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 Sivart and Delson (1974), the Order Primates is divided into three suborders, the extinct Plesiadapiformes, the Strepsirrhini (lower primates), and the Haplorhini, including the infraorders Tarsiformes (tarsiers and fossil relatives—see Schwartz, this volume), Platyrrhini (New World anthropoids), and Catarrhini (Old World anthropoids). The formal status of Anthropoidea was not recognized in order to reduce the number of ranks allowed, but it may be considered a hyrork (between suborder and infraorder; see Delson 1977) including Platyrrhini and Catarrhini. The nomen Siniformes Hoffstetter 1974, may be substituted for Anthropoidea Miiller 1854, if desired, to avoid confusion with earlier contrasts between Anthropoidea and "Prosminis", a grade term including all non-primates. We shall briefly review the evolutionary history of each anthropoid infraclass 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 primate species were more numerous and more diverse taxonomically than their relatively derived pliopithecid contemporaries (Pliopithecidae), including Aegyptopithecus, species, but the former do not appear to have left any descendants or close relatives. During the Early and Middle Miocene, pliopithecid occurrences 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-opo-like Strepsirrhini and the Cercopithecids (Old World monkeys). One cercopithecoid 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 *Stegotherium* group is currently the subject of much debate (see papers in Cochoch and Corruccini 1983), and both its position in ape phylogeny and a meaningful family-group nomen within Hominoidea is 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 (*Pongo*-nae) but perhaps also to the African ape-human lineage (*Homininae*) of the Pliocene and Pleistocene. The later Late Miocene saw the diversification of the Cercocebusidae (and the brief flowering of the cercopithecoid *Oreopithecus*), with a peak in generic diversity probably occurring in the Late Pliocene. The sequence of re-placement therefore might be seen as: Parapithecidae, Pliopithecidae, Dryopithecidae, *Stegotherium* group, and Cercocebusidae, with Homininae coexisting with the latter and eventually dominating all surviving forms ecologically. The living Hylabatidae (gibbons) has essentially no fossil record, other than rare Pleistocene teeth, although it has often been incorrectly linked to the piliopithecid. 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: *Hylabates*, *Pongo*, and *Macaca*.

The Gibbons

*Hylabates* has been linked to Cenozoic fossils as old as the Oligocene by Simons (1965), among others. The genus *Aerolopithicus* is now seen to be merely a species of the common Fayum taxon *Propithecus* (Szalay and Delson 1979; Kay et al. 1981), and its putative gonial features have been refuted as better material appeared. The Miocene *Propliopithecus* (and *Dendropithecus*) have been linked to *Hylabates* 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 1971). 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, *Hylabates* (only known genus of the Hylabatidae) 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, *Hylabates* species are also relatively conservative compared to the inferred common ancestor of eucatarhines (nonparapithecids), with many similarities to piliopithecids. Their derived features, however, include some lengthening of upper cheek teeth and clungul reduction, loss of protocone, reduction of M1 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 isochal collagen acids also conform to reconstructions of the ancestral eucatarhine conditions. On the other hand, below the neck, so to speak, *Hylabates* is one of the most derived catarrhines. It shares the hominoid synomorphies 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 antibrachium) and other adaptations to ricochetal brachiation (such as relative elongation of metacarpals and nonhallucal phalanges). Thus, although *Hylabates* does retain a number of specific features nearly unchanged from the Oligocene eucatarhine ancestor, it shows derived features even within the same system 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 *Semi-pithecus* 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 sympathy among members of several species groups, although the underlying morphological of the taxa is fairly uniform (Toothen 1982). In a wide variety of characters, macaques retain what Dehson (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 envelope 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 *Panopio* (Fig. 1), the potential ancestor of the living African papionins *Papio, Theropithecus*, and *Cercocetus*, 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 (Dehson 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 (Dehson 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* from India, after Gregory (1951, Fig. 21.4B; courtesy of the American Museum of Natural History; (B) *Panopio broomi*, middle to late Pliocene of southern Africa, from Szalay and Dehson (1979; Fig. 169A, courtesy Academic Press). The facial profiles are nearly identical.
Fig. 2. Morphology of left lower molars: (A) P4 of *Macaca* and early cercopithecoids; (A-C) ventral views; (D-F) lingual; (G-H) buccal. 1A, D, G *Macaca schweizeri* florentina, early Pleistocene of Italy. P4-M2 from partial corpus (P); removed in D-F, H. 1B, E *Marauxia* sp., late Miocene of Algeria. Isolated teeth aligned as M4s, *C*. F, D *Von der Deckenii*. 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 Phytirhini

The fossil record of the phytirhynine 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 *Bransella*, whose affinities are not demonstrable near any of the other ceboid monkeys. Morphologically highly primitive (e.g., Heiwetstetter 1980), *Bransella* 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 assignment to extant clades. Thus phytirhynine 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 manifesta-
tion of this historical pattern.

The Marmosets

The living platyrhines comprise some 15 or 16 genera (Szalay and De locomotive 1979; Rosen-
berger 1970s) and be grouped into two fam-
ilies (Cebidae and Atelidae) each containing a
pair of subfamilies. In contrast to many other
taxonomic schemes (e.g., Napier and Napier
1967; Napier 1978; Hershkovitz 1973), our divi-
sions are designed to conform to a cladistic hy-
pothesis of the affinities of both living and ex-
tinct forms, and we think it very likely that all of
the higher taxa that we recognize are monophy-
letic. Of these, the Callitrichidae (marmosets)
have long been regarded as the most conserva-
tive (Hershkovitz 1977), hence the best can-
didates for preserving living fossils. However,
many authorities have also argued that marmo-
sets are a highly modified lineage. Independent
analyses of numerous anatomical systems (re-
viewed in Rosenberger, in press), including the
skull, dentitions, aspects of the postcranial 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 rec-
ord, given its scarcity and incompleteness, can-
not be called upon to "prove" or "disprove,"
this notion, none of the cranial/teeth features of
the complex appear among the Paleogene fossil
platyrhines, and none are elements of the
cavities assemblage type (Szalay and De locomotive
1979). The evidence thus does not uphold
Hershkovitz's theory that marmosets are a ples-
ion. For now, we would predict that none of the
living callitrichines will be found to be living
called marmosets 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, Dulichius (the Late Oligo-
ceene and Neosaimiri of the Middle Miocene,
Another species, "Saimiri" bernesianus 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 platyrhine morphotype,
such as a relatively low hypsognathous, highly
concave occlusal relief, and elevated trigonids. On
the other hand, as with all other ceboid genera,
Saimiri presents a suite of unique characters or
clades that distinguishes it from all living relatives.

The Middle Miocene Neosaimiri is known
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 circular developmen (Fig. 3). Given the limited mate-
rial, and by analogy with the diversity and tax-
onomy of the catarhines, it is reasonable to
suggest that Neosaimiri fields 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 Seto-
guchi, but we do wish to emphasize the continui-
ty of morphology within this lineage.

In fact, this continuity may extend back even
further into the Miocene Centose. There are im-
portant similarities in the cranial anatomy of the
Late Oligocene Dolichus 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 pilar (Feagle and Rosenberger, 1983), narrow and
elongate nasals, a prolonged frontal process,
re-
duction of the interorbital sinuses, and a probably
fenestrated interorbital septum (Rosenberger
1979) are present in both (but see Hershkovitz
1982). Other details of the neurocranium sug-
gest additional "Saimiri-like" aspects in the masticatory apparatus and the soon to be described
(Rosenberger and Hell). In preparation) middle-
earth region. The overall endocast of Dolichocel-
bus also suggests a frontal lobe that is relatively
enlarged and positioned much as it is in Saimiri
as well as a markedly crested Sylvian sulcus, perhaps a unique Saimiri-like feature. The ev-
ident differences in the configuration of the fa-
cial 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 Dolichocel-
bus 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* (now believed to be a species of *Saimiri*), Middle Miocene of Colombia.

*Saimiri*, but possibly its direct Oligocene ancestor, has autapomorphies that 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 (top left) and right lateral views of male *Saimiri sciureus* (above, living taxon) and female *Dolichocebus guianensis* (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 atelines, both pitheciine and ateline 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 platyrhines 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 hower 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 platyrhines, are also represented in the record by several genera. One of these, *Cebu-
(Králjevich 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 hypertropic 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 pithecine morphotype and that crown morphology was much more primitive in Tremacebus—in having an off-set 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 catarhine 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" pithecine 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 platyrhines, 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 platyrhines are overall more sensitive to change than the ctenoid catarhines. A combination of cladistic analysis and paleontology indicates that there have been two large-scale adaptive radiations among the catarhines since the Late Oligocene, the hominoids 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 cercopithecoid and hominoid radiations occurred in broadly distinct adaptive zones. Old World monkeys are probably a terrestrial diversion of the primate arboreal way of life that apes retained, with only a few exceptions. No such ecological diversion occurred in the New World (Rosenberger 1980). Thus the earlier initiation of the monophyletic platyrhine 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. Alternately, or perhaps predictably, if Vrba's (1980, 1983) "effect hypothesis" of macroevolutionary trends has validity, the cercopithecids and perhaps other catarhine groups may have been genetically more "dispersed" toward producing numerous lineages continuously, while the platyrhines radiated early and persisted.

A second factor derives from these considerations. The highly successful cercopithecoid radiation became ever more numerous in surviving taxa and also apparently reinforced 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 hominoids 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, they 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 muasatomys may have diversified as a result of the opening of this new habitat, but on no level higher than the species or subspecies. 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 cebids, 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 ecosystem 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 Kuznetzov 1976; Hershkovitz 1977). Postcranially, cercopithecids are relatively uniform (e.g., Schultz 1970), whereas the platyrrhines display nearly all variations, except sterility, 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 anagenesis (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 (Foden 1982) from a form 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). Simias 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 handsomely, be-
ing phenetically quite similar to relatively ancient clade relatives. Among the catarhines, or Old World anthropoids, the hylobatids have often been suggested as tracing ancestry back to the Miocene or even Oligocene plesiothecids, but this concept has now been widely rejected; the many postcranial, behavior, facial, and dental apomorphies of gibbons far outweigh their several dental and cranial eucatarhine synapomorphies, 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 Saupithicus group of hominids; until the phenetic similarities have been analyzed in detail, we refrain from too readily considering the orangutan as a living fossil. Of all the catarhines, only the cercopithecoid genus Macaca appears to qualify for this role. It corresponds closely in dental, cranial, and postcranial details to the inferred morphotype of the cercopithecine or even cercopithecoid ancestor of 10-15 million years ago. Moreover, the species M. sylvestris can be extended back to the beginning of the Miocene on the basis of circum-Mediterranean gnathic and partial postcranial evidence, while the genus as a whole may be traced through Late Miocene North African teeth to approach the 15 million-year-old Vicanthopithecus leakeyi of East Africa both dentally and in elbow morphology.

Among the New World platyrhines, generic lineages are much more readily traced into the middle Cenozoic. Although the callicebine ceboids (marmosets) have been suggested by Hershkovitz as persistently primitive (essentially 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 Oligocene Dolichopithecus presents a large number of specifically Saimiri-like features (several autapomorphic) in the skull, as well as the lesser known brach, suggesting a true continuation of the generic lineage over some 25 million years. A second clear case of a platyrhine living fossil is the pithecanthrope Aegyptopithecus. The mosaic of cranial features related to this form's nocturnal adaptation are foreshadowed in Tremacebus, a contemporary of Dolichopithecus.

The persistence of these two rather "specialized" lineages indicates unexpectedly early differentiation of the cebids at fairly low taxonomic levels. The resistant implication of numerous other such lineages in the (now meagre) fossil record is supported by the presence in the Middle Miocene of taxa rather similar to the living Ateles and the common pithecanth in stock. Because these similarities seem less close than that seen between Pongo and Saupithicus, although La Venta is comparable in age to the oldest viviparids, the forms involved are not grunted living fossil status.

Why was the pattern of differentiation so dissimilar 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 catarhines. In South America, family-group and even generic lineages with unique specializations appeared early and persisted; apart from Brantilia, only one early fossil genus, Early Miocene Homunculus, cannot be placed more closely than in a modern subfamily. The isolation of South America, as opposed to the free 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, platyrhines began to diverge earlier and were less directly affected by Miocene climatic shifts (no terrestriality) or intercontinental migration. Instead, they emphasized angiosperm except when offered wholly new geographic zones, as in the Caribbean, whose two novel generic lineages are known from latest Pleistocene (Mid-Holocene) fossils.

In contrast, the catarhines (especially the cercopithecoids) may have been more canalized toward producing numerous short-lived lineages that responded to competition mainly by speciating or becoming extinct, rather than through niche specialization and character displacement. This follows Vrba's "effect hypothesis" model of macroevolution. The competition provided by intercontinental faunal exchange combined with internal replacement to reduce the character for extinct catarhine lineages to survive as living fossils. Moreover, the relative morphological homogeneity of the highly successful cercopithecoids further suggests they were likely to replace each other as
rather small adaptive novelties became selec-
tively advantageous. Nonetheless, the several
extreme eurytypes among the Cercopithecoidae,
such as Macaco and Papio, did manage to per-
sist 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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Literature
Andrews, P. J. 1981. Species diversity and diet in
monkeys and apes during the Miocene, pp. 75-61.
In: Stringer, C. B. (ed.). Aspects of human evolu-
Andrews, P. J., Cronin, J. E. 1982. The relationships
of Sts 500 and Ramapithecus and the evolu-
Berner, R., L. In press. A zoogeographic theorem
and biochronologic play: the time/biofacies phenom-
ena of Eurasian and African Miocene mammal
provinces. In: Meen, P. (ed.). Proc. RCMNS Col-
lege. 1983.
interpretations of ape and human ancestry. New
York: Plenum.
Delson, E., 1975a. Evolutionary history of the Cerco-
Delson, E. 1975b. Paleoecology and zoo geography
of the Old World monkeys, pp. 37-64. In: Tuttle,
R. (ed.). Primate functional morphology and evo-
Delson, E. 1977. Catarhine phylogeny and classifi-
cation: principles, methods and comments. J. Hu-
man Evol. 6:433-459.
Delson, E. 1980. Fossil macaques, phylogenetic rela-
tionships and a scenario of deployment, pp. 10-36.
In: Lindburg, D. E. (ed.). The Macaques: studies in
ecology, behavior and evolution. New York: Van
Nostrand.
Delson, E., Andrews, P. 1975. Evolution and interre-
relationships of the catarhine primates, pp. 405-
466. In: Luckett, W. P. and Salkai, F. S. (eds.).
Phylogeny of the primates: a multidisciplinary ap-
proach. New York: Plenum.
Eldredge, N. 1979. Alternative approaches to evolu-
tionary theory. In: Schwartz, J. H., Rollin, H. B.
(eds.). Models and methodologies in evolutionary
Erikson, G. E. 1963. Brachiation in New World mon-
morphology of the earliest anthropoids, pp. 141-
153. In: Sakka, M. (ed.). Morphology evolving,
morphogenesis du crane et origine de l'homme.
Paris: C.N.R.S. (Centre National de la Recherche
Scientifique).
Foooden, J. 1982. Ecogeographic segregation of ma-
Geraud, D. 1982. Paleobiogeographie de l'afrique
de nord depuis le Mioceen terminal, d'apres les
grands mammiferes. Geobios Mem. Spec. 6:473-
481.
Hershkovitz, P. 1972. The Recent mammals of the
Neotropical Region: a zoogeographic and ecologi-
cal review, pp. 311-431. In: Keast, A., Erik, F. C.,
Glass, R. (eds.). Evolution, mammals and south-
Press.
Hershkovitz, P. 1977. Living New World monkeys
Hershkovitz, P. 1982. Supposed squirrel monkey af-
finites of the late Oligocene Dolichochehus
Hofstetter, R. 1974. Apatodus et l'origine des Si-
278:1715-1717.
Hofstetter, R. 1980. Origine and deployment of the
New World monkeys emphasizing the southern
continents route, pp. 103-122. In: Ciochon, R. L.,
Chirelli, A. B. (eds.). Evolutionary biology of the
New World monkeys and continental drift. New
York: Plenum.
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