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Fossil New World Monkeys Dispute the Molecular Clock

New World monkeys offer an empirical test of the accuracy of molecular clocks. A phylogenetic reconstruction based upon craniodental morphology suggests that platyrrhine clades and generic lineages are far older than albumin and transferrin "clocks" indicated. It is unjustified to accept the molecular clock's timescale when protein and morphological evidence do not generate symmetrical cladograms. Such a dichotomy in evidence for New World anthropoids exists and, by implication, casts doubt upon molecular divergence dates of Old World monkeys, apes and hominids.

Ever since it was first introduced by Sarich & Wilson (1967), the molecular clock of primate evolution, which projects the divergence times of living lineages based upon their immunological differences, has received criticism from various disciplines (e.g., Lovejoy *et al.*, 1972; Read, 1975; Korey, 1981; Goodman, 1976). Because paleontology offers the most direct empirical test of such historical hypotheses, the molecular clock's timing of adaptive radiations has been independently checked against the fossil record of hominoid apes and hominids (Simons, 1976; Uzzel & Pilbeam, 1971; Walker, 1976), cercopithecine Old World monkeys (Cronin & Meikle, 1982) and the broad outlines of Cenozoic primate evolution (Romero-Herra *et al.*, 1978). Although the consensus once claimed that the albumin-transferrin clock seriously underestimated divergence dates, a rethinking of hominoid evolution during the past few years has forced a turnabout among paleoanthropologists. Many now tend to agree with the basic framework of an adjusted immunological timescale (Andrews, 1982; Pilbeam, 1982) which places the origin of hominids at about 5 ± 1 million years (Myr) ago (Pilbeam, 1984; Greenfield, 1980; Cronin & Sarich, 1975; Sarich & Cronin, 1980).* Implicit in this new perception of the resolving power of proteins is the thought that primate paleontology is incapable of testing the central doctrine of the molecular clock hypotheses, that biomolecular differences among extant species are directly proportional to the time elapsed since common ancestry. If this theorem is true, then independently developed, "correct" cladograms must be symmetrical with a biomolecular tree and the fossil record should accord with its timescale.

The paleontological evidence of New World monkey phylogeny suggests that the timescale for their evolution set by the molecular clock is, in fact, inaccurate. This may have special significance for evaluating controversies regarding splitting times and for calculating protein evolutionary rates within the primate order because neotropical monkeys provide a superior test of biomolecular models for a number of reasons. Represented by some sixteen modern genera, they are more diverse taxonomically than the extant hominoids and cercopithecoids, which number about five and eleven genera, respectively (Szalay & Delson, 1979). Anatomically and adaptively, the neotropical

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* While quoted divergence dates still vary among authors, Pilbeam (1984), for one, observed that "The earlier debate between physical anthropologists and molecular biologists over the pattern and timing of hominoid evolution is now basically settled" (p. 85).

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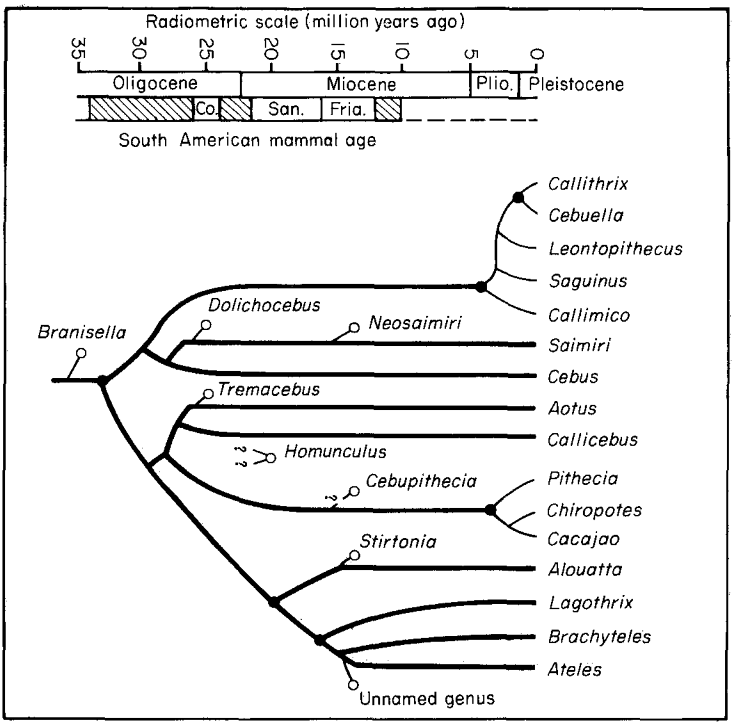
platyrrhines are considered to surpass the collective variety of the Old World anthropoids (Schultz, 1970). This increases the reliability of genealogical reconstructions, being less hampered by disguising parallelisms and the primitive retentions that are of lesser value than share derived homologies. Such diversity also offsets the fact that the platyrrhine fossil record is still quite meager: in spite of its richness, it is the very uniformity of form which makes the systematics of hominoids so difficult. Finally, the platyrrhines are the product of a single, long lasting adaptive radiation spanning at least 35 Myr, and many surviving genera can be traced paleontologically well into the Tertiary. The living catarrhines comprise two arrays, neither having exceptional temporal depth. In fact, in only two cases can lineal and collateral relatives of extant Old World apes and monkeys be confidently recognized before the Pliocene Epoch (Delson & Rosenberger, 1984).

Dating the history of platyrrhine differentiation is now possible due to a vastly improved calibration of South American Land Mammal Ages (Marshall, Pascual *et al.*, 1977) and recent advances in our knowledge of their morphology (Hershkovitz, 1970; 1977) and genealogy (Rosenberger, 1977, 1980, 1981*a*). Six to eight relevant fossils whose affinities are considered well delineated permit the development of a paleontological time scale (Figure 1). Several of these may actually be ancestral to modern genera (Delson &

Figure 1. The genealogical relationships of extant New World monkey genera and fossils relevant to the timing of their differentiation. Estimated ages of fossils based upon their corresponding South American land mammal ages. Thick lines denote lineages with durations fixed by the fossil record; thin lines represent lineages without a real time framework, shown here for cladistic significance. Black circles mark the monophyletic groups agreed upon by both morphological and albumin-transferrin data.



Rosenberger, 1984) but I here take the conservative view that they are only sister-taxa for illustrative purposes. It should be noted that my phylogram markedly disagrees with the genealogy implied by the albumin-transferrin dendrogram (Cronin & Sarich, 1975; Sarich & Cronin, 1980). Indeed only six nodes defining the cladistic affinities of the living coincide, and one of these refers merely to the monophyly of the platyrrhines themselves. Whereas four major lineages are suggested by the comparative anatomy, the biomolecular interpretations calls for no less than seven independent lineages, all unrooted. This is a high percentage given the number of taxa sampled and their relatively low hierarchical level.

Of the four major groups that I recognize, the callitrichine (Szalay & Delson, 1979) marmosets are still without any fossil representatives. The immunological data posits their diversification from a common ancestor at about 10 Myr ago, well after the inferred origin of the lineage at 17 Myr ago. Indirect paleontological and cladistic analysis places the differentiation of callitrichines prior to 25 Myr ago, however (Rossenberger, 1979). This is demonstrated by the late Oligocene appearance of *Dolichocebus,* the earliest close relative of *Saimiri.* Along with *Dolichocebus, Cebus* and *Saimiri* (and *Neosaimiri,* see below) form the sister-group of the callitrichines (Szalay & Delson, 1979; Rosenberger, 1979). Since a large body of morphological and behavioral data conflict with the biomolecular interrelationships of four out of the five marmoset genera (Hershkovitz, 1977; Rosenberger, 1977, 1980, 1981*a*; Rosenberger & Coimbra-Filho, 1985), it is likely that cladistic errors have adversely affected both of the dates projected by the molecular clock.

The branching sequence of the atelines appears to pose no serious conflicts, although *Brachyteles* has not been sampled immunologically. Nevertheless, paleontological data points dispute the more recent dates given by the clock. *Stirtonia tatacoensis,* from the Colombian middle Miocene, about 15 Myr ago, is widely accepted as morphologically highly similar (Hershkovitz, 1970) and very closely related to the howler monkey (Szalay & Delson, 1979; Delson & Rosenberger, 1984; Setoguchi *et al.,* 1981). Both are characterized by an unmistakable, highly derived folivorous dental complex. This makes the *Alouatta* lineage about 5 Myr older than its molecular divergence data. New material from the same La Venta locality now being described by Dr T. Setoguchi, comes from a species more closely related to the spider monkeys than is any other ateline. It bears the indelible, derived stamp on an *Ateles*-like molar pattern. This evidence, combined with the contemporaneous presence of howler monkey relatives, makes it highly unlikely that the *Lagothrix-Ateles* split could have occurred as recently as the 4–5 Myr ago indicated by the molecular clock. The monophyletic (Szalay & Delson, 1979; Rosenberger, 1981*a*) saka-uakari clade, *Pithecia-Chiropotes-Cacajao,* are of late origin as well, according to the biomolecular view. The La Ventan *Cebupithecia sarmientoi* has some relevance here. Although its systematic position is still not clear (Delson & Rosenberger, 1984), the genus is earmarked by most of the derived features of the peculiar saki-uakari feeding mechanism (Szalay & Delson, 1979; Rosenberger, 1977). Since *Chiropotes* and *Cacajao* are somewhat more derived than either *Pithecia* (Pocock, 1925) or *Cebupithecia,* the fossil may logically occupy different positions on the phylogram. All of them confirm that this lineage is more than 15 Myr ago in age.

The anatomical and protein data are in serious conflict regarding the phylogenetic interpretations of the four remaining living genera. Nevertheless, the comparative anatomy strongly supports a monophyletic *Cebus-Saimiri* clade (Rosenberger, 1981*a*; Pocock, 1925) and another for *Aotus* and *Callicebus* (Pocock, 1925). Both are represented by good fossil material. *Tremacebus harringtoni,* from late Oligocene Patagonian deposits, reveals several derived orbital characters shared with the night monkey, *Aotus,* as well as some synapomorphic facial features (Fleagle & Rosenberger, 1983). This extends the duration of the *Aotus* lineage, and its unique adaptive shift toward nocturnality, to about 25 Myr ago. The La Ventan *Neosaimiri fieldsi* and the Colhuepahipan late Oligocene *Dolichocebus gaimanensis* show derived dental (Szalay & Delson, 1979; Delson & Rosenberger, 1984) and cranial (Rosenberger, 1979; Fleagle & Rosenberger, 1983) similarities, respectively, to the squirrel monkeys, *Saimiri.* Obviously, the sister-taxa of each of these enduring generic lineages, leading to the extant *Cebus* and *Callicebus,* must be equally as old. The phylogenetically ambiguous genus *Homunculus,* possibly related to *Callicebus* or some other segment of this cladistic division (Pocock, 1925), confirms the group's relative antiquity. Although the absolute dates given by the molecular clock fall short in this comparison too, there may be an important commonality in that both approaches agree that the origins of each of the four genera are quite ancient.

Finally, the differentiation of the monophyletic modern platyrrhines appears to have occurred significantly earlier than the 20 Myr ago predicted by the clock. Both *Tremacebus* and *Dolichocebus* provide solid evidence for this. Still, one cannot be very precise about the timing of this event. *Branisella boliviana* appears in the early Oligocene, about 35 Myr ago, but its affinities are debatable (Szalay & Delson, 1979; Hershkovitz, 1977). Although undoubtedly a platyrrhine, *Branisella* may represent a lineage apart from what the mainstream of ceboid evolution (Rosenberger, 1981*b*). Therefore, the ultimate ancestor of the New World monkeys must have lived prior to the early Oligocene, but the last common

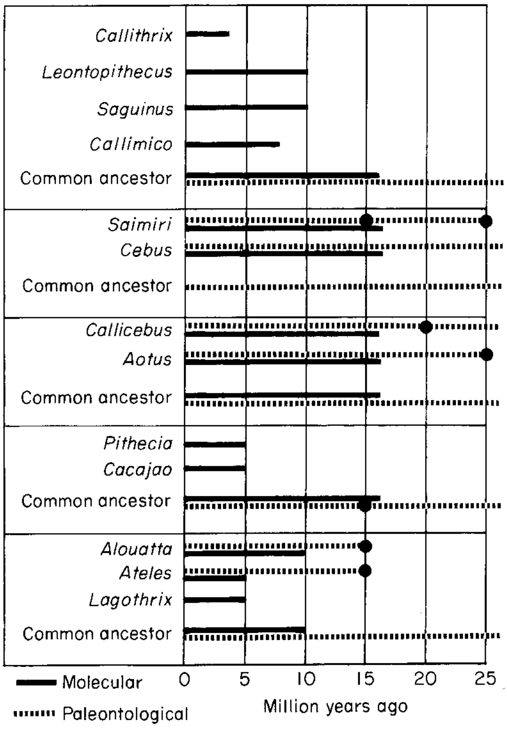


Figure 2. A comparison of the splitting times determined from the fossil record with those generated immunologically. Molecular dates were estimated from the dendrogram of Sarich & Cronin (1980). Paleontological ages of hypothetical common ancestors were inferred by bracketing the known ages of reference fossils (black circles). See text for their identification. *Homunculus* is here shown in its possible position as a sister-taxon to *Callicebus. Cebupithecia* is shown as affirming the minimal age of origin for the *Pithecia-Cacajao* clade.

ancestor of the extant forms could have appeared sometime between that point and 25 Myr ago.

Molecular clocks are dependent upon the fossil record for calibration. When comparing a molecular clock of New World monkey evolution scaled against the estimated first appearance of primates 60–70 Myr ago (Pilbeam, 1984; Cronin and Sarich, 1975), with the known fossil evidence, major inconsistencies in splitting times are apparent (Figure 2). Some discrepancies are probably due to contradictory phylogenetic hypotheses, while others could be reflecting varying evolutionary rates of proteins within lineages. Since no other group of anthropoids presents such a rich temporal and taxonomic spread of paleontological points, the New World monkeys are an ideal baseline for rescaling hominoid albumin and transferrin clocks, thereafter, reassessing hominoid divergence.

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