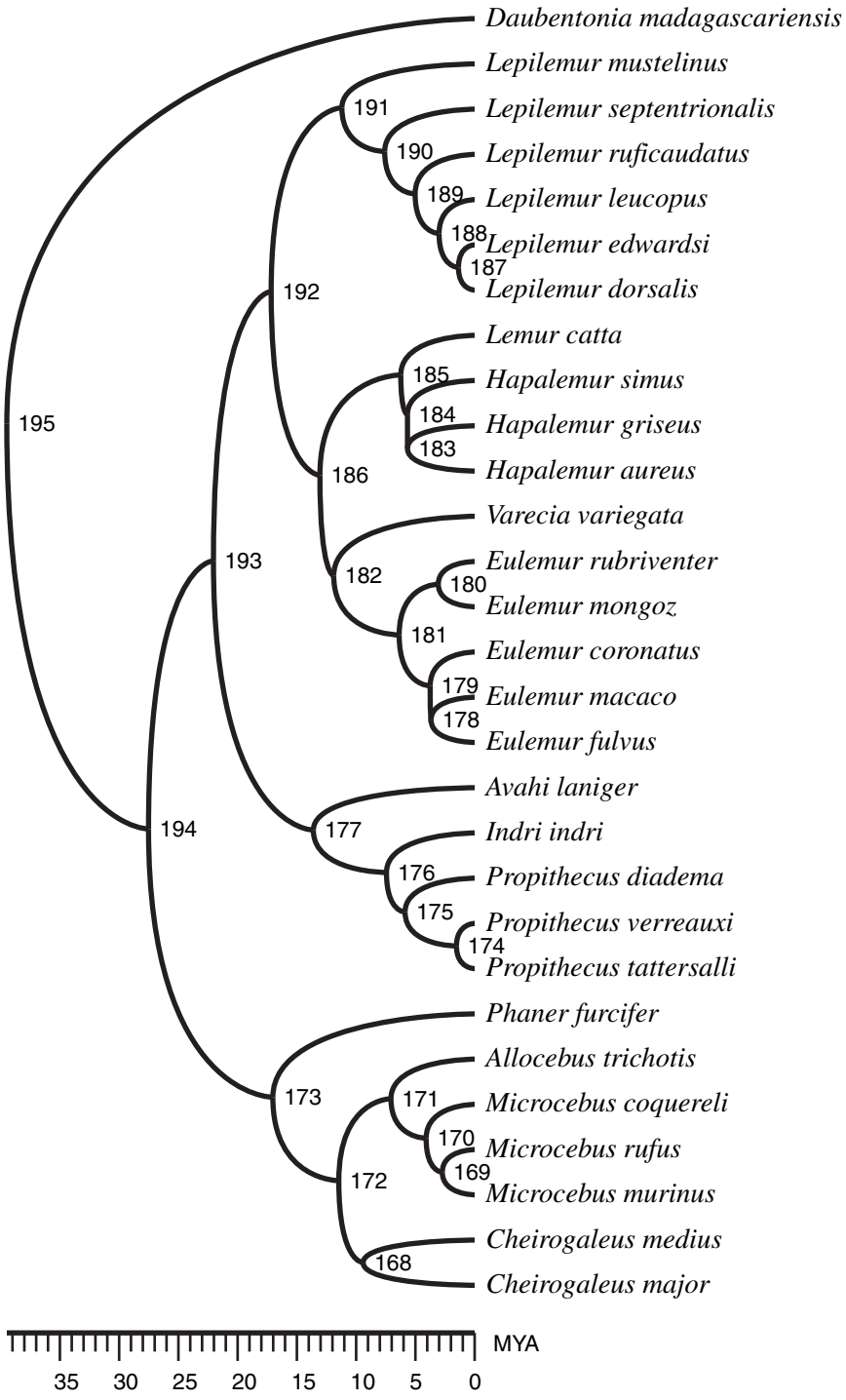


FIGURE V-13. GALAGO, OTOLEMUR, GALAGOIDES, EUOTICUS, NYCTICEBUS, LORIS, ARCTOCEBUS, PERODICTICUS

The node labels are unique identifiers over the whole tree, and correspond with the entries in Table 2. See text for details.

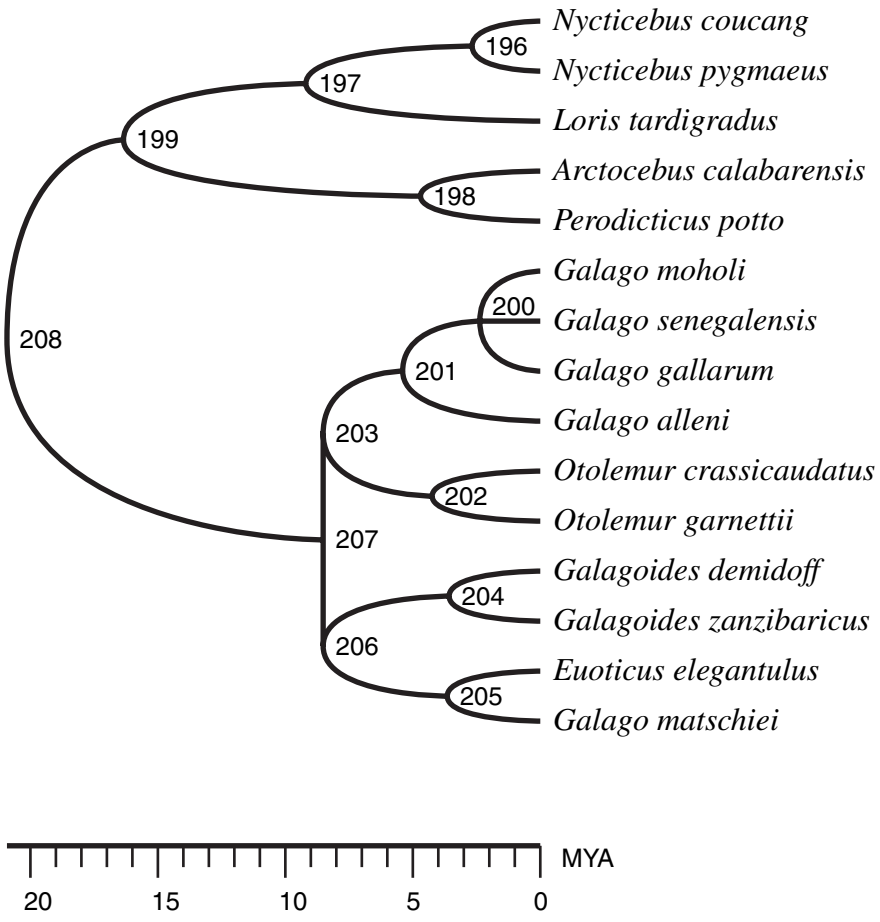


FIGURE V-14. DISTRIBUTION OF MODELED VERSUS MOLECULAR NODE DEPTHS

Distribution of modeled node depths versus depths estimated from calibrated near-clocklike sequences. Diamond boxes indicate mean and 95% confidence interval. See text for details.

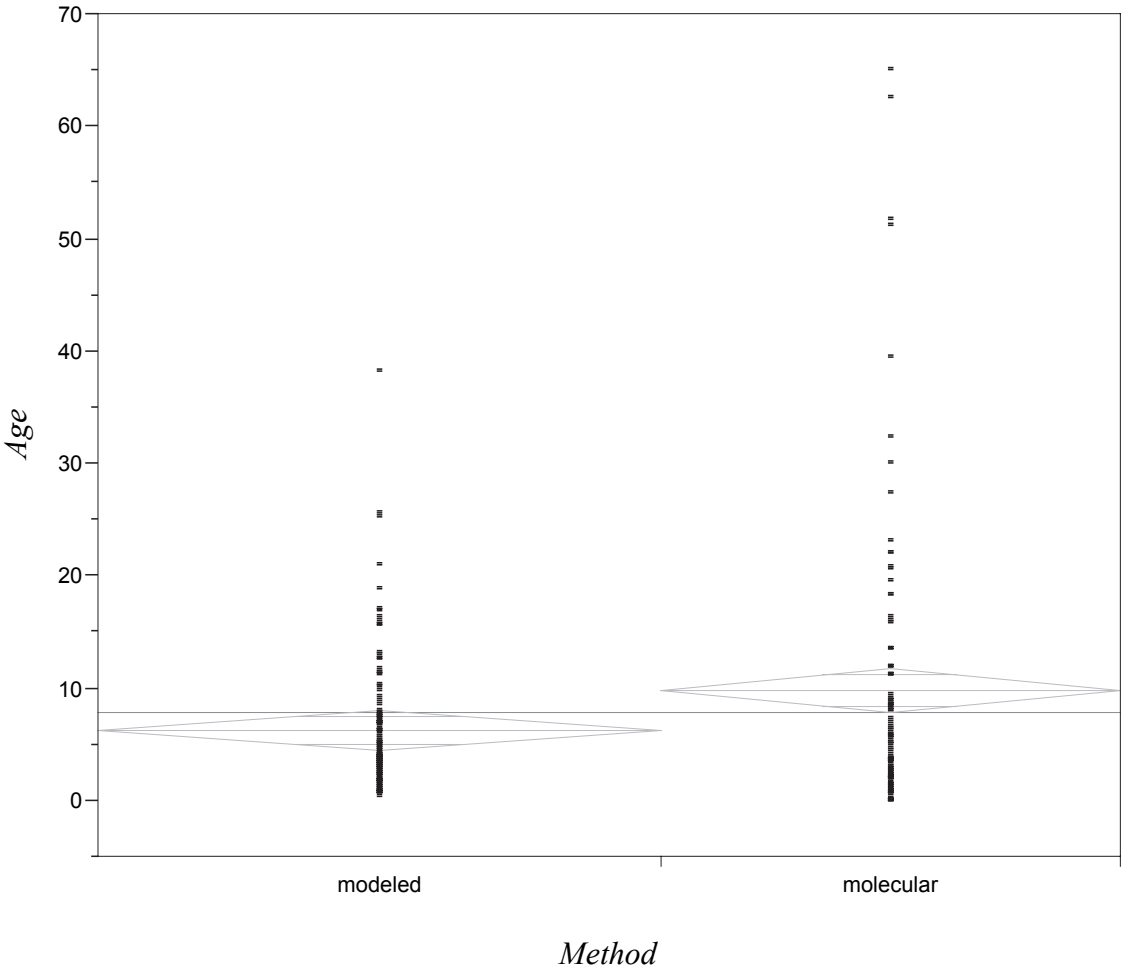


FIGURE V-15. LINEAGE THROUGH TIME PLOTS

Lineage through time plots for the order Primates (log transformed number of lineages). The gray curve shows lineage through time growth when both molecular estimates of divergence dates, as well as interpolated (pure birth) based divergence dates are considered. The black curve shows lineage through time curve only considering lineages for which molecular estimates are available. See text for details.