A Composite Estimate of Primate Phylogeny

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A composite estimate of primate phylogeny

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SUMMARY

This paper presents an estimate of the phylogeny of all 203 species of primate. The composite tree is derived by applying a parsimony algorithm to over a hundred previous estimates, and is well resolved, containing 160 nodes. The ages of over half the clades in the tree have been estimated from information in the literature. Bootstrapping has been used to indicate the degree of certainty associated with each clade. The tree will be a useful framework for comparative biologists and shows which areas of primate phylogeny are still only sketchily known.

1. INTRODUCTION

I present an estimate, derived from over a hundred previously published studies, of the phylogeny of the whole order Primates. The resulting tree has 160 branching points, 90 with estimates of age, linking 203 species.

The tree should prove useful for comparative studies of the order. Comparative biology has repeatedly given valuable insights into why primates show the adaptations they do (see, for example: Clutton-Brock & Harvey 1977; Harcourt *et al.* 1981; Jungers 1985; Ridley 1986; Smuts *et al.* 1987; Fleagle 1988; Martin 1990; Dunbar 1992; Charnov & Berrigan 1993; Tardif & Garber 1994). However, analysis of cross-species data is complicated by the tendency for close relatives to inherit characteristics from a common ancestor, rather than evolve them independently; species values are therefore not statistically independent (see Harvey & Pagel (1991) and Miles & Dunham (1993) for reviews). Many methods have been designed to overcome the problems of comparative data (Ridley 1983; Felsenstein 1985; Cheverud *et al.* 1985; Grafen 1989; Gittleman & Kot 1990; Harvey & Pagel 1991; Martins & Garland 1991; Maddison & Maddison 1992; Pagel 1994), all of them requiring estimates of phylogeny. The methods perform best when the phylogeny is well resolved, and many require knowledge of the relative lengths of branches.

Recent work (Kirkpatrick & Slatkin 1993; Slowinski & Guyer 1993; Nee *et al.* 1994; Harvey *et al.* 1995) shows how phylogenies can also be used to make inferences about macroevolutionary processes. The phylogeny presented here is the largest well resolved estimate of a complete clade, and so will be useful for studies of large-scale patterns of evolution. Additionally, it may be a useful 'Aunt Sally', provoking further research into unresolved issues in primate phylogeny and ways of combining trees.

It would not be feasible to compile a morphological or molecular data set representing all or even most of the living primate species. However, a large body of literature has accumulated that bears on the interrelations of primate lineages. My aim here has been to use information from as wide a range of published estimates as possible, in keeping with the principle of total evidence (Kluge 1989).

Attempts to combine estimates of phylogeny to produce a consensus run up against two practical problems. The first is that strict and semi-strict consensus trees lose resolution as more estimates are added, whenever there is any conflict among source trees (Lanyon 1993). Given the debate about the position of so many primate taxa over the years (e.g. tarsiers, *Daubentonia*, callitrichids and *Homo*; see Martin (1990) for a review), such a consensus tree of the order would be almost completely unresolved. Secondly, methods avoiding the first pitfall (e.g. Nelson consensus; Page 1989) require that all of the trees being combined have the same set of taxa at the tips, which they rarely do.

A new technique, matrix representation with parsimony (Baum 1992; Ragan 1992), modified to eliminate potentially misleading redundant information from the data matrix (Purvis 1995), circumvents both problems. Briefly, each of the source trees to be combined is recoded as a matrix of binary characters by using the following simple algorithm (taken from Purvis (1995), where a more detailed explanation and examples can be found).

```
For each node in the source tree in turn:
    score taxa in the clade defined by the node as 1;
    score taxa in the sister clade as 0;
    score any other taxa and missing taxa as ?
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Figure 1 illustrates the process for the estimate by Haimoff *et al.* (1982) of gibbon (*Hylobates*) phylogeny. The binary matrices from the different trees are then combined into a single matrix, the outgroup coded as 0 (primitive), and the matrix analysed by using parsimony. The resulting tree can be resolved even when there is disagreement among source trees, in the same way that a resolved tree can result from a character matrix even when characters disagree. As when character data are analysed, some parts of the

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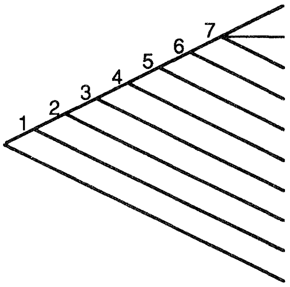

	1	2	3	4	5	6	7
agilis	1	1	1	1	1	1	1
lar	1	1	1	1	1	1	1
muelleri	1	1	1	1	1	1	1
moloch	1	1	1	1	1	1	0
pileatus	1	1	1	1	1	0	?
klossii	1	1	1	1	0	?	?
hoolock	1	1	1	0	?	?	?
syndactylus	1	1	0	?	?	?	?
concolor	1	0	?	?	?	?	?
outgroup	0	0	0	0	0	0	0

Figure 1. An illustration of how trees are recoded as binary characters. The left part of the figure shows the phylogeny of *Hylobates* according to Haimoff *et al.* (1982). Numbers of nodes correspond to columns in the table on the right. See text for the algorithm used.

tree are known with much more certainty than are others; I have used bootstrapping to give a very rough indication of the relative robustness of the different clades.

Estimates of the ages of nodes give a timescale for primate evolution and so are useful when asking questions about the rates of evolution or diversification. I have estimated the ages of over half of the nodes in the composite tree, by using a range of methods, and also estimated the uncertainty associated with them.

2. METHODS

Source trees were generally found by on-line searches. I searched Bath Information and Data Services (BIDS) (1981–1993) for titles or keywords with any of cladistic*, clado*, phylogen*, systematic* and taxonom*. Recent issues of *Zoological Record* and *Biological Abstracts* were searched for references containing, in any field, primat* and any one or more of phylogen*, clado* and cladistic*.

I accepted the following kinds of information as source trees:

(A) maximum likelihood trees;

(B) cladistic or compatibility analyses of morphological, molecular (sequence, restriction site, or allele presence/absence), karyotypic or behavioural characters;

(C) neighbour-joining trees based on sequence data;

(D) trees based on molecular (DNA–DNA hybridization, allele frequencies, sequence divergence) data when rate constancy was not assumed or was demonstrated to be reasonable;

(E) trees based on molecular data with rate constancy assumed but not demonstrated;

(F) phenograms based on morphology or behaviour;

(G) trees based on non-cladistic analysis of the distribution of morphological or behavioural characters; and

(H) taxonomies.

In all, 112 publications provided source trees. There are many cases of an author or group publishing in more than one place virtually the same set of relations based on more or less the same data. In such instances, I have counted each clade only once, irrespective of how often it appears.

Clearly some of these lines of evidence are much more likely to reflect phylogeny than are others: some were never *intended* to estimate phylogenetic relations. I have taken the view, however, that each of the lines of evidence listed above will tend to point to phylogeny, and that any information is better than none: there are not enough cladograms or maximum likelihood trees to defend ignoring the rest. Note that it is currently only possible to combine characters (as advocated by many supporters of total evidence, e.g. Barrett *et al.* (1991) and Kluge (1989)) when the characters are of the same type (e.g. discrete characters), which they are not here.

Because different kinds of source tree differ in their likelihood of being right, equal weighting of source trees cannot be defended (Barrett *et al.* 1991). However, it is far from clear what weighting scheme should be adopted instead. I have assigned a relative weight of four to binary characters derived from source trees in categories A–D above, reflecting their sounder theoretical basis and better performance in simulations (see, for example: Felsenstein 1981; Huelsenbeck & Hillis 1993; Stewart 1993; Hillis *et al.* 1994). The final tree is not unduly sensitive to different values of the weighting factor (see results section).

Over much of the order, there is a shortage of information about phylogeny. In contrast, there is an almost endless stream of studies of the relation of *Homo* to its close relatives, the great apes. I therefore restricted myself to just the first 23 studies I came to that bore on this question.

To ensure that the most parsimonious trees were found, I used the branch-and-bound algorithm (Hendy & Penny 1982) of PAUP (Swofford 1993). Branch-and-bound becomes prohibitively slow with more than about 20 taxa; so I broke the phylogeny into monophyletic nested pieces of manageable size. Conflict among source trees was so extensive that there was no such set of taxa on which all the source trees agreed; so I followed the (generally overwhelming) majority opinion whenever a choice had to be made. I have assumed that each of the following taxa is monophyletic (names as in Corbet & Hill 1991): Cheirogaleidae + Lemuridae + Indriidae + Daubentoniidae + Lorisidae, Cheirogaleidae, *Galago* + *Galagoides* + *Otolemur* + *Euoticus*, *Loris* + *Nycticebus* + *Perodicticus* + *Arctocebus*, *Tarsius*, Cebidae + Callitrichidae, Callitrichidae, *Saguinus*, *Cebus*, *Aotus*, *Callicebus*, *Saimiri*, *Pithecia*, *Alouatta*, *Ateles*, Cercopithecinae, *Cercopithecus* + *Erythrocebus* + *Miopithecus* + *Allenopithecus*, *Macaca*, *Papio*, Colobinae, *Pygathrix*, *Presbytis*, *Hylobates*, Pongidae + Hominidae.

Different primate systematists differ in their view of what constitutes a species, and therefore how many species particular groups contain. I have used as a standard the 203 species names listed by Corbet & Hill (1991), a recent and widely available work; others who prefer other arrangements can therefore work out synonyms where necessary. There is nothing definitive about the particular list I have chosen, given recent instability in the alpha taxonomy of many groups, especially the New World monkeys. I have also followed the taxonomic scheme of Corbet & Hill (1991); technically, *Eulemur* should be used in place of *Petterus* for the non-*catta* lemurs, because the former name has priority (Simons & Rumpler 1988).

The appendix gives references to all source trees used. It is clear that some parts of the order have received more coverage than others. Unsurprisingly, hominoids have been studied in most depth (with, on average, 4.5 binary characters per species), followed by strepsirhines (3.2), cercopithecines (2.5), platyrrhines (2.4), colobines (1.1) and tarsiers (0.5). The estimate of the interrelations among these groups is based upon 5.4 characters per taxon. The data matrices cannot be included because of space constraints, but are available from me on request. When maximum parsimony trees had been obtained, 100 bootstrap replicates were generated (with the same weighting scheme in place) to give a rough idea of the relative strength of support for different clades. The characters are not logically independent, whereas bootstrapping requires that they are; however, tree structure is partitioned among characters without repetition (Purvis 1995), which makes bootstrapping more reasonable than it might otherwise be. For groups containing many taxa (*Macaca*, Strepsirhini and *Cercopithecus* + *Erythrocebus* + *Miopithecus* + *Allenopithecus*), bootstrapping was done using heuristic searches, rather than branch-and-bound, for reasons of time. For the latter group, the effectiveness of the heuristic search was reduced further by tree-buffer overflow.

Dating the composite tree

When the most parsimonious tree had been found, I used information from the source papers and elsewhere to assign dates to branching events. Dates from sources were of two types: absolute (generally derived from the fossil record; e.g. dates from Szalay & Delson (1979)) or relative (derived by calibrating a molecular clock against one or more nodes of known date). Because miscalibrations can lead to correlated errors among estimates, I have recalculated all clock dates according to a local molecular clock (Bailey *et al.* 1991).

I have taken dates only where the source node defines the same monophyletic group as a node in the composite tree: the structure below the node need not be the same. I relaxed this requirement occasionally where there was only very minor conflict (e.g. Szalay & Delson (1979) date the split between the atelines and the *Chiropotes–Cacajao–Pithecia* lineage at 28 million years ago; I have used this date even though they have *Callicebus* within this clade while I do not). When a source is a refinement of the composite tree, I have taken the ages of the various source nodes as estimates of the age of the corresponding polytomy in the composite tree. When the source is less resolved, I have used the age of the source polytomy as a value for the age of each corresponding node in the composite tree.

Absolute dates

To calibrate relative dates to absolute time, I estimated the dates of the following four nodes using only non-molecular sources: strepsirhine–haplorhine divergence, platyrrhine–catarrhine divergence, Cercopithecidae–Hominoidea divergence, and *Pongo*–Homonidae divergence.

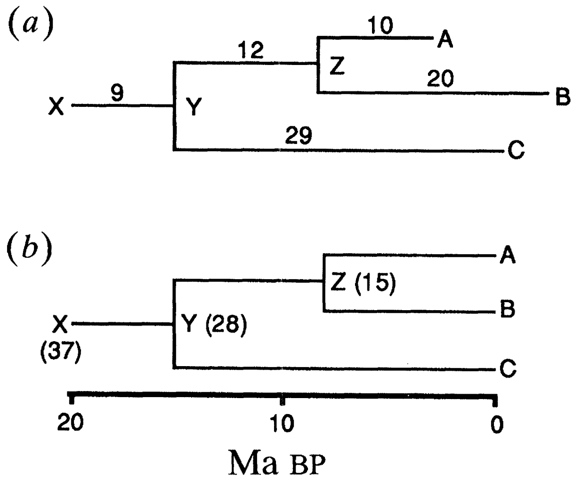

Figure 2. Calculating dates based on the assumption of a local molecular clock. (*a*) Relationships among three extant species (A–C); numbers of substitutions are shown above each branch. (*b*) After application of local molecular clock; mean number of substitutions since each node shown in parentheses. The timescale applies only to (*b*).

There is probably more agreement over the dates of these nodes than over the dates of any others. Absolute dates for these and other nodes came from a range of sources (Covert 1986; Fa 1989; Niemitz 1988; Rosenberger & Strier 1989; Szalay & Delson 1979; Wayne *et al.* 1991); values for other nodes were combined with estimates from elsewhere (see below). I have also used estimates of single dates from other molecular work (Cronin *et al.* 1984; Nakamura *et al.* 1983; Zhang *et al.* 1993). Because the fossil record has only been very incompletely sampled, dates of nodes based on fossil evidence are likely to be consistently underestimated (Martin 1993). The dates of other nodes have been calibrated against these and so all dates in the tree may be too young; this point will be returned to in the discussion.

Relative dates

Different lineages often evolve at different rates (Gillespie 1991); so calibration of a whole tree against a single node of known age is likely to lead to large and correlated errors in the dates assigned to different nodes. Bailey *et al.* (1991) suggest that local molecular clocks will be a better way to date nodes when there are rate differences among lineages. Local molecular clock calculations use information about only those branches in the region of the node to be dated. Figure 2 illustrates how I have implemented their suggestion. Suppose that extant species A, B and C are related as shown in figure 2*a*, with numbers of substitutions indicated along each branch. The median of several estimates of the age of X is 20 million years; the aim is to estimate the ages of Y and Z. I have proceeded as follows. First, A and B are separated from Z by 10 and 20 substitutions, respectively, an average of 15. Z is, in turn, 12 substitutions from Y. Z is therefore estimated to be 15/(12+15) as old as Y. On moving up the tree,

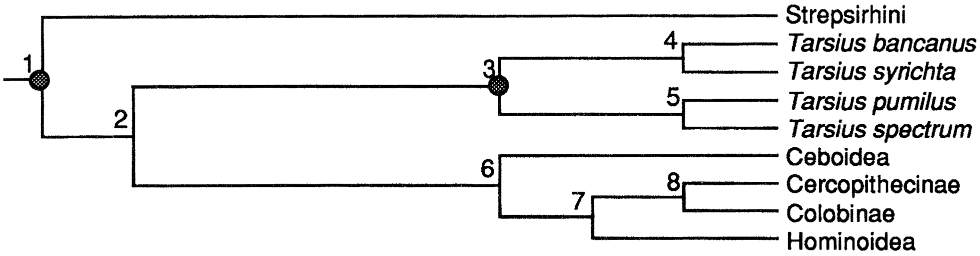

Figure 3. The composite tree for the major groups and *Tarsius*. Node numbers refer to table 1. In this and subsequent figures, nodes marked with a dot were assumed to be monophyletic (see text). No meaning should be assigned to the lengths of branches in this figure or in figures 4–8.

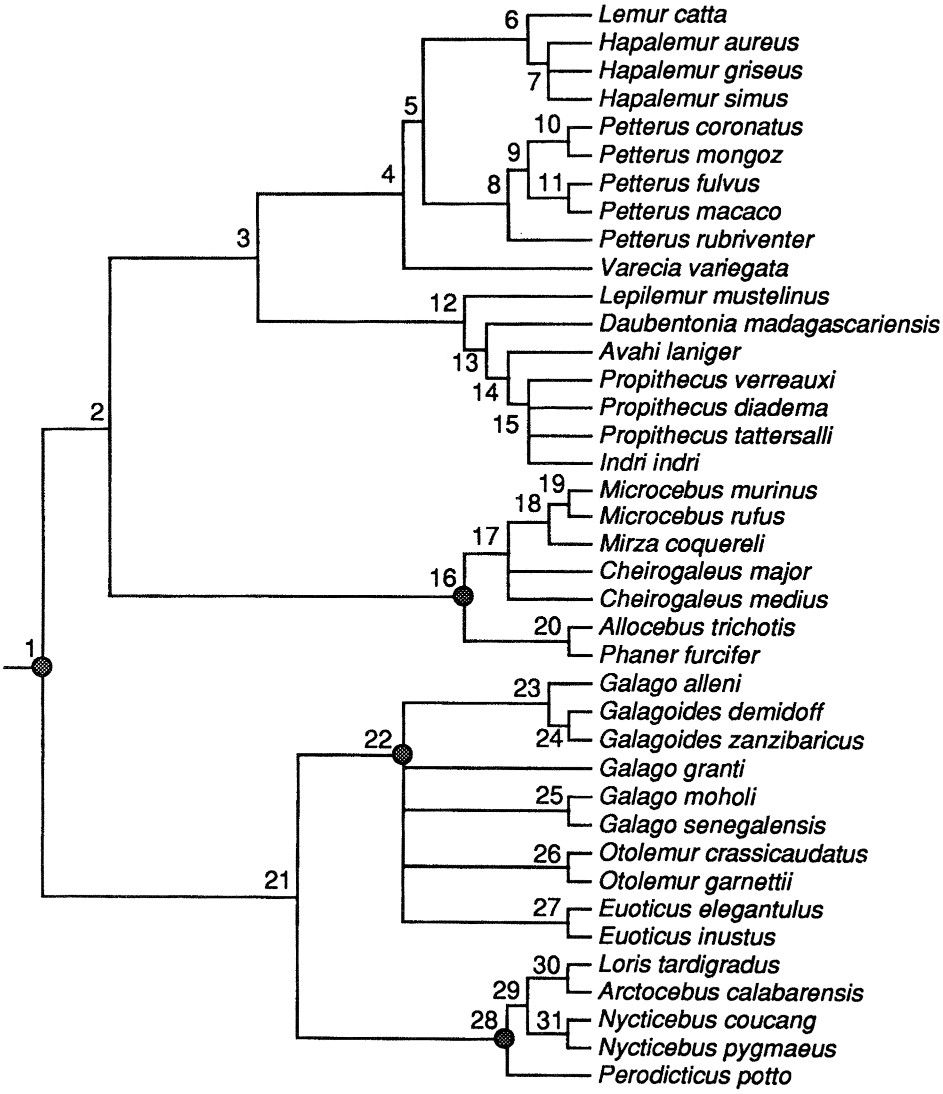

Figure 4. The composite tree for the Strepsirhini. Node numbers refer to table 2.

Y is on average 27 substitutions away from A and B, and 29 from C; the average of these is 28, and so Y is 28/(28+9) as old as X. The median estimate of X's age is 20 million years; so Y is estimated to be 15.1 million years old. If there are other estimates of Y's age, then the median of all the estimates should be used to calibrate Z. In the absence of other estimates, the method is the same as assuming a constant rate below the top node being considered; figure 2*b* shows the dated tree that would result. Note that, in contrast to Bailey *et al.* (1991), I use information from both daughter lineages in the calculations.

I applied the local molecular clock procedure to data from a number of papers (Baba *et al.* 1980; Bailey *et al.* 1991; Bonner *et al.* 1980; Coppenhaver *et al.* 1988; Disotell *et al.* 1992; Fooden & Lanyon 1989; Goodman *et al.* 1982; Kohne 1975; Melnick *et al.* 1993; Ruvolo 1988; Saitou 1991; Schneider *et al.* 1993; Zhang & Shi 1993).

Information from other molecular studies was also used to estimate node dates. I applied the local molecular clock logic to DNA–DNA hybridization distances (Miyamoto & Goodman 1990) and genetic distance values (Meireles *et al.* 1992). Other papers

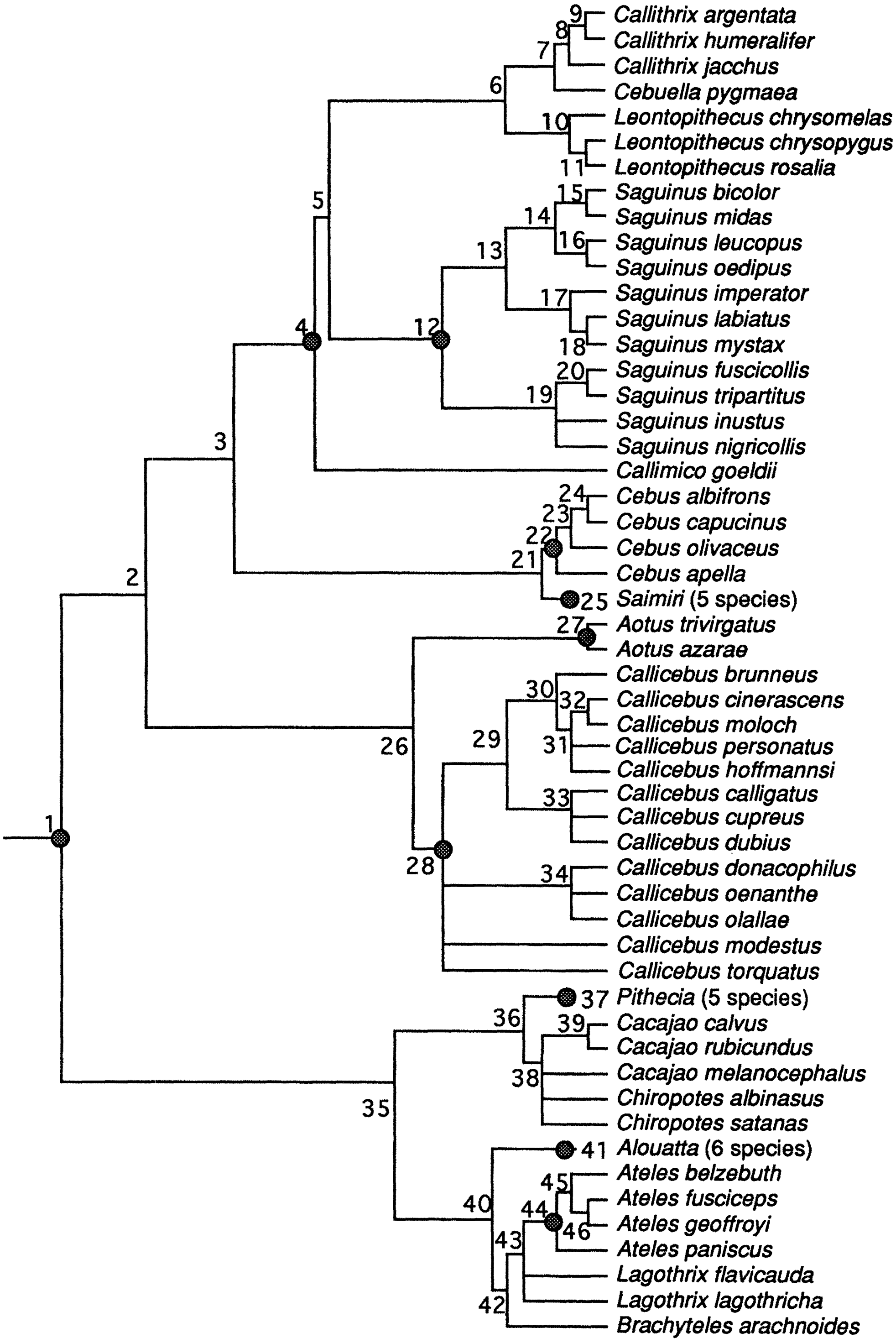

Figure 5. The composite tree for the Cebidae and Callitrichidae. Node numbers refer to table 3.

(Cronin & Meikle 1989; Cronin *et al.* 1984; Dene *et al.* 1980; Lucotte 1982; Nozawa *et al.* 1977; Sarich & Cronin 1980; Sibley & Ahlquist 1984) present dates derived with the assumption of an overall molecular clock. To avoid problems due to differences of calibration I have, wherever possible, recalibrated dates relative to higher nodes for which other estimates were available.

The methods described so far yielded a total of 192 estimates, covering 76 of the 160 nodes. Further estimates can be obtained by applying the clock logic to the numbers of karyotypic changes reported by Dutrillaux (1988) and Rumpler *et al.* (1988). Within higher clades, the numbers of rearrangements between common ancestor and all descendants is surprisingly constant, suggesting a clock-like accumulation of changes. A further 22 estimates, 14 of them for previously undated nodes, were obtained in this way. If the clock approach cannot validly be applied to these data, the estimates that result should tend to differ to an unusual degree from other estimates of the same node. Five nodes permit such a test, and the 'karyotypic clock' dates do not tend to be outliers: they differ from the mean of the other estimates by an average of 0.68 standard deviations (range 0.16 to 1.75). I have therefore accepted the 'karyotypic clock' estimates as no worse than the others.

3. RESULTS

The composite estimates of phylogeny are shown in figures 3–8. The bootstrap proportion and estimated time of divergence (Ma BP) associated with each node are given in tables 1–6, which also indicate whether the node was found in the composite tree with weighting factors of 2 or 8.

Tree topology: degree of resolution and robustness

Overall, the composite tree has 160 nodes. A fully bifurcating tree would have 202; so the estimate is 79 % resolved. The degree of resolution varies among major groups, reflecting both the number of source trees available and how well they agree with each other. The cercopithecine tree is over 90 % resolved, whereas the resolution for colobines is just 63 %.

It is likely that bootstrapping tends to underestimate absolute robustness when applied to matrices derived from source trees, because the coding procedure and

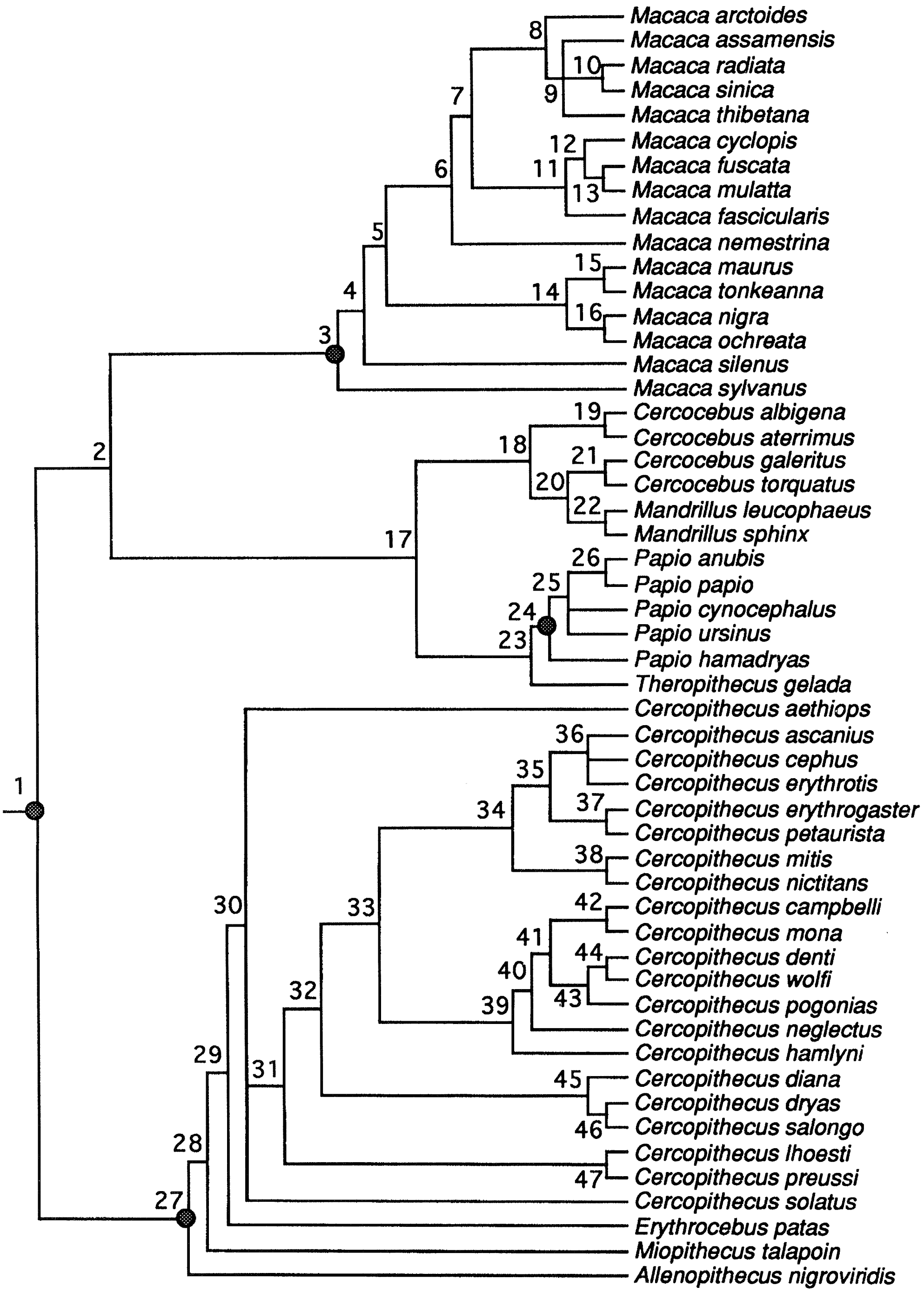

Figure 6. The composite tree for the Cercopithecinae. Node numbers refer to table 4.

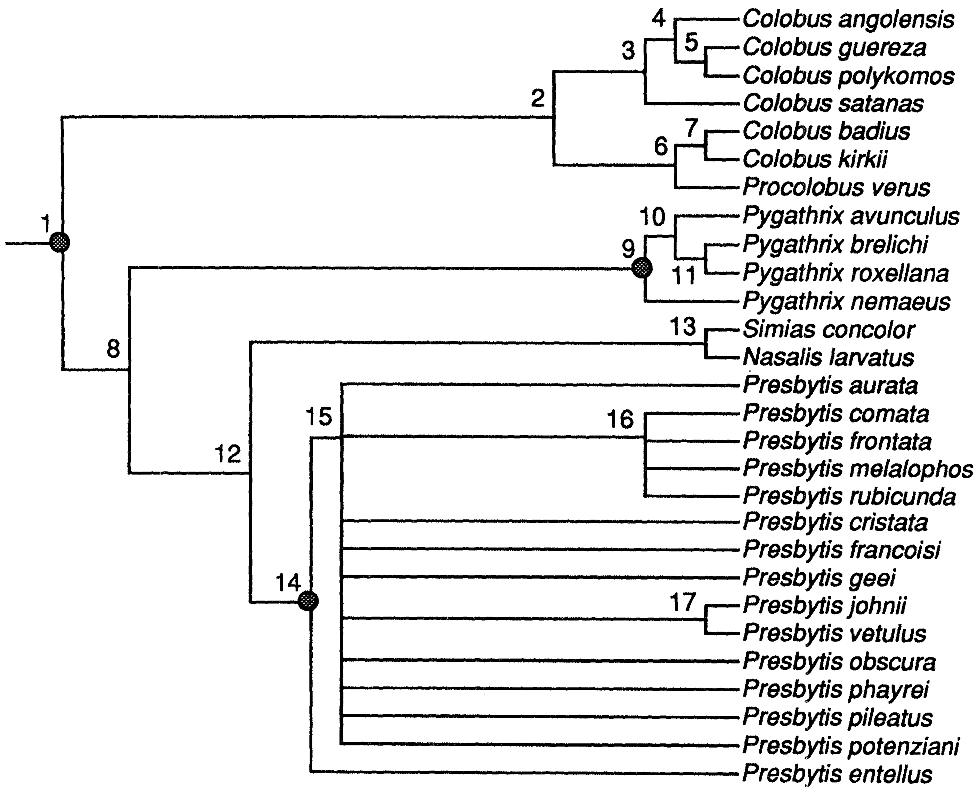

Figure 7. The composite tree for the Colobinae. Node numbers refer to table 5.

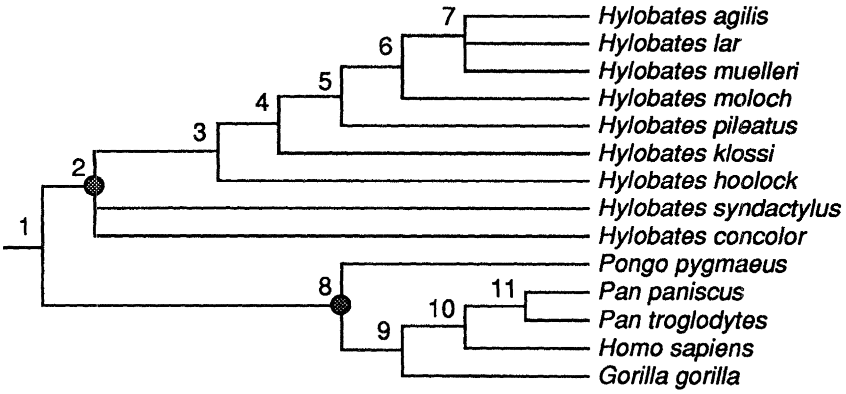

Figure 8. The composite tree for the Hylobatidae, Pongidae and Hominidae. Node numbers refer to table 6.

Table 1. *The major groups and* Tarsius

(Node numbers refer to figures 3–8; *n*, number of estimates from which medians and means were calculated; s.e., standard error of the mean; bootstrap, bootstrap proportion as judged from 100 bootstrap replicates; weight 2? and weight 8? indicate whether a node was also present in the most parsimonious tree when weighting schemes of 2:1 and 8:1 were used instead of 4:1 (parentheses indicate that all relevant characters had the same weight); equal? indicates whether the clade was present when taxonomic information was not considered and the remainder weighted equally. The last four columns have no meaning for those nodes where I assumed monophyly. See text for further explanation. See also figure 3.)

node	*n*	median	mean	s.e.	bootstrap	weight 2?	weight 8?	equal?
1	3	57.50	57.17	1.74	NA	NA	NA	NA
2	6	52.10	49.61	3.00	98	yes	yes	yes
3	0	—	—	—	NA	NA	NA	NA
4	0	—	—	—	72	(yes)	(yes)	yes
5	0	—	—	—	73	(yes)	(yes)	yes
6	4	40.50	39.88	3.39	100	yes	yes	yes
7	2	27.50	27.50	4.50	100	yes	yes	yes
8	4	14.38	14.65	1.14	97	yes	yes	yes

Table 2. *Strepsirhini*

(See also figure 4.)

node	*n*	median	mean	s.e.	bootstrap	weight 2?	weight 8?	equal?
1	8	45.11	41.79	3.46	NA	NA	NA	NA
2	1	39.62	39.62	—	85	yes	yes	yes
3	1	20.00	20.00	—	88	yes	yes	yes
4	2	16.64	16.64	5.01	96	yes	yes	yes
5	1	14.04	14.04	—	51	yes	yes	yes
6	1	10.92	10.92	—	57	yes	yes	yes
7	1	8.19	8.19	—	97	yes	yes	yes
8	1	10.43	10.43	—	98	yes	yes	yes
9	2	8.51	8.51	3.30	50	yes	yes	no
10	0	—	—	—	48	yes	yes	no
11	0	—	—	—	55	yes	yes	no
12	1	18.60	18.60	—	78	yes	yes	yes
13	1	14.00	14.00	—	79	yes	yes	yes
14	0	—	—	—	98	yes	yes	yes
15	0	—	—	—	80	yes	yes	yes
16	1	30.68	30.68	—	NA	NA	NA	NA
17	1	10.23	10.23	—	45	no	yes	yes
18	0	—	—	—	88	yes	yes	yes
19	0	—	—	—	64	yes	yes	no
20	0	—	—	—	71	yes	yes	no
21	2	22.11	22.11	0.72	93	yes	yes	yes
22	1	1.86	1.86	—	NA	NA	NA	NA
23	0	—	—	—	51	(yes)	(yes)	no
24	0	—	—	—	85	(yes)	(yes)	no
25	0	—	—	—	76	(yes)	(yes)	no
26	0	—	—	—	78	(yes)	(yes)	no
27	0	—	—	—	65	(yes)	(yes)	no
28	1	10.38	10.38	—	NA	NA	NA	NA
29	2	11.95	11.95	1.94	62	yes	yes	no
30	0	—	—	—	66	no	yes	no
31	1	2.70	2.70	—	92	yes	yes	yes

weighting scheme do not take into account the strength of support for different nodes in the source tree. Despite this conservatism, the bootstrap proportions can still give an indication of which nodes are more strongly supported than others. Generally, older nodes are more robust: there is relatively little disagreement about relations among most families. At lower taxonomic levels, however, estimates are often based on only a small body of work and are much more tentative.

Use of different weighting schemes provides an alternative indication of robustness. As tables 1–6 indicate, only ten nodes from the composite tree were not found if a weighting factor of 2 was used in place of 4, and only four nodes were affected if the weighting factor was 8. One referee felt that taxonomic information should not be used, and that equal weighting would be preferable. Rejection of taxonomic information makes the composite tree considerably less well resolved (largely because many species have never been included in other kinds of study and so had to be excluded from the analysis). As the last column in tables 1–6 shows, 42 of the nodes in the composite tree are not found under that weighting scheme. However, there are only four points of conflict: the analysis suggested by the referee groups *Galago senegalensis* with *G. granti*, *Nycticebus* with *Loris*, *Arctocebus* with *Perodicticus*, and *Saguinus* with *Leontopithecus*. In all other cases, the difference between the trees is that the one presented in figures 3–8 is more resolved.

Many source trees list higher taxa, rather than individual species, as terminals. Such source trees assume the monophyly of the higher taxon, and so may have caused fewer genera to appear paraphyletic than is really the case.

Estimates of dates: distribution, uncertainty and robustness

The 90 dated nodes are not spread evenly across the tree. Again, least is known about colobines (only 4 of 17 nodes dated), whereas the 15 estimates of the timing of the human–chimp divergence are far from an exhaustive survey of published estimates. Seven of the date estimates imply that a node is older than the previous one; such negative branch lengths can arise because different nodes are often used to calibrate the local molecular clock estimates of different dates. The negative branch lengths are always small compared with the age of the node, except within the genus *Cercopithecus*. There, a node dated at 0.62 million years ago is ancestral to several nodes estimated to be more than 3 million years old. If 'global' clocks were used instead, negative branch lengths would be more likely.

Table 3. *Cebidae + Callitrichidae*

(See also figure 5.)

node	*n*	median	mean	s.e.	bootstrap	weight 2?	weight 8?	equal?
1	5	32.19	28.76	4.95	NA	NA	NA	NA
2	0	—	—	—	16	no	no	no
3	3	34.50	32.19	3.09	67	yes	yes	yes
4	5	13.41	15.55	1.76	NA	NA	NA	NA
5	4	13.50	13.51	4.13	72	yes	yes	yes
6	2	9.50	9.50	3.50	39	yes	yes	no
7	4	4.51	5.08	1.13	99	yes	yes	yes
8	1	6.72	6.72	—	88	yes	yes	yes
9	1	2.65	2.65	—	87	yes	yes	yes
10	0	—	—	—	95	yes	yes	yes
11	0	—	—	—	85	yes	yes	yes
12	1	5.72	5.72	—	NA	NA	NA	NA
13	0	—	—	—	27	yes	yes	no
14	0	—	—	—	32	yes	yes	no
15	0	—	—	—	76	yes	yes	yes
16	0	—	—	—	59	yes	yes	no
17	0	—	—	—	61	yes	yes	no
18	0	—	—	—	83	yes	yes	yes
19	1	1.79	1.79	—	48	yes	yes	no
20	0	—	—	—	63	yes	yes	no
21	1	21.00	21.00	—	78	yes	yes	yes
22	1	17.88	17.88	—	NA	NA	NA	NA
23	1	8.94	8.94	—	66	yes	yes	yes
24	0	—	—	—	94	yes	yes	yes
25	0	—	—	—	NA	NA	NA	NA
26	1	14.00	14.00	—	54	yes	no	yes
27	1	8.64	8.64	—	NA	NA	NA	NA
28	1	7.30	7.30	—	NA	NA	NA	NA
29	0	—	—	—	60	(yes)	(yes)	no
30	0	—	—	—	40	(yes)	(yes)	yes
31	0	—	—	—	54	(yes)	(yes)	no
32	0	—	—	—	74	(yes)	(yes)	yes
33	0	—	—	—	84	(yes)	(yes)	yes
34	0	—	—	—	70	(yes)	(yes)	yes
35	2	23.00	23.00	5.00	50	yes	no	yes
36	3	8.05	9.45	1.79	100	yes	yes	yes
37	0	—	—	—	NA	NA	NA	NA
38	1	5.98	5.98	—	98	yes	yes	yes
39	0	—	—	—	59	yes	yes	no
40	3	15.00	15.09	1.08	99	yes	yes	yes
41	1	3.98	3.98	—	NA	NA	NA	NA
42	3	14.00	14.12	2.44	95	yes	yes	yes
43	2	8.88	8.88	1.38	50	yes	no	no
44	0	—	—	—	NA	NA	NA	NA
45	1	1.33	1.33	—	74	(yes)	(yes)	yes
46	0	—	—	—	58	(yes)	(yes)	yes

Standard errors of the mean require at least two estimates of a date. However, most dates in tables 1–6 are based on a single estimate. It is possible to assess the average error associated with a single estimate by using a one-way analysis of variance (ANOVA), with node number as the grouping factor. Dates were logarithmically transformed (base 10) to equalize variance (otherwise estimates for older nodes have more scope for error). The pooled standard deviation for the logarithmically transformed estimates was 0.177; back-transformation indicates an average error margin of just over ±50%. Clearly, not too much reliance should be placed on single estimates.

An ANOVA on the absolute values of residuals (excluding nodes for which there was only a single estimate) indicates that there are differences among clades in the proportional error associated with each estimate ($F_{5,168} = 3.08$, $p = 0.011$). By inspection, cercopithecines have the highest proportional error. The large error margin is probably because cercopithecines radiated relatively recently: most of the dates are therefore small numbers and so errors that are small in absolute terms can still be proportionately large.

Because node ages are estimated with respect to the ages of older nodes, changes of an estimate may have ramifications for a cascade of nodes throughout the tree. Nodes against which the largest number of estimates are calibrated are the ape–Old World monkey divergence (39 calibrations), the colobine–

Table 4. *Cercopithecinae*

(See also figure 6.)

node	*n*	median	mean	s.e.	bootstrap	weight 2?	weight 8?	equal?
1	3	9.53	9.62	0.20	NA	NA	NA	NA
2	6	7.47	9.25	2.15	93	yes	yes	yes
3	1	5.00	5.00	—	NA	NA	NA	NA
4	2	2.37	2.37	0.62	70	yes	yes	no
5	2	2.99	2.99	1.24	35	yes	yes	yes
6	1	2.78	2.78	—	45	yes	yes	yes
7	2	2.13	2.13	0.39	44	yes	yes	yes
8	2	1.67	1.67	0.67	87	yes	yes	yes
9	2	1.02	1.02	0.01	62	yes	yes	yes
10	2	0.67	0.67	0.17	84	yes	yes	no
11	4	1.64	1.60	0.23	85	yes	yes	yes
12	4	0.89	1.43	0.58	91	yes	yes	yes
13	2	0.63	0.63	0.33	83	yes	yes	yes
14	3	0.75	1.13	0.62	38	yes	yes	yes
15	0	—	—	—	58	yes	yes	yes
16	0	—	—	—	58	yes	yes	yes
17	2	6.59	6.59	0.21	84	yes	yes	yes
18	1	6.72	6.72	—	73	yes	yes	yes
19	0	—	—	—	85	yes	yes	yes
20	1	3.19	3.19	—	69	yes	yes	yes
21	0	—	—	—	56	yes	yes	yes
22	0	—	—	—	81	yes	yes	yes
23	2	4.22	4.22	1.01	55	yes	yes	yes
24	4	0.77	1.36	0.77	NA	NA	NA	NA
25	1	0.58	0.58	—	74	(yes)	(yes)	yes
26	1	0.49	0.49	—	65	(yes)	(yes)	yes
27	2	5.20	5.20	0.60	NA	NA	NA	NA
28	1	4.00	4.00	—	70	yes	yes	no
29	0	—	—	—	35	yes	yes	no
30	1	3.00	3.00	—	45	yes	yes	yes
31	0	—	—	—	11	yes	yes	no
32	1	1.11	1.11	—	47	yes	yes	yes
33	1	0.62	0.62	—	29	yes	yes	no
34	1	3.38	3.38	—	71	yes	yes	yes
35	0	—	—	—	60	yes	yes	yes
36	0	—	—	—	65	yes	yes	yes
37	0	—	—	—	65	yes	yes	yes
38	1	0.25	0.25	—	88	yes	yes	yes
39	0	—	—	—	20	yes	yes	no
40	1	4.38	4.38	—	35	yes	yes	no
41	1	3.61	3.61	—	50	yes	yes	yes
42	1	2.59	2.59	—	91	yes	yes	yes
43	1	3.23	3.23	—	56	yes	yes	yes
44	0	—	—	—	65	yes	yes	no
45	0	—	—	—	63	yes	yes	no
46	0	—	—	—	66	yes	yes	no
47	0	—	—	—	55	yes	yes	yes

cercopithecine split (37), the first bifurcation within Cercopithecinae (28) and the catarrhine–platyrrhine divergence (20). It follows that the set of date estimates is most sensitive to changes in the estimates of these dates. However, few calibrations are made to nodes that have been dated from a single estimate: one node in *Macaca* is used in seven calibrations, but no other singly estimated node is used in more than four.

4. DISCUSSION

Because all of the information on which it is based has been published previously, the composite tree cannot contain any clades that have not been implied by any previous study. Discussion of the evidence supporting particular clades can therefore be found in the source papers (referenced in the appendix) and would be out of place here. However, the composite tree is a summary of findings on some controversial issues in primate systematics, and it is worth noting whether the clear majority of opinion is on one side. For instance, there is broad consensus that tarsiers are the sister clade of the monkeys and apes – the haplorhines are a monophyletic group – and that the orangutan is the outgroup to a chimp–human–gorilla clade. Also, the Callitrichidae make the other New World monkeys (often grouped together as Cebidae) paraphyletic in the composite tree and in all the

Table 5. *Colobinae*

(See also figure 7.)

node	n	median	mean	s.e.	bootstrap	weight 2?	weight 8?	equal?
1	3	8.85	9.27	1.75	NA	NA	NA	NA
2	0	—	—	—	89	yes	yes	yes
3	0	—	—	—	66	yes	yes	yes
4	1	0.23	0.23	—	57	yes	yes	yes
5	1	0.10	0.10	—	69	yes	yes	yes
6	0	—	—	—	58	yes	yes	no
7	0	—	—	—	49	yes	yes	no
8	1	4.50	4.50	—	95	yes	yes	yes
9	0	—	—	—	NA	NA	NA	NA
10	0	—	—	—	55	yes	yes	no
11	0	—	—	—	95	yes	yes	yes
12	0	—	—	—	52	no	yes	yes
13	0	—	—	—	99	yes	yes	yes
14	0	—	—	—	NA	NA	NA	NA
15	0	—	—	—	61	(yes)	(yes)	no
16	0	—	—	—	66	(yes)	(yes)	no
17	0	—	—	—	92	(yes)	(yes)	no

Table 6. *Hylobatidae + Pongidae + Hominidae*

(See also figure 8.)

node	n	median	mean	s.e.	bootstrap	weight 2?	weight 8?	equal?
1	12	18.22	17.58	1.34	100	yes	yes	yes
2	3	7.83	6.25	1.88	NA	NA	NA	NA
3	0	—	—	—	95	yes	yes	yes
4	0	—	—	—	83	yes	yes	yes
5	1	1.31	1.31	—	89	no	yes	yes
6	0	—	—	—	55	no	yes	yes
7	0	—	—	—	45	no	yes	yes
8	2	14.50	14.50	2.50	NA	NA	NA	NA
9	14	8.29	8.09	0.67	100	yes	yes	yes
10	15	7.01	7.04	0.42	80	yes	yes	yes
11	4	2.35	2.49	0.15	98	yes	yes	yes

bootstrap replicates, although the exact placement of the former is less certain. Elsewhere, opinion is more divided: the composite tree has Lemuridae paraphyletic, with *Lepilemur* as sister group of a *Daubentonia*–Indriidae clade; but *Lepilemur* groups with the other Lemurids in 13% of bootstrap replicates. *Daubentonia* is sister to the Indriidae in 79% of bootstrap replicates, but lies outside the Indriidae–*Lepilemur* clade in the remainder, without ever being linked particularly closely to any other taxon. Humans and chimps are sister groups in the composite tree and in 88% of bootstrap replicates, but chimps and gorillas form a clade in the remainder. Other issues were not addressed: several taxa (e.g. Strepsirhini, Callitrichidae) were assumed to be monophyletic for reasons given earlier.

Although the analysis presented here assumes that source trees are independent, they will not always be. Often, characters will be common to more than one study. Furthermore, the criteria for publication may affect the sample of source trees, if it is harder to publish trees that are either identical to received wisdom or wildly discrepant. The source trees are not therefore entirely independent 'votes' in the choice of composite phylogeny: as one referee put it, 'bandwaggoning, lobby groups and peddling of influence have all played their part'. This is undoubtedly true, but similar and other processes (see, for example, Doyle 1992) can also compromise the independence of characters within any single study.

The composite tree has 160 nodes. If branching has been dichotomous, there are therefore 42 nodes that are not shown in the composite tree. This 'unrecognised phylogeny' (Grafen 1989) need not invalidate comparative studies, provided that each node contributes only one piece of information to the final test (Grafen 1989; Harvey & Pagel 1991; Pagel 1992). Simulations (Grafen 1989; Purvis *et al.* 1994) show that methods retain reasonable power when trees are incompletely resolved.

Many comparative methods require estimates of the relative lengths of all the internodes in the estimate of phylogeny. For this purpose, it is possible to extrapolate from the available estimates. There are many ways one might do this. Losos (1990) spaced the nodes on a branch evenly along its length. Grafen (1989) suggests that the age of each node might be taken to be proportional to the number of species ultimately

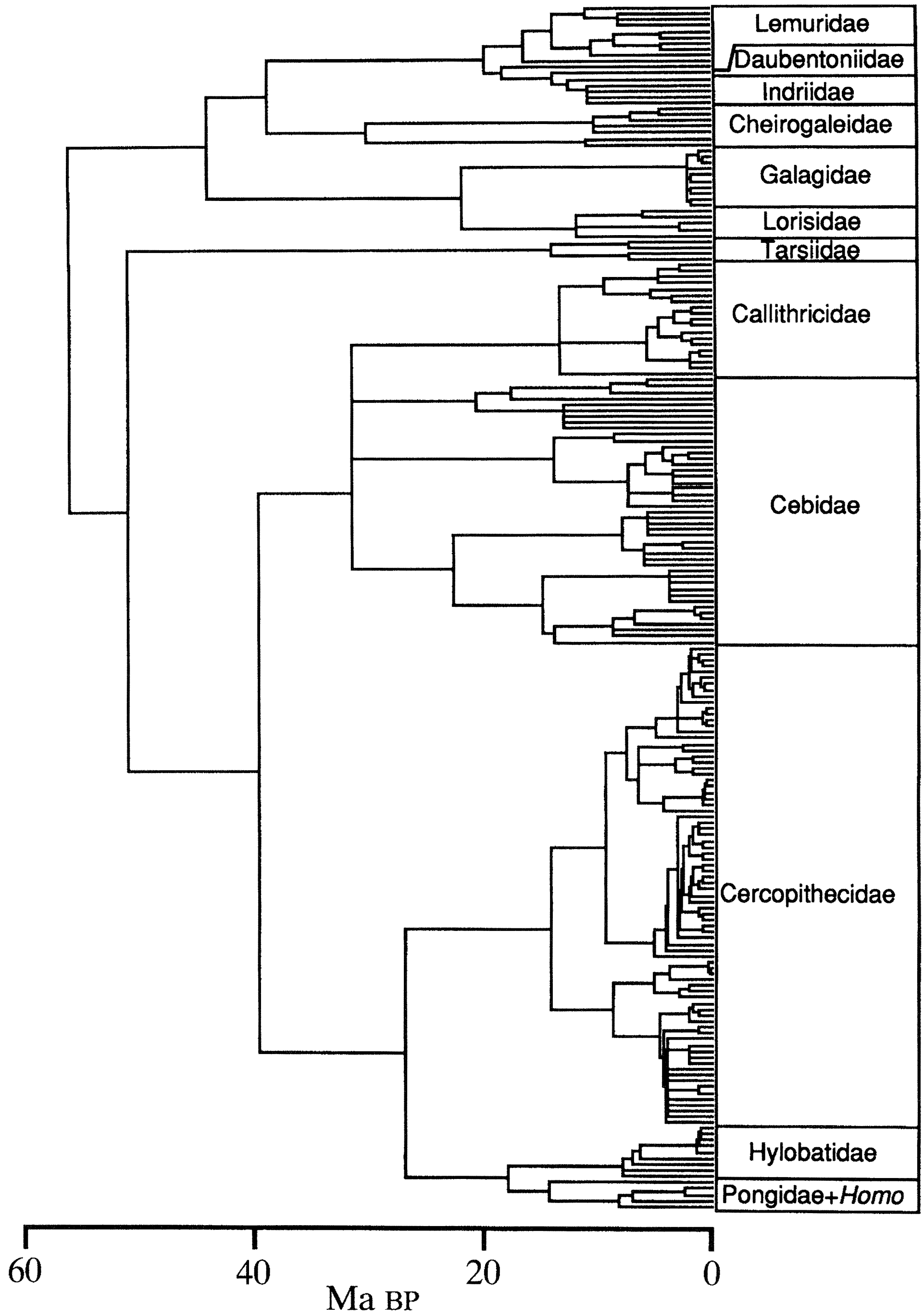

Figure 9. The composite tree for the whole order. Within major taxa, species are in the same order as in figures 3–8. Tables 1–6 give the node ages, where known. The remaining nodes had 'dates' assigned to them according to the method described in the text. Negative branch lengths are drawn as having zero length.

descended from it. S. Nee (personal communication) notes that models of cladogenesis as either a pure birth process or a random birth–death process would result in the ages of clades being proportional to the logarithm of the number of species they contain. In figure 9, I have used this suggestion to 'date' the unknown nodes relative to dated ancestral nodes, according to

$$\text{`date' of daughter} = \text{`date' of ancestor}\cdot\frac{\log\,(\text{daughter clade size})}{\log\,(\text{parent clade size})}.$$

The 'dates' produced in this way might be useful for comparative studies, though their efficacy should be tested when they are used (Garland *et al.* 1992). Figure 9 shows, in broad outline, the pattern of radiation of living primates. Martin (1993) points out that the very incomplete sampling of the fossil record means that ages of taxa based on fossil evidence will tend to be underestimates. All the dates in the phylogeny presented here are either based on or calibrated against fossil evidence; so they may all be too low. If fossil sampling is more or less uniformly incomplete, then dates should be underestimated by a roughly constant factor. Such a pattern would not invalidate the use of the phylogeny with comparative methods, which require only the relative lengths of branches. Additionally, simulations (Purvis *et al.* 1994) suggest that comparative methods are not greatly invalidated by even very inaccurate branch length information.

The estimate of phylogeny proposed in the paper is undoubtedly wrong in many details, of both branching order and branching times. It is, however, the first attempt to combine the evidence that has accumulated on the systematics of the whole order. It provides a useful starting point for comparative analyses and investigations of phylogeny shape. 'Meta-analyses' such as this are useful because they point out where broad agreement exists and where it does not, and so can serve as useful pointers for further research.

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APPENDIX

This appendix gives, for each assumed clade in turn, the binary characters corresponding to each source tree and the weights they were assigned.

Major groups and Tarsius (*see figure 3*)

Weight = 4. Baba *et al.* (1980); Clemente *et al.* (1990); Dutrillaux (1988); Hasegawa (1990); Hayasaka *et al.* (1988*a*); Koop *et al.* (1989); Miyamoto & Goodman (1990); Saitou (1991); Strasser & Delson (1988); Winkler (1984).

Weight = 1. Musser & Dagosto (1987); Sarich & Cronin (1980); Schwartz (1986); Szalay & Delson (1979); Wayne *et al.* (1991).

Strepsirhini (*see figure 4*)

Weight = 4. Absher (1993); Coppenhaver *et al.* (1988); Crovella *et al.* (1993); Darga *et al.* (1984); Dutrillaux (1988); Eaglen (1982, 1983); Groves & Eaglen (1988); Jung *et al.* (1992); Koop *et al.* (1989); Miyamoto & Goodman (1990); Pettigrew & Jamieson (1987); Porter *et al.* (1993); Rumpler *et al.* (1987, 1988); Schwartz & Tattersall (1988); Tattersall & Schwartz (1991); Yoder (1989, 1992, 1994).

Weight = 1. Dahl (1981); Dene *et al.* (1980); Goodman *et al.* (1974); Honacki *et al.* (1982); Nowak (1991); Olson (1979); Schwartz (1986); Schwartz & Tattersall (1985); Szalay & Delson (1979); Tattersall & Schwartz (1991); Zimmermann *et al.* (1988).

Platyrrhini (*see figure 5*)

Weight = 4. Baba *et al.* (1980); Darga *et al.* (1984); Dickinson *et al.* (1989); Dutrillaux (1988); Ford (1986); Galbreath (1983); Hershkovitz (1983); Jacobs (personal communication, 1993); Kay (1990); Kinzey (1992); Natori (1986, 1988, 1989, 1990); Rosenberger & Strier (1989); Schneider *et al.* (1993); Seuánez *et al.* (1989).

Weight = 1. Cheverud & Moore (1990); Chiarelli (1980); Cronin & Sarich (1978); Darga *et al.* (1984); Dickinson *et al.* (1990); Froehlich *et al.* (1991); Groves (1992); Hershkovitz (1987, 1988); Kaufman (1987); Martin (1992); Meireles *et al.* (1992); Moore & Cheverud (1992); Natori & Hanihara (1992); Schmitt *et al.* (1990); Schwartz (1986); Snowdon *et al.* (1986); Szalay & Delson (1979).

Cercopithecinae (*see figure 6*)

Weight = 4. Darga *et al.* (1984); Disotell *et al.* (1992); Dutrillaux (1988); Dutrillaux *et al.* (1982, 1988); Fooden & Lanyon (1989); Gautier (1988); Hayasaka *et al.* (1988*a*, *b*); Jablonski & Peng (1993); Melnick & Kidd (1985); Melnick *et al.* (1993); Nakamura *et al.* (1983, 1985); Ruvolo (1988); Stanyon *et al.* (1986); Strasser & Delson (1988); Zhang & Shi (1993).

Weight = 1. Colyn *et al.* (1991); Cronin & Meikle (1989); Delson (1980); Dugougon *et al.* (1989); Horn (1987); Lernould (1988); Lucotte (1982, 1983); Nozawa *et al.* (1977); Ruvolo (1988); Szalay & Delson (1979).

Colobinae (*see figure 7*)

Weight = 4. Jablonski & Peng (1993); Peng *et al.* (1993); Strasser & Delson (1988).

Weight = 1. Nowak (1991); Oates & Trocco (1983); Schultz (1986); Szalay & Delson (1979).

Hominoidea (*see figure 8*)

Weight = 4. Dunlap & Aziz (1985); Dutrillaux (1988); Gonzalez *et al.* (1990); Groves & Paterson (1991); Haimoff *et al.* (1982); Hasegawa (1990); Hixson & Brown (1986); Holmes *et al.* (1989); Holmquist *et al.* (1988); Izor *et al.* (1981); Koop *et al.* (1989); Marks (1993); Miyamoto & Goodman (1990); Saitou (1991); Schwartz (1985); Shea (1985); Stanyon *et al.* (1986); Templeton (1985); Ueda *et al.* (1989); van Tuinen & Ledbetter (1983, 1987).

Weight = 1. Creel & Preuschoft (1984); Groves (1984); Hayasaka *et al.* (1988*a*); Schmitt *et al.* (1990); Szalay & Delson (1979); Wayne *et al.* (1991).

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