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Are There Any Anthropoid Primate Living Fossils?

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Introduction

The concept of "living fossil" as employed by Simpson (1953) and others has been somewhat altered for the purposes of this volume. As we understand it, the implication is of a living taxon that differs only slightly if at all in known morphology from an early fossil member of its clade, at whatever taxonomic rank. In this spirit, we will examine the "higher" or anthropoid primates to determine if any taxa, including some previously suggested, qualify for this status. Following Szalay and Delson (1979), the Order Primates is divided into three suborders, the extinct Plesiadapiformes, the Strepsirhini (lower primates), and the Haplorhini, including the infraorders Tarsiiformes (tarsiers and fossil relatives—see Schwartz, this volume), Platyrrhini (New World anthropoids), and Catarrhini (Old World anthropoids). The formal taxon Anthropoidea was not recognized in order to reduce the number of ranks allowed, but it may be considered a hyporder (between suborder and infraorder; see Delson 1977) including Platyrrhini and Catarrhini. The nomen Simiiformes Hoffstetter 1974, may be substituted for Anthropoidea Mivart 1864, if desired, to avoid confusion with earlier contrasts between Anthropoidea and "Prosimii", a grade term including all non-anthropoids. We shall briefly review the evolutionary history of each anthropoid infraorder here, searching for taxa that may fall under the expanded living fossils rubric and commenting on any that have been implied as such previously; the contrasting patterns of evolution in these two groups will then be analyzed. Unless otherwise indicated, background material and references for this chapter may be found in Szalay and Delson (1979).

Evolution and Living Fossils Among the Catarrhini

The evolutionary record of the Old World anthropoids reveals a pattern of temporal replacement of one successful, radiating group by a distant "cousin." Briefly, the Oligocene parapithecids were more numerous and more diverse taxonomically than their relatively derived pliopithecid contemporaries (*Propliopithecus*, including *Aegyptopithecus*, species), but the former do not appear to have left any descendants or close relatives. During the Early and Middle Miocene, pliopithecids occurred rarely alongside a third radiation, the early Hominidae (Dryopithecinae or Proconsulinae) especially in Africa. By the Middle Miocene, two new groups arose that, for the first time, represent close relatives of living taxa: the modern-ape-like *Sivapithecus* group and the Cercopithecidae (Old World monkeys). One cercopithecid tooth is known from the Early

Miocene, and there are suggestions of links to some Oligocene taxa, but no morphology amenable to analysis is known until after 16 million years ago.

The *Sivapithecus* group is currently the subject of much debate (see papers in Ciochon and Corruccini 1983), and both its position in ape phylogeny and a meaningful family-group nomen within Hominidae are still uncertain. This group of species appeared in the later Middle Miocene, diversified in the earlier Late Miocene, and then essentially disappeared; it is clearly related to the Asian orangutan (Ponginae) but perhaps also to the African ape–human lineage (Homininae) of the Pliocene and Pleistocene. The later Late Miocene saw the diversification of the Cercopithecidae (and the brief flowering of the cercopithecoid *Oreopithecus*), with a peak in generic diversity probably occurring in the Late Pliocene. The sequence of replacement therefore might be seen as: Parapithecidae, Pliopithecidae, Dryopithecinae, *Sivapithecus* group, and Cercopithecidae, with Homininae coexisting with the latter and eventually dominating all surviving forms ecologically. The living Hylobatidae (gibbons) has essentially no fossil record, other than rare Pleistocene teeth, although it has often been incorrectly linked to the pliopithecids. This pattern of taxic succession (linked to ecological adaptations by Andrews 1981 and Ripley 1979) leads to a picture of mainly short-lived modern groups mostly separated from their closest fossil relatives. There are three taxa, however, that merit closer examination in terms of this paper: *Hylobates, Pongo,* and *Macaca.*

The Gibbons

Hylobates has been linked to Cenozoic fossils as old as the Oligocene by Simons (1965), among others. The genus *Aeolopithecus* is now seen to be merely a species of the common Fayum taxon *Propliopithecus* (Szalay and Delson 1979; Kay et al. 1981), and its putative gibbonlike features have been refuted as better material appeared. The Miocene *Pliopithecus* (and *Dendropithecus*) have been linked to *Hylobates* on the bases of shared conservative features of the dentition and face, along with postcranial characters that are now seen to depend

mainly on the relative gracility of long bones that do not show the extreme elongation typical of living gibbons (Simons and Fleagle 1973). Thus, there are no significant fossils known that are cladistically (as opposed to merely phenetically) linked to the hylobatids. In light of this review, then, *Hylobates* (only known genus of the Hylobatidae) cannot be readily termed a "living fossil," even under the broad definition of this volume.

On the other hand, can one argue that the gibbons are conservative enough of ancestral catarrhine morphologies in general to be treated as a "living morphotype"? Their facial architecture has long been known as retentive of various features deduced for the catarrhine morphotype (see Vogel 1966; Delson and Andrews 1975), but it also presents such derived characters as the protruding circumorbital rims and shallow mandibular corpus. Dentally, *Hylobates* species are also relatively conservative compared to the inferred common ancestor of eucatarrhines (nonparapithecids), with many similarities to pliopithecids. Their derived features, however, include some lengthening of upper cheek teeth and cingulum reduction, loss of protoconule, reduction of M_3 length, and especially near loss of canine sexual dimorphism. The cerebral contours and sulcal pattern of gibbons are probably the most conservative of living catarrhines, although the relative brain size is larger than in cercopithecids. The diploid chromosome number and presence of ischial callosities also conform to reconstructions of the ancestral eucatarrhine conditions. On the other hand, below the neck, so to speak, *Hylobates* is one of the most derived catarrhines. It shares the hominoid synapomorphies of shoulder, elbow, and thorax morphology, presents a slightly different wrist articulation (with a lunula between ulna and carpus), and is highly derived in its strongly elongated limbs (especially the antebrachium) and other adaptations to ricochetal brachiation (such as relative elongation of metacarpals and nonhallucal phalanges). Thus, although *Hylobates* does retain a number of specific features nearly unchanged from the Oligocene eucatarrhine ancestor, it shows derived features even within the same systems and a highly derived locomotor–behavioral complex that clearly removes it from consideration as a living morphotype.

The Orangutan

Until recently, it was widely assumed that the ancestry of the orangutan, *Pongo pygmaeus*, lay among the Asian "dryopithecines" of 13–8 million years ago, but without any known fossil showing especially close affinities. Numerous isolated teeth known mainly from Pleistocene deposits in China and Java were the only "real" orangutan fossils. In the last few years, however, more detailed studies by Pilbeam, Andrews, Wu, and others on older and newly found specimens of what is here called the *Sivapithecus* group showed that these materials shared detailed similarities with the derived orangutan facial architecture (Pilbeam 1982; Andrews and Cronin 1982; Wu et al. 1983). In addition, the Chinese specimens display a pattern of enamel wrinkling that may be similar to that of living orangutans. It is important to note, therefore, that the orangutan lineage extends back to at least 8 million years ago based on known derived facial morphology and to around 14 million years ago if the apparent identity of 9–14 million-year-old gnathic remains with those in 8 million year old crania imply identity of facial structure as well. No author has yet claimed or even implied that *Pongo* is a living fossil, nor do we do so at this stage in the discovery and study of the fossils, but the possibility should be seriously considered.

The Macaques

The genus *Macaca* is represented today by about 15 species ranging across southern and southeast Asia and one in North Africa. The Asian forms occur in a wide variety of local environments, both arboreally and terrestrially, with sympatry among members of several species groups, although the underlying morphology of the taxa is fairly uniform (Fooden 1982). In a wide variety of characters, macaques retain what Delson (1975a and later) inferred to be the ancestral condition for the subfamily Cercopithecinae, if not the family as a whole. These features include all dental structures except for the reduction of lingual lower incisor enamel that characterizes the tribe Papionini and perhaps the cercopithecine enlarged incisors overall. Cranially, *Macaca* preserves the facial morphology of a hypothesized ancestral cercopithecine, an inference supported in part by its similarity to the Pliocene *Parapapio* (Fig. 1), the potential ancestor of the living African papionins *Papio*, *Theropithecus*, and *Cercocebus*, which have divergently derived faces. The brain, postcranium, chromosomes, and other soft tissues of macaques are also essentially unchanged from the cercopithecine morphotype condition.

To be a living fossil, however, a modern taxon must match early fossil relatives. Macaque fossils in Asia are relatively few in number and fragmentary, although a Middle Pleistocene form may indicate a link between two modern subgroups (Delson 1980). The circum-Mediterranean record is more continuous, with a sampling of mandibular remains that cannot be specifically distinguished from the living North African *M. sylvanus* stretching back to nearly 5 million years ago (Delson 1980). In addition, the Late Miocene site of Marceau, Algeria, has yielded a collection of isolated teeth
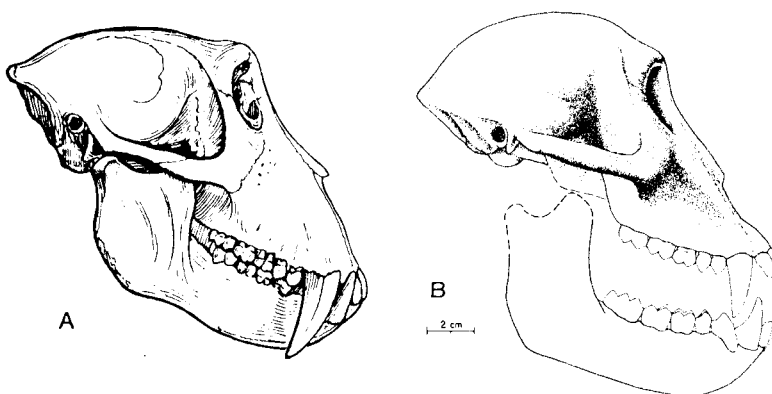

Fig. 1. Right lateral views of male skulls in Frankfurt orientation, at approximately same scale. (A) *Macaca nemestrina leonina*, living today in Indochina, after Gregory (1951, Fig. 23.44b, cut D3, courtesy of the American Museum of Natural History; (B) *Parapapio broomi*, middle to late Pliocene of southern Africa, from Szalay and Delson (1979; Fig. 169A, courtesy Academic Press). The facial profiles are nearly identical.
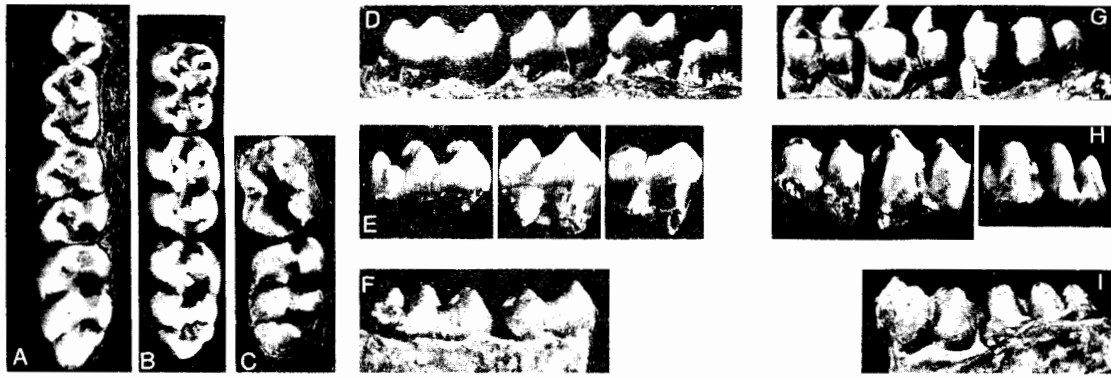
Fig. 2. Morphology of left lower molars (and P₄) of macaques and early cercopithecids. (A–C) occlusal views; (D–F) lingual; (G–I) buccal. (A, D, G) *Macaca sylvanus florentina*, early Pleistocene of Italy, P₄–M₃ from partial corpus (P₄ removed in D). (B, E, H) ?*Macaca* sp., late Miocene of Algeria, isolated teeth aligned as M₁₋₃. (C, F, I) "*Victoriapithecus*" *leakeyi*, middle Miocene of Kenya, M₂₋₃ of partial corpus (scaled up to molar length equal to two younger fossils). Some retouching of the prints has covered portions of corpus and supporting clay, but not affected morphology, which is quite constant across this 13 million year span.

(Fig. 2) that are morphologically inseparable from those of modern macaques of comparable size. It is not clear that these specimens confirm the presence of *Macaca*, because they might also be assigned to the phenetically identical *Parapapio* (of the sub-Saharan Pliocene), but biogeographic indicators suggest that the Saharan region was already a barrier to migration at this date, thus enhancing a referral to *Macaca* (Delson 1975b; Thomas 1979; Thomas et al. 1982; but compare Geraads, 1982).

Finally, the earliest evidence for modern-type cercopithecids comes from the Middle Miocene (ca. 15 million years ago) site of Maboko, Kenya. Here are found two morphs that have been termed *Victoriapithecus macinnesi* and "*V.*" *leakeyi*. The former appears to show some derived dental features in common with colobines but the latter is more "generalized" and thus cercopithecine-like. This second form is represented by only a few teeth and uncertainly referred limb bones, but a partial mandible (Fig. 2) and elbow fragments are hard to separate from those of modern macaque species. The overall indication is that in terms both of morphotype conservatism and phenetic similarity to ancient cercopithecines, *Macaca* may be termed a living fossil under our working definition. The earliest fossils of *Papio* are about 2.5 million years old and so close to modern forms that they are placed in the same species.

Nonetheless, the time scale involved is so much shorter than we would hardly consider the baboon a living fossil.

Evolution and Living Fossils Among the Platyrrhini

The fossil record of the platyrrhine primates is exceedingly meager compared with that of the catarrhines. Nonetheless, it hints at a broadly different pattern of diversification that, in some ways, seems confirmed by the taxonomic and morphologic composition of the surviving forms. The record opens in the early Oligocene with *Branisella*, whose affinities are not demonstrably near any of the other ceboid monkeys. Morphologically highly primitive (e.g., Hoffstetter 1980), *Branisella* possibly represents an early branch antedating the last common ancestor of all other fossil and living New World monkeys (Rosenberger 1981a). From the Late Oligocene onwards, however, the record reveals an intriguing number of examples that are surprisingly modern in appearance and assignable to extant clades. Thus platyrrhine evolution may not have unfolded in waves of successive adaptive radiations but rather as long-stemmed branches of persistent lineages (Rosenberger 1980). The impressive anatomical

variety of the living genera may be a manifestation of this historical pattern.

The Marmosets

The living platyrrhines comprise some 15 or 16 genera (Szalay and Delson 1979; Rosenberger 1981b) and may be grouped into two families (Cebidae and Atelidae) each containing a pair of subfamilies. In contrast to many other taxonomic schemes (e.g., Napier and Napier 1967; Napier 1976; Hershkovitz 1977), our divisions are designed to conform to a cladistic hypothesis of the affinities of both living and extinct forms, and we think it very likely that all of the higher taxa that we recognize are monophyletic. Of these, the Callitrichinae (marmosets) have long been regarded as the most conservative (Hershkovitz 1977), hence the best candidates for preserving living fossils. However, many authorities have also argued that marmosets are a highly modified lineage. Independent analyses of numerous anatomical systems (reviewed in Rosenberger, in press), including the skull, dentition, aspects of the postcranium and reproductive system, which together define what may be termed the Marmoset Anatomical Complex, indicate that callitrichines are indeed a very derived assemblage. While the fossil record, given its scarcity and incompleteness, cannot be called upon to "prove" or "disprove" this notion, none of the craniodental characters of the complex appear among the Paleogene fossil platyrrhines, and none are elements of the euprimate morphotype (Szalay and Delson 1979). The evidence thus does not uphold Hershkovitz's theory that marmosets are a plesion, and we would predict that none of the living callitrichines will be found to be living fossils with any significant temporal dimension.

The Squirrel Monkey

The subfamily Cebinae, sister-group of the callitrichines, is represented in the fossil record by two genera, *Dolichocebus* of the Late Oligocene and *Neosaimiri* of the Middle Miocene. (Another species, *"Saimiri" bernensis* of the latest Pleistocene, probably is a third.) Of the two living genera, *Cebus* and *Saimiri*, the latter

seems to conserve some of the dental traits characterizing the platyrrhine morphotype, such as a relatively low hypocone, highly cuspate occlusal relief, and elevated trigonids. On the other hand, as with all other ceboid genera, *Saimiri* presents a suite of unique characters or mosaics that distinguishes it from all its living relatives.

The Middle Miocene *Neosaimiri* is known only by a nearly complete mandible lacking the rami and a few teeth. Although slightly larger than *Saimiri*, it differs from the living form solely in a few minor occlusal details, such as cuspal acuity, basin constriction, and cingular development (Fig. 3). Given the limited material, and by analogy with the diversity and taxonomy of the catarrhines, it is reasonable to suggest that *Neosaimiri fieldsi* be ranked as a subgenus of *Saimiri*. We do not take this step formally here, as full revision of the Miocene ceboids is under way by Rosenberger and Setoguchi, but we do wish to emphasize the continuity of morphology within this lineage.

In fact, this continuity may extend back even farther into the Middle Cenozoic. There are important similarities in the cranial anatomy of the Late Oligocene *Dolichocebus gaimanensis* and *Saimiri* (Fig. 4). At least two derived diagnostic features of the modern genus, a dolichocephalic neurocranium and a pattern of circumorbital traits including a very narrow interorbital pillar (Fleagle and Rosenberger, 1983), narrow and elongate nasals, a prolonged frontal process, reduction of the interorbital sinus, and a probably fenestrated interorbital septum (Rosenberger 1979) are present in both (but see Hershkovitz 1982). Other details of the neurocranium suggest additional *Saimiri*-like aspects in the masticatory apparatus and the soon to be described (Rosenberger and Mills, in preparation) middle-ear region. The natural endocast of *Dolichocebus* also suggests a frontal lobe that is relatively enlarged and positioned much as it is in *Saimiri* as well as a markedly creased Sylvian sulcus, perhaps a uniquely *Saimiri*-like feature. The evident differences in the configuration of the facial skull and in what can be discerned of the auditory bulla that set the fossil apart from the living *Saimiri* are easily transformable into a fully modern pattern. Thus we regard *Dolichocebus* not only as a close relative of the living
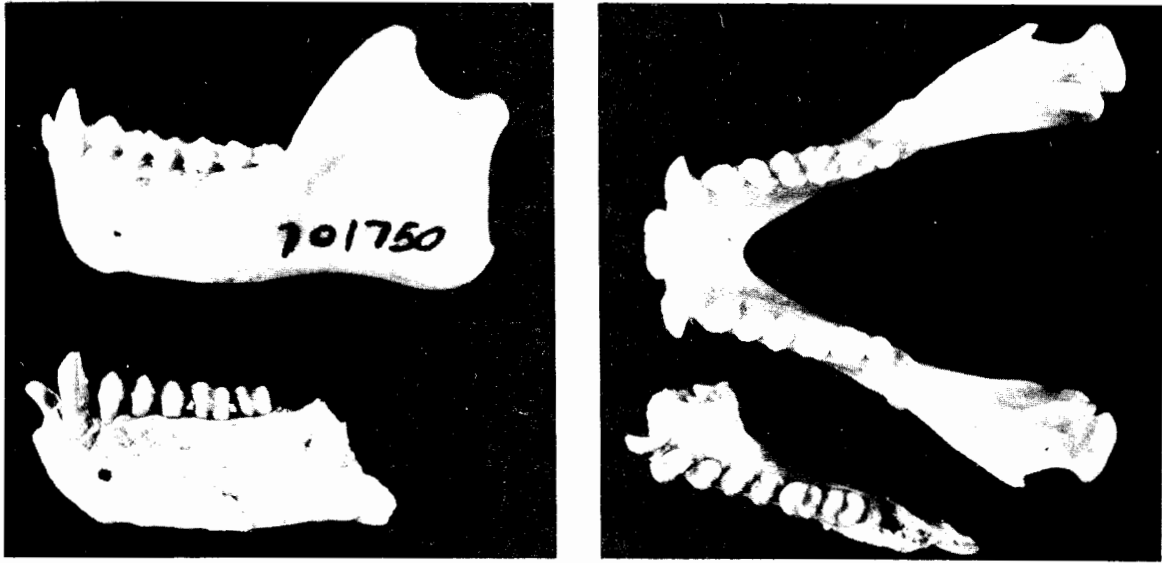
Fig. 3. Left lateral and occlusal views of *Saimiri sciureus* (complete jaw of living widespread Neotropical species) and *Neosaimiri* (=*Saimiri*?) *fieldsi*, Middle Miocene of Colombia.

Saimiri, but possibly its direct Oligocene ancestor; no autapomorphies are yet known that would preclude this hypothesis. In either case, *Saimiri* is an excellent example of an anthropoid living fossil and perhaps the sequence *Dolichocebus–Neosaimiri–Saimiri* represents one of the longest generic lineages among all primates.
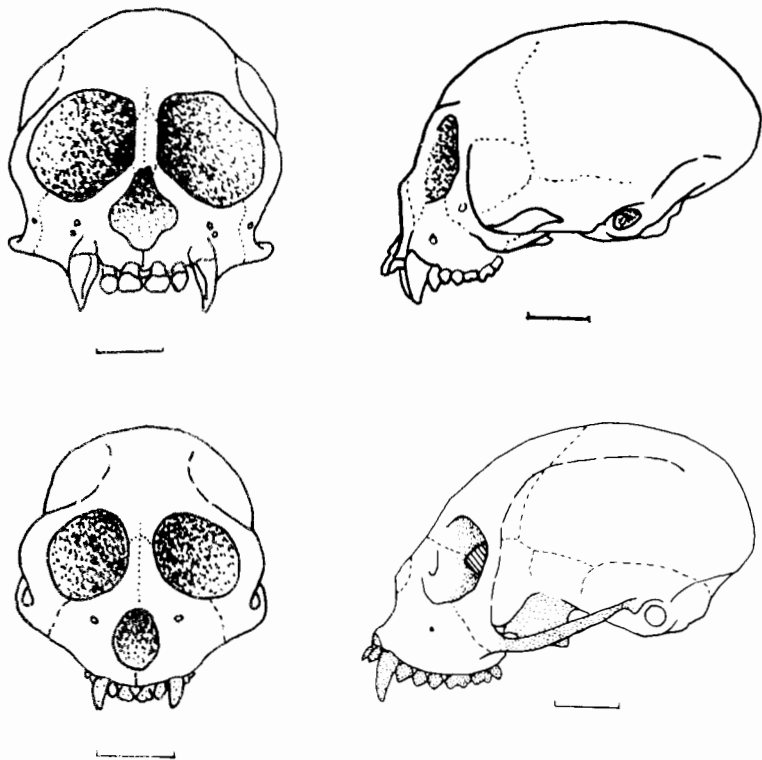

Fig. 4. Frontal (to left) and right lateral views of male *Saimiri sciureus* (above, living taxon) and ?female *Dolichocebus gaimanensis* (below, restored, Late Oligocene of Argentina). Scale bars represent 1 mm; reconstructed areas are uniformly stippled; the interorbital fenestra is hatched. Lower right figure after Rosenberger (1979).

The Howler Monkey

Among the atelids, both pitheciine and ate-line subfamilies are represented in the Tertiary record. The atelines are known from the Miocene form *Stirtonia*, which very closely resembles the living *Alouatta* in dental anatomy (but see Setoguchi et al. 1982), although not in mandibular form. Significantly, it is the shape of the mandible and presumably correlated modifications of the skull that set the living genus apart from all other platyrrhines most strikingly—a complex of characters that many have argued are related to the elaboration of the vocalization mechanism. We take this to mean that the howler lineage may also be as ancient as the Middle Miocene, but the evidence is still too spotty to discern if its most obvious autapomorphies were then existent; certainly its predilection for a folivorous diet was, as judged by the dentition of *Stirtonia*.

The Saki-Uakaris

The pitheciines, which present some of the most unusual dental and gnathic specializations of all platyrrhines, are also represented in the record by several genera. One of these, *Cebu-*

pithecia, comes from the same Middle Miocene fauna as does *Stirtonia*. It has been likened to *Pithecia* (e.g., Stirton and Savage 1951), and one can draw the erroneous conclusion that *Pithecia* is thus a living fossil. However, a recent reconsideration of the holotype (Rosenberger and Mills, in preparation) indicates that the genus shows no positive derived features that are exclusively shared with *Pithecia;* it may be a sister-taxon of the entire saki-uakari (Pitheciini: Rosenberger 1981b) radiation.

The Owl Monkey

Another pitheciine comes from an earlier period. *Tremacebus harringtoni* occurs in Late Oligocene beds and bears a remarkable resemblance to the living owl monkey, *Aotus*. Two of the more startling apomorphies of *Aotus* are its enlarged orbits, reflecting its shift to a nocturnal/crepuscular activity cycle, and its greatly enlarged incisors (of uncertain adaptive explanation). The latter are exceedingly broad teeth, especially the upper central, and require a much broader premaxilla and anterior maxilla. *Tremacebus* is known by a fossil cranium that displays both of these osseous characteristics
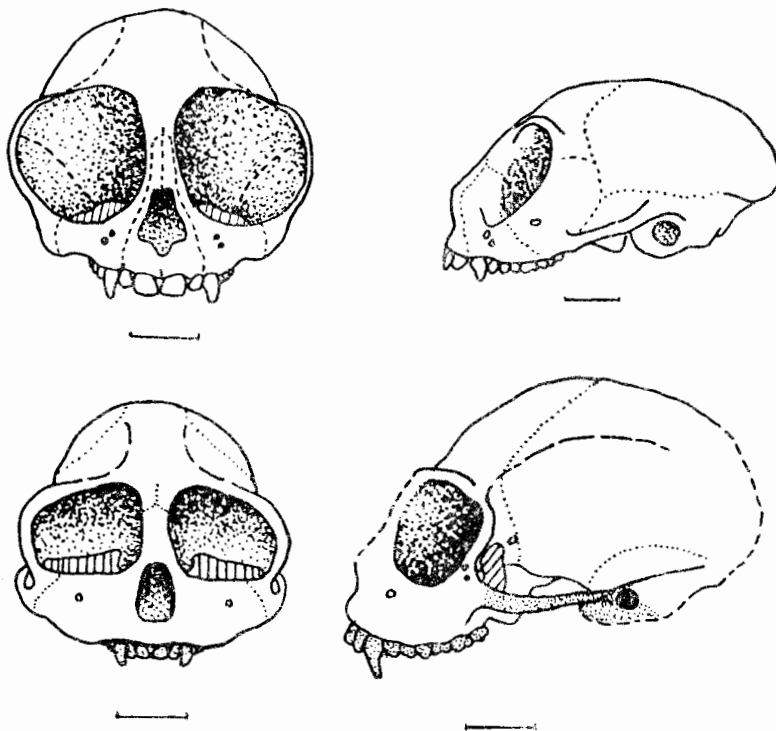

Fig. 5. Frontal (to left) and right lateral views of *Aotus trivirgatus* (above, modern, South America) and *Tremacebus harringtoni* (below, restored, late Oligocene of Argentina). Scale bars represent 1 mm; reconstructed areas are uniformly stippled or indicated by broken line; the orbitotemporal fenestra is hatched.

(Kraglievich 1951; Rosenberger 1980; see Fig. 5). Although the orbits are not quantitatively as enlarged as are those of some populations of *Aotus* (Fleagle and Rosenberger, 1983), both forms show the flaring orbital margin, enlarged secondary postorbital fenestra, capacious postorbital plate, and depressed orbital floor that are elements of the hypertrophic eyeball complex. Additionally, although anterior teeth are missing in the fossil, the anterior aspect of the palate is notably squared off, as in *Aotus,* despite the fact that the preserved canine roots are relatively small, implying large incisors. Thus it appears that at least two of the most important functional adaptations of *Aotus* are evident in *Tremacebus*. The few features visible on the badly damaged molar teeth of the fossil indicate that molar proportions would have been as predicted for the pitheciine morphotype and that crown morphology was much more primitive in *Tremacebus*—in having an offset hypocone, for example. Whatever else can be studied of the skull shows no important differences, however.

Therefore, *Aotus* becomes the second platyrrhine living fossil, paralleling *Saimiri* in its close morphological and phylogenetic linkage to a Late Oligocene fossil. The time depth of these two apparent lineages is truly astounding, especially by comparison to the more familiar catarrhine pattern of successive replacement. On the other hand, lest we be accused of making all platyrrhine fossils direct ancestors of living forms, it may be noted that the well-known Miocene *Homunculus* is a "primitive" pitheciine not readily linked more closely to any modern genus.

Adaptation, Ecology, and Time: A Comparison of the Two Patterns

Knowing full well that we are prone to grand error because the fossil record forever surprises us with new information, and especially because so little is available for Tertiary platyrrhines, we take this opportunity to explore some of the possible implications of our analysis and of the patterns of diversification evident among New and Old World anthropoids.

While none of the modern anthropoids can be unequivocally viewed as epitomizing arrested evolution, there seem to be indications that platyrrhines are overall more retentive of ancient Cenozoic morphologies than are the catarrhines. A combination of cladistic analysis and paleontology indicates that there have been two large-scale adaptive radiations among the catarrhines since the Late Oligocene, the hominids and then the cercopithecids. Modern subfamilies are not definitively represented until the Late Miocene. Neither line of evidence, in contrast, shows this pattern in the Neotropics: The only side lineage to the mainstream would have antedated the Late Oligocene, when two of the four modern subfamilies (if not generic lineages) first appear; a third dates at least to the Middle Miocene. Significantly, the cercopithecid and hominid radiations occurred in broadly distinct adaptive zones. Old World monkeys are probably a terrestrial diversion of the primitive arboreal way of life that apes retained, with only a few exceptions. No such ecological division occurred in the New World (Rosenberger 1980). Thus the earlier initiation of the monophyletic platyrrhine radiations would make it likely that should living fossils occur, they would be expected to be of more ancient origin in the New World than in the Old. Alternatively, or perhaps predictably, if Vrba's (1980, 1983) "effect hypothesis" of macroevolutionary trends has validity, the cercopithecids and perhaps other catarrhine groups may have been genetically more "disposed" toward producing numerous lineages continuously, while the platyrrhines radiated early and persisted.

A second factor devolves from these considerations. The highly successful cercopithecid radiation became ever more numerous in surviving taxa and also apparently reinvaded the arboreal milieu. This says as much for the severity of selective pressures in the changing Old World biosphere as it does of the competition between rather closely related primates. In both arboreal and terrestrial habitats, the cercopithecids tend to be more abundant than hominids in species and genera. This also implies that they may have outcompeted at least some of their ape contemporaries, leaving fewer possible living fossil survivors. While South America was also certainly subject to large climatic changes and faunal turnovers, the primates were apparently less affected, or were affected in other

ways. No terrestrial sublineages appeared (so far as we know), despite the proliferation of savannah-like grasslands across the continent (Hershkovitz 1972). It is conceivable that some of the living marmosets may have diversified as a result of the opening of this new habitat, but on no level higher than the species or subgenus. Two points can be made: Competition between taxa occupying the same habitat would have been more intense, leading to more character divergence and finer niche partitioning; but no innovative higher morphological complexes emerged under novel selective pressures to enter into competition with established genetic potentials. Thus generic differences among the platyrrhines could have become marked over time without wholesale extinction eliminating large portions of the fauna. This makes for a greater opportunity to preserve living fossils.

A similar phenomenon would have resulted from the contrasting continental circumstances in the New and Old World. Essentially isolated throughout much of the Tertiary (Marshall et al. 1982; Patterson and Pascual 1972; Hershkovitz 1972), the South American primate fauna was self-contained and free from invasion by closely related forms. On the other hand, Europe, Asia, and Africa experienced intermittent contacts at various times since the Late Oligocene (Bernor, in press; Savage and Russell 1983), enabling faunas to mix and competitors to pressure taxa to transform or become extinct. The waves of extracontinental migrants may have severely affected the survivorships of early lineages especially. A possible test of both these hypotheses is offered by the several Latest Pleistocene Caribbean ceboids, all of which appear to have diverged quite strongly from their closest relatives despite rather short time spans involved (Rosenberger 1978; MacPhee and Woods 1982). This implies that once a novel ecozone became available, divergence occurred rapidly.

Another aspect may have influenced the diversification of cercopithecids in a restrictive sense. Although they have occupied much more continental land than the platyrrhines and invaded such contrasting ecological situations as the arboreal and terrestrial zones, they still exhibit less anatomical variety than do the platyrrhines. It may be suggested that this is because platyrrhines appeared earlier than cercopithecids. However, we think it is also significant

that Old World monkeys are possibly more canalized anatomically than the platyrrhines. For example, their bilophodont molar dentition manifests a surprising homogeneity in form, suggesting an all-purpose design irrespective of diet. Platyrrhines, in contrast, are highly diverse dentally (Rosenberger and Kinzey 1976; Hershkovitz 1977). Postcranially, cercopithecids are relatively uniform (e.g., Schultz 1970), whereas the platyrrhines display nearly all variations, except terrestriality, that the order Primates has produced (e.g., Erikson 1963). If true, this canalization might mean that cercopithecids are evolutionarily "interchangeable," producing short-lived taxa that may succumb to extinction if a competitor gains a relatively small adaptive advantage. This would again support the "effect hypothesis" interpretation noted above. On the other hand, wider adaptive differences separate platyrrhine generic lineages in which the potential for anagensis (slow phyletic evolution) is dominant so long as the essential ecological balance is not destroyed.

If we assume that extinction has more or less randomly influenced the survivorship of adaptive types in both the New and Old World, than what can explain the survivorship of living fossils in each group? *Macaca* represents an archetypal eurytope, or ecological generalist (see Eldredge 1979), whose species differ in minor ways (Fooden 1982) from a norm unchanged over millions of years. The African *Papio* has a much shorter known duration, although fossils nearly 3 million years old can be placed in the living species, and its degree of eurytopy is even greater as evidenced by its monotypy (Vrba 1980). *Saimiri* may have achieved success for much the same reasons. *Aotus*, however, has taken itself out of competition with close relatives by moving into an entirely different ecological realm, that of the night.

Summary

The anthropoid primates are not usually considered as candidates for the position of living fossils, which often implies great antiquity as well as a lineage that has shown morphological conservatism throughout its existence. Under the broadened definition of this volume, however, several taxa appear to qualify handily, be-

ing phenetically quite similar to relatively an-
cient cladistic relatives. Among the catarrhines,
or Old World anthropoids, the hylobatids have
often been suggested as tracing ancestry back
to the Miocene or even Oligocene pliopithecids,
but this concept has now been widely rejected;
the many postcranial, behavior, facial, and den-
tal apomorphies of gibbons far outweigh their
several dental and cranial eucatarrhine symple-
siomorphies, so that they cannot be considered
as living morphotypes either. The orangutan
lineage, on the other hand, can now be traced
back at least 8 (if not nearly 15) million years to
the *Sivapithecus* group of hominids; until the
phenetic similarities have been analyzed in de-
tail, we refrain from too readily considering the
orangutan as a living fossil. Of all the catar-
rhines, only the cercopithecid genus *Macaca*
appears to qualify for this role. It corresponds
closely in dental, cranial, and postcranial de-
tails to the inferred morphotype of the cerco-
pithecine or even cercopithecid ancestor of 10–
15 million years ago. Moreover, the species *M.
sylvanus* can be extended back to the beginning
of the Pliocene on the basis of circum-Mediter-
ranean gnathic (and partial postcranial) evi-
dence, while the genus as a whole may be
traced through Late Miocene North African
teeth to approach the 15 million-year-old *"Vic-
toriapithecus" leakeyi* of East Africa both den-
tally and in elbow morphology.

Among the New World platyrrhines, generic
lineages are much more readily traced into the
middle Cenozoic. Although the callitrichine ce-
bids (marmosets) have been suggested by
Hershkovitz as persistently primitive (essen-
tially living fossils), they are in fact a highly
autapomorphic group. The cebine *Saimiri*, on
the other hand, is both relatively conservative
dentally and so close to the Middle Miocene
Neosaimiri as to bring their generic distinction
into serious question. In addition, the Late Oli-
gocene *Dolichocebus* presents a large number
of specifically *Saimiri*-like features (several
autapomorphic) in the skull, as well as the
lesser known brain, suggesting a true continua-
tion of the generic lineage over some 25 million
years. A second clear case of a platyrrhine liv-
ing fossil is the pitheciine atelid *Aotus*. The mo-
saic of cranial features related to this form's
nocturnal adaptation are foreshadowed in *Tre-
macebus*, a contemporary of *Dolichocebus*.

The persistence of these two rather "special-
ized" lineages indicates unexpectedly early dif-
ferentiation of the ceboids at fairly low taxo-
nomic levels. The resultant implication of
numerous other such lineages in the (now mea-
ger) fossil record is supported by the presence
in the Middle Miocene of taxa rather similar to
the living ateline *Alouatta* and the common
pitheciin stock. Because these similarities seem
less close than that seen between *Pongo* and
Sivapithecus, although La Venta is comparable
in age to the oldest sivapiths, the forms in-
volved are not granted living fossil status.

Why was the pattern of differentiation so dis-
similar in the New and Old World anthropoids?
In the Old World, a set of sequentially replacing
sister-taxa or collateral relatives characterized
not only the family-group but also the generic
history of the catarrhines. In South America,
family-group and even generic lineages with
unique specializations appeared early and per-
sisted; apart from *Branisella*, only one early
fossil genus, Early Miocene *Homunculus*, can-
not be placed more closely than in a modern
subfamily. The isolation of South America, as
opposed to the freer intercontinental passage
and competition in the Old World, more than
anything else, appears to be at the root of the
differences. In the New World, platyrrhines be-
gan to diverge earlier and were less directly af-
fected by Miocene climatic shifts (no terrestrial-
ity) or intercontinental migration. Instead, they
emphasized anagenesis except when offered
wholly new geographic zones, as in the Carib-
bean, where two novel generic lineages are
known from Latest Pleistocene (Mid-Holocene)
fossils.

In contrast, the catarrhines (especially the
cercopithecids) may have been more canalized
toward producing numerous short-lived lin-
eages that responded to competition mainly by
speciating or becoming extinct, rather than
through niche separation and character dis-
placement. This follows Vrba's "effect hypoth-
esis" model of macroevolution. The competi-
tion provided by intercontinental faunal
exchange combined with internal replacement
to reduce the chances for ancient catarrhine lin-
eages to survive as living fossils. Moreover, the
relative morphological homogeneity of the
highly successful cercopithecids further sug-
gests they were likely to replace each other as

rather small adaptive novelties became selectively advantageous. Nonetheless, the several extreme eurytopes among the Cercopithecidae, such as *Macaca* and *Papio,* did manage to persist for reasonably long intervals with little change, once their underlying adaptations were fixed. Only additional fossils, as always, will tell if these interpretations are defensible.

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