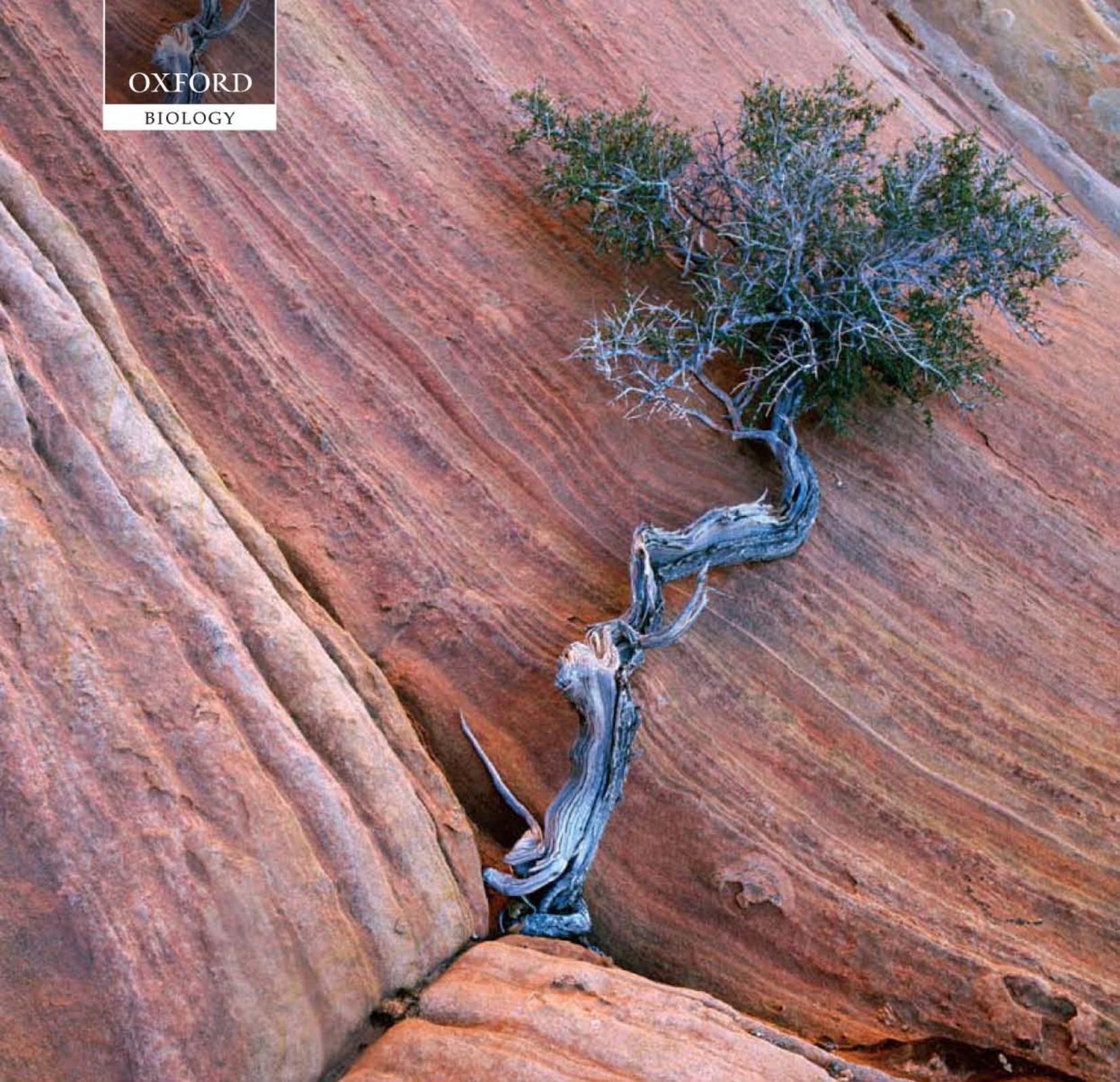


OXFORD  
BIOLOGY



*the* **TIMETREE** *of* **LIFE**

*edited by* **S. BLAIR HEDGES** *and* **SUDHIR KUMAR**  
*foreword by* James D. Watson

# Primates (Primates)

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## Abstract

**The Order Primates (ca. 350 species) consists of six major extant groups: lemurs, lorises, tarsiers, New World monkeys, Old World monkeys, and apes (including humans). These groups are organized into two suborders: strepsirrhines (lemurs, lorises) and haplorrhines (tarsiers, monkeys, apes, and humans). The timetree indicates that these two suborders diverged before the Mesozoic–Cenozoic boundary at about 78 million years ago (Ma), with individual families mostly diversifying during the later Paleogene (~45 Ma) and early Neogene (20 Ma).**

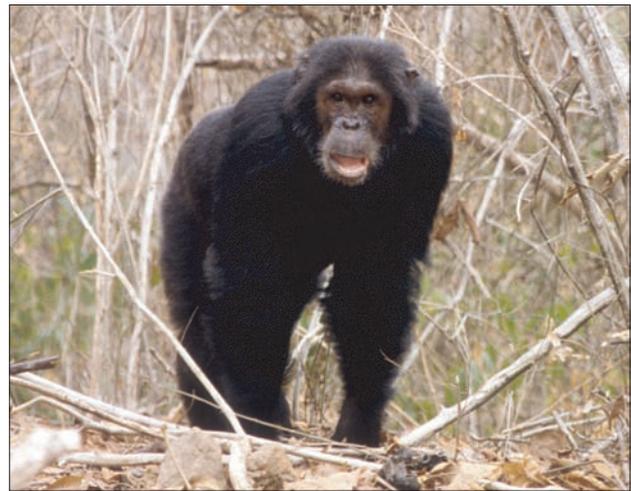
Living primates comprise an order of placental mammals characterized by forward facing eyes, a petrosal-derived auditory bulla, grasping hands and feet, nails instead of claws, a large brain relative to body size, and a slow life history (1). There are over 350 extant primate species (2) (Fig. 1). Aside from our own widely distributed species, primates are native to habitats throughout Central and South America, Africa, and Asia. Here, molecular divergence times of the 15 extant primate families (2) are reviewed.

Currently, there is general consensus on the overall shape and structure of the subordinal through family-level phylogeny of the primates, with some exceptions (Fig. 2) (3–6). Lemurs and lorises, collectively known as the strepsirrhines, are united by the presence of derived features including a toothcomb and grooming claw. Within the lemurs, there is as yet no consensus on the relationships among the five extant families, except that Daubentoniidae is likely to be the most basal taxon based on molecular evidence (7). Therefore, we represent the relationships among the remaining four families as

a polytomy and use the oldest date for included nodes given in each study (8–10).

The phylogenetic position of Tarsiidae is perhaps the most enigmatic within the primates. Tarsiers have been linked to strepsirrhines based on overall adaptive similarities (6). However, shared-derived morphological traits, such as a continuous lip, link this lineage with anthropoids (monkeys and apes) in the Suborder Haplorrhini (5). Although there is some discordance among molecular studies, recent work on short interspersed nuclear elements (SINEs) support a taxon Haplorrhini (11, 12), which we use here. Extant anthropoids, composed of platyrrhines (New World monkeys) and catarrhines (Old World apes and monkeys), have a fused mandibular symphysis and complete postorbital closure. Platyrrhines have broad nostrils, three premolars, and lack a tympanic tube.

In studies of platyrrhine molecular phylogenetics there is disagreement as to the most basal taxon (13), although SINEs support Pitheciidae in this role (14). Here we represent this node as a trichotomy and use the deepest date for that node. For Aotidae, we choose to place this family with Cebidae because these families are phylogenetically linked in most molecular studies, although its exact position remains unresolved (13).



**Fig. 1** A Chimpanzee (*Pan troglodytes*) from Gombe National Park, Tanzania. Credit: Martin N. Muller.

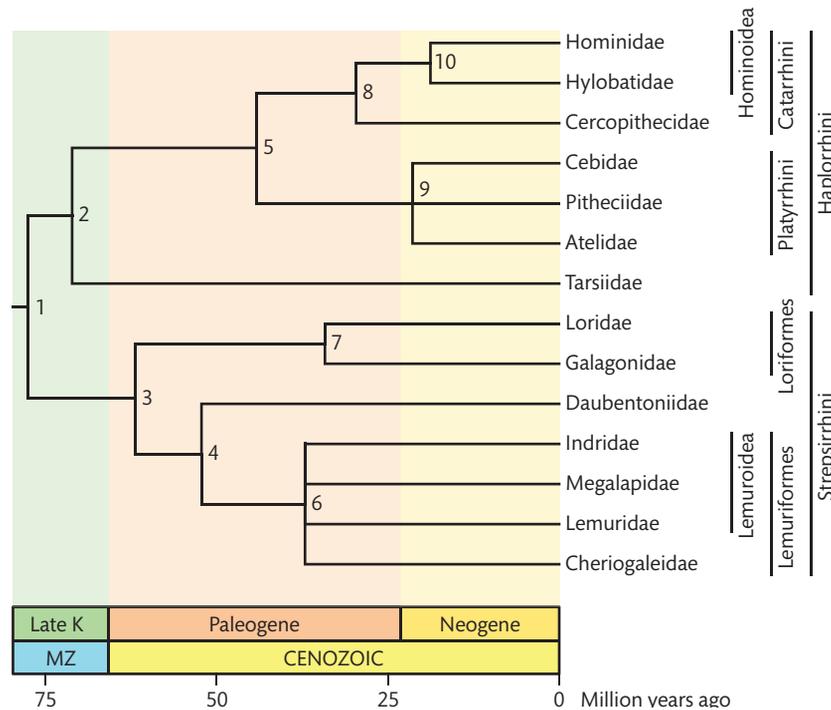


Fig. 2 A timetree of primates. Divergence times are shown in Table 1. *Abbreviations:* MZ (Mesozoic) and K (Cretaceous).

Catarrhines, composed of Old World monkeys (Cercopithecidae) and apes (Hominoidea; includes Hylobatidae and Hominidae), have narrow nostrils, a reduction in premolars, and a long and continuous tympanic tube. Cercopithecidae is distinguished by the presence of bilophodont molars and ischial tuberosities, whereas the hominoids lack tails and are larger bodied with relatively large brain size.

Beginning with its application to hominoids by Sarich and Wilson (15), the molecular clock approach has been widely applied to dating primate divergences. Despite this, few studies have comprehensively estimated all or most of the family-level nodes in a single analysis (3, 10, 16–18), focusing instead on resolving lower-level taxonomic units or areas of special interest (e.g., catarrhines, 19). Within primates, there is extensive evidence for lineage specific rate variation, for example, the “hominoid slowdown” (20–23). This complicates the usage of the molecular clock and requires methods for its useful application within primates, including removal of non-clocklike genes from analyses (e.g., 24), usage of “local-clocks” (e.g., 3), relaxation of a strict clock (e.g., 18) using the methods of Thorne *et al.* (25, 26), and/or application of multiple fossil calibration points (e.g., 10) (Table 1).

Although the oldest fossils bearing on the earliest divergence among living primates (divergence of strepsirrhines and haplorrhines) are known from the Paleocene and earliest Eocene (27), molecular clock studies continue to place that divergence event in the Upper Cretaceous (77.5 Ma) (3, 10, 16–18, 28–30). Many of these studies analyzed samples of genes from throughout the nuclear and mitochondrial genomes using a Bayesian dating method. These studies employed a range of fossil calibrations to date the crown primate node, including dates from outside of the primate radiation (28, 30), and both in- and outside of primates (16–18). Other studies chose to at least partly calibrate their trees within primates, at the strepsirrhine/haplorrhine divergence (3, 10, 29, 31). A date based solely from studies that did not constrain the node being timed results in a similar estimate (78.9 Ma vs. 77.5 Ma). A Cretaceous estimate for this node is also consistent with a date derived from a model based on primate fossil preservation (32).

The deepest divergence between the major extant strepsirrhine lineages is dated to 61.9 Ma, which is close to the Mesozoic–Cenozoic boundary (66 Ma). However, the earliest representatives of strepsirrhines are only known from the earliest part of the late Eocene (33,

**Table 1.** Divergence times (Ma) and 95% confidence/credibility (CI) intervals among primates.

Timetree		Estimates										
Node	Time	Ref. (3)	Ref. (18)		Ref. (10)		Ref. (28)	Ref. (17)		Refs. (29, 50)	Ref. (16)	
		Time	Time	CI	Time	CI	Time	Time	CI	Time	Time	CI
1	77.5	63	77.5	93–66	84.9	90–77	73.1	77.2	96–63	78.9	87.7	88–85
2	71.1	58	-	-	-	-	70.2	-	-	-	85.0	85–82
3	61.9	50	57.1	69–48	68.5	75–61	-	59.6	75–48	60.4	75.5	76–71
4	52.2	45	-	-	62.0	73–58	-	-	-	49.6	-	-
5	44.2	45	42.9	51–36	49.4	56–44	37.5	43.6	50–37	37.0	54.1	54–50
6	37.1	28	40.9	51–32	42.3	50–35	-	-	-	-	-	-
7	34.2	23	-	-	39.1	42–38	-	-	-	-	40.5	41–32
8	29.6	25	30.5	36–26	34.7	38–32	25.5	28.1	34–24	26.8	36.6	37–34
9	21.4	25	20.8	26–17	-	-	-	20.1	25–15	16.8	24.5	25–21
10	18.8	18	-	-	-	-	15.6	17.9	23–14	-	23.5	24–22

Note: Node times in the timetree represent the mean of time estimates from different studies. The time estimates of Goodman *et al.* (3) are based on globin and IRBP sequence data with the calibrations given. No CIs were indicated. Steiper and Young (18) used an alignment of contiguous genomic sequence data with calibrations from within and outside of primates. Credibility intervals are given. Yoder and Yang (10) used multiple independent mitochondrial and nuclear data sets in the context of calibrations including primates (90.0–63.0 Ma), Galagonidae–Loridae (42.0–38.0 Ma), and Catarrhini (38.0–32.0 Ma). Non-primate calibrations were also used. Credibility intervals are given. Hasegawa *et al.* (28) reanalyzed the data of Murphy *et al.* (49), which comprises multiple independent mitochondrial and nuclear data sets, using non-primate calibrations. Eizirik *et al.* (17) also analyzed the data set of Murphy *et al.* (49), but with additional taxa. Calibrations included 50.0–36.0 Ma for the anthropoid node, <26.0 Ma for the platyrrhine node, and >23.0 Ma for the catarrhine node. The 95% confidence intervals are given. Both Poux *et al.* (29, 50) studies used multiple independent mitochondrial and nuclear data sets, in the context of a calibration at the root primate node from 90.0 to 63.0 Ma and a host of non-primate calibrations. In one of the two studies a hominoid–cercopithecoïd calibration was also used (35.0–32.5 Ma) (50). Bininda-Emonds *et al.* (16) dated a very large and taxon-rich data set comprising multiple independent mitochondrial and nuclear loci and multiple calibrations, including a >44.5 Ma date for the haplorhine node.

34). Among the Malagasy primates, studies yielded an average estimate of 52.2 Ma for the deepest divergence of Daubentoniidae from the remaining lemur families. The deepest node within the remaining four families of lemurs is dated to 37.1 Ma, also based on three studies. Two of these converged at similar dates using different calibration points and data sets [40.9 Ma (18, 35) and 42.3 Ma (10)]. The divergence of Loridae and Galagonidae is estimated at 34.2 Ma. This result is particularly interesting because the aforementioned fossils (*Karanisia* and *Saharagalago*) belong to the Loriformes and are dated to ~37 Ma (33, 34). This is the only example where fossil evidence for a taxon antedates the mean given in Table 1. However, this divergence may have occurred earlier than 34.2 Ma. Only three of the studies estimated a date for this node and one used a calibration point for the strepsirrhine/haplorrhine divergence of 63.0 Ma (3), which may be too young. Indeed, although Yoder and Yang (10) calibrated the divergence of Loridae and Galagonidae at 42.0–38.0 Ma based on this fossil evidence, in an earlier study where this divergence was not constrained, they

estimated the node at 40.5 Ma (8). Based on all of the evidence, this divergence date is likely to be closer to ~40 Ma.

The earliest divergence within haplorrhines is estimated to be 71.1 Ma. The oldest members of Tarsiidae, *Tarsius eocaenus* and *Xanthorhysis*, are dated to the middle Eocene, ~45 Ma, while the earliest stem anthropoid, *Eosimias*, is similar in age (36, 37). Therefore, the molecular estimate for the divergence date of this node is at least 20 Ma older than the earliest fossil evidence. This suggests that the diversification of primates belonging to living groups may have occurred substantially within the Cretaceous, opening a range of interesting biogeographical questions (38).

Based on eight studies, anthropoids are estimated to have split into Platyrrhini and Catarrhini at 44.2 Ma. The earliest catarrhine is *Catopithecus* (35–34 Ma) (33) and the earliest platyrrhine is *Branisella* (26–25 Ma) (39). The oldest members of the living platyrrhine radiation come from the early Miocene of South America (6) and a date of 21.4 Ma for the divergence of the living families of

platyrrhines fits well with these fossil data. The estimate for the split of platyrrhines from catarrhines at ~44 Ma and the diversification of the living platyrrhine families at ~21 Ma indicates that the ancestor of New World monkeys migrated to South America sometime during this period. This is particularly interesting, as South America was an island continent during this time. While it is unresolved whether platyrrhine primates derive from North America or Africa, current evidence favors the latter (6).

The divergence of the catarrhine groups Hominoidea and Cercopithecoidea is estimated to have occurred 29.6 Ma. The oldest cercopithecoids are *Victoriapithecus* and *Prohylobates*, dated from the early to middle Miocene, 19–12 Ma (40), while the oldest hominoids are *Proconsul* and *Morotopithecus*, both dated to ~20 Ma (41, 42). The fossil record of Africa between 29 and 21 Ma contains few good localities preserving primates. A single hominoid-like fossil (*Kamoyapithecus*) is dated 27.8–23.9 Ma (43), but the affinities linking this specimen to apes are not diagnostic, making its relevance unclear. Within hominoids, Hylobatidae is estimated to have diverged from Hominidae at 18.8 Ma.

The molecular estimates reported here are generally concordant with each other and for the most part are consistent with a timetree based on fossils. However, there are some nodes where molecular estimates greatly exceed the earliest fossil evidence of a taxon. For example, both crown primates and haplorrhines are estimated to originate before the Mesozoic–Cenozoic boundary, while hominoids and cercopithecoids are estimated to have diverged in the earlier part of the Oligocene (~30 Ma). In these instances, molecular estimates are anywhere from 20% to 30% older than those derived from fossil evidence. There are several nonexclusive and potentially overlapping reasons for this result. Critical portions of the fossil record may be undersampled (44), taxa may lack recognizable characters near their origins (45), and homoplasy may make diagnostic traits unreliable (e.g., 46). Alternatively, current molecular estimation techniques may not accurately model important sources or patterns of rate variance that differentially affect these particular nodes (e.g., 47, 48). A combination of paleontological fieldwork targeted on underrepresented portions of the fossil record and empirical research on rates of molecular evolution will help to resolve these areas of contention.

## Acknowledgment

We thank E. Seiffert for comments.

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