

.....

Evolutionary History of Lorisiform Primates

D. Tab Rasmussen, Kimberley A. Nekaris

Department of Anthropology, Washington University, St. Louis, Mo., USA

Key Words

Lorisidae · Strepsirhini · *Plesiopithecus* · *Mioeuoticus* · *Progalago* · *Galago* · Vertebrate paleontology · Phylogeny · Primate adaptation

Abstract

We integrate information from the fossil record, morphology, behavior and molecular studies to provide a current overview of lorisoid evolution. Several Eocene prosimians of the northern continents, including both omomyids and adapoids, have been suggested as possible lorisoid ancestors, but these cannot be substantiated as true strepsirhines. A small-bodied primate, *Anchomomys*, of the middle Eocene of Europe may be the best candidate among putative adapoids for status as a true strepsirhine. Recent finds of Eocene primates in Africa have revealed new prosimian taxa that are also viable contenders for strepsirhine status. *Plesiopithecus teras* is a *Nycticebus*-sized, nocturnal prosimian from the late Eocene, Fayum, Egypt, that shares cranial specializations with lorisoids, but it also retains primitive features (e.g. four premolars) and has unique specializations of the anterior teeth excluding it from direct lorisiform ancestry. Another unnamed Fayum primate resembles modern cheirogaleids in dental structure and body size. Two genera from Oman, *Omanodon* and *Shizarodon*, also reveal a mix of similarities to both cheirogaleids and anchomomyin adapoids. Resolving the phylogenetic position of these Africa primates of the early Tertiary will surely require more and better fossils. By the early to middle Miocene, lorisoids were well established in East Africa, and the debate about whether these represent lorisines or galagines is reviewed. Neontological data are used to address the controversial branching sequences among extant lorisid clades. Data from the skin and scent glands, when integrated with other lines of evidence, suggest that Asian and African lorisines share a common lorisine ancestry. The hypothesis of an African clade containing both pottos and galagos to the exclusion of Asian lorisines is less tenable. True galagines are found in the fossil record of Namibia, while true lorisines are known from the Miocene of Asia. The hypothetical branching sequences can be integrated with behavioral and morphological features to develop an adaptive model of lorisoid divergence. By specializing on two different foraging modes early in their radiation, lorisines and

Table 1. Some shared specializations of extant lorisisids^a

Presence of a complete longitudinal septum through the auditory bulla
Major blood supply to the brain via an ascending pharyngeal artery ^b
Tympanic ring is fused to external bullar wall ^c
Usual absence of a zygomaticofacial foramen ^d
Highly pneumatized mastoid region ^e
Hypothesized homologies of the karyotype

^a Sources include [4, 12, 17].
^b Also found in cheirogaleids.
^c Also found in platyrrhines.
^d Also absent spottily among other primate groups.
^e Also found in some anthropoids.

galagines subsequently underwent a chain of integrated evolutionary changes eventually having an impact on many components of locomotor behavior, anatomy, physiology, reproduction, life history, and social behavior. Ongoing evolutionary studies of extant galagines are illuminating population phenomena and processes of speciation in an ecological context.

Introduction

Lorisiform primates have been subjects of an ever increasing number of behavioral, ecological, morphological and reproductive studies [1, 2]. Only a little attention has been directed towards some of the basic questions about lorisiform evolutionary history [3, 4]. When and where did the lorisiform clade originate? Are any of the Eocene fossils close relatives of the lorisiform primates? What was the branching sequence among the known lorisiform lineages? What were the key adaptive features of the lorisiform radiation? When and where did adaptive divergence occur among groups?

Extensive, long-term research in paleontology and various fields of neontology will be required to obtain answers to all of these questions. The purpose of this paper is to review current understanding of lorisiform evolution, and to make contributions in four areas: (1) to review new fossil evidence relevant to lorisiform origins; (2) to evaluate the Miocene fossil record of lorisisids in the context of new information on lorisiform origins; (3) to assess the branching sequences among extant lorisid lineages, and (4) to provide an adaptive model of lorisid evolutionary divergence.

Classification of Lorisiform Primates

Monophyly of Lorisiidae

Extant lorises, pottos and galagos comprise a monophyletic group (the shared specializations of which are listed in table 1). Members of this group are usually classified together in one family, Lorisiidae, with two subfamilies, Lorisiinae for the slow-climbing forms (lorises and pottos), and Galaginae for the leaping forms (galagos).

Raising these subfamilies to family rank has become a common practice, but there is really no rationale for splitting the two groups at the family level.

Whether one splits or lumps at the family level is not simply a matter of taste; such decisions should be governed by considerations of adaptive diversity, cladistic relationships, and nomenclatural conservatism and stability. Several families of mammals contain as great or greater internal diversity than that which is found between lorises and galagines, even in their locomotor adaptations. For example, compare burrowing *Cynomys* (prairie dogs) and gliding *Glaucomys* (flying squirrels) of the family Sciuridae, marine *Enhydra* (sea otter) and desert *Taxidea* (American badger) of the family Mustelidae, suspensory *Ateles* (spider monkey) and leaping *Saimiri* (squirrel monkey) of the family Cebidae. Greater divergence occurs among other primate families than between lorises and galagines (with the possible exception of the hominoid families). No cladistic information is gained by separating the groups at the family level rather than the subfamily level. The use of Galagidae is a non-conservative choice that introduces nomenclatural instability without providing any gains in expressing the diversity or natural genealogy of the group.

Monophyly of Strepsirhini

The monophyly of lorises has never really been questioned. The interesting phylogenetic debates about extant lorises have been about their relationship to cheirogaleids and other Malagasy primates. Gregory [5] placed Malagasy primates and Eocene adapoids in a prosimian infraorder Lemuriformes, while lorises were placed in an equally ranked Lorisiformes, a classification still used by some researchers today [4]. It is now widely accepted that the Lorisiformes and the Malagasy primates are more closely related to each other than either is to omomyids or adapoids (but there are exceptions [6]). The proper name to apply to this combined clade of lorises and Malagasy primates is not at all obvious.

Several authors, beginning with Szalay and Delson [7], have used the infraorder Lemuriformes Gregory, 1915, for the tooth-combed prosimian clade, containing Malagasy primates and lorises, but not adapoids. However, this version of 'Lemuriformes' differs substantially from the initial use of the taxon by Gregory [5] and many subsequent authors who excluded the lorises, and included Eocene adapoids which lack a tooth comb. The use of Lemuriformes by Szalay and Delson [7] does not just 'telescope' the taxon, enlarging it to include the lorises – it revamps the relationships among groups. Therefore, Gregory's Lemuriformes should not be used as a taxon delimiting the tooth-combed prosimians; by simply eliminating adapoids from the group, it may be applied in a more restricted sense to the clade of Malagasy primates.

Another taxon commonly used to denote the tooth-combed prosimian clade is Strepsirhini Pocock, 1918. However, this taxon has been even more confusing than Lemuriformes when applied specifically to tooth-combed prosimians because Strepsirhini has been used often as a primitive wastebasket taxon to accommodate anything not perceived as haplorhine, itself a very problematic taxon. However, if used in a strict sense, the term Strepsirhini is available for the clade of tooth-combed prosimians. Membership in a strictly defined Strepsirhini must be demonstrated by the presence of shared *specializations*. For primates lacking a tooth comb, such as the aye-aye (*Daubentonia*), the hypothesis of membership within the strepsirhine clade must be documented by other lines of evidence [8].

Relationship between Lorisidae and Cheirogaleidae

The possibility has been raised that lorisids and cheirogaleids share a close phylogenetic relationship exclusive of any other Malagasy taxa [9–13]. This hypothesis was based mainly on shared patterns of arterial blood flow to the head and pneumatization of the mastoid portion of the temporal bone. A classification was adopted that put cheirogaleids within Lorisiformes [7]. As this shift in consensus was occurring during the late 1970s through the 1980s, molecular and karyotypic data became available that either indicated cheirogaleids to be a member of the Malagasy radiation [14–20], or were unable to resolve branching sequences [21]. Finally, Martin [4] conducted a thorough review of all published data, and Yoder [22, 23] compiled new data on mitochondrial nucleotide sequences. Martin and Yoder concluded that cheirogaleids do belong in the Malagasy clade, and that the basicranial traits shared between cheirogaleids and lorisids must be primitive for strepsirhines (as suggested by Le Gros Clark [24]), or must have been attained convergently. In this paper, we accept the conclusion that the family Cheirogaleidae does not belong within Lorisiformes.

The Problem of Lorisiform Origins

Conceptual Issues in Strepsirhine Origins

Researchers have less avidly sought lorisiform ancestors among Eocene primates than they have looked for anthropoid ancestors, but the same kinds of conceptual and empirical troubles that beset the question of anthropoid origins [25, 26] also come into play when investigating lorisiform origins. A central issue is whether or not an early Tertiary primate is strepsirhine or haplorhine. The question of lorisiform origins cannot be successfully addressed until ‘strepsirhinism’ (in the strict sense advocated here) can be identified in the fossil record [27, 28]. Such action requires that strepsirhinism be judged on the basis of preserved morphology in the fossil record, not soft tissues such as placentas, retinas and nose structures.

The broad, paraphyletic concept of Strepsirhini emerged in part from the incorrect perception that some degree of primitive uniformity occurs among strepsirhines. Modern strepsirhines share several specializations of the cranium and dentition not found in other primates. These traits can be used as a guide for assessing membership within the strepsirhine clade among fossil forms. How the clade based on hard tissue matches with the one that would be devised if fossil soft tissues were available cannot be determined. The true match between a clade based on hard tissues and an ontogenetically independent one based on soft tissues is probably almost always a nested relationship, rather than a congruous one. The two clades may be exactly equivalent when examining only those primates that happened to survive to the present, but things become much more complicated when diverse early Tertiary radiations are also considered. When primate diversity is viewed against a backdrop of time, one clade is almost certainly a broader paraphyletic taxon containing the other. To be more precise, this problem is not restricted to the contrast between hard tissue clades and soft tissue clades. The same concept holds true for any clade defined by more than one apparent synapomorphy, even if all synapomorphies are osteological or all are molecular. For a clade defined by n independent synapomorphies, there are likely to be, in reality, n nested clades, unless two or more synapomorphies had their evolutionary origins at exactly the same time. The important difference between hard and soft tissues is

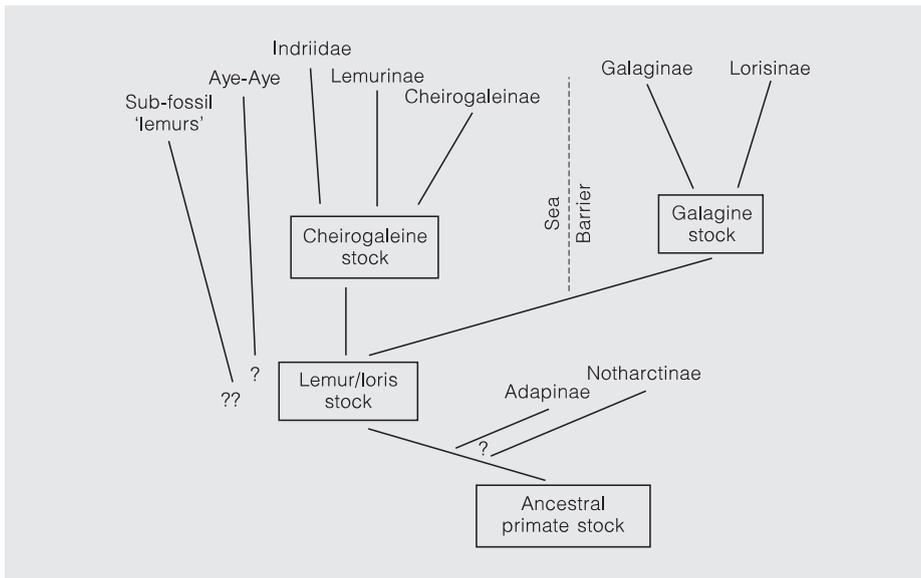


Fig. 1. Phylogenetic hypothesis about the ancestral strepsirhine ('lemur/loris stock') posed by Charles-Dominique and Martin [34]. This hypothesis excludes the superficially lemur-like notharctines and adapines from the true strepsirhine clade, and suggests that basal strepsirhines exhibited an assemblage of characters shared in common by the 'cheirogaleine stock' and the 'galagine stock'. Reproduced from *Nature*.

that the nested sequence of clades can be discovered for the former but not for the latter.

Based on phenetic similarities between Eocene adapoids and Malagasy lemurs, some early researchers concluded that adapoids gave rise to lemurs [29, 30], but there was early dissent from this view [31–33]. According to this hypothesis, non-lemurid Malagasy primates (cheirogaleids, indrids, aye-ayes, several subfossil taxa) and lorises must have been secondarily derived from a primitive, lemur-like primate. Gregory [5, p. 215] discussed how the postcrania of *Galago* and *Perodicticus* could be 'derived directly from the *Notharctus* type', which Gregory considered to be essentially lemurid.

The myth of an ancestral lemur was challenged in a paper titled 'Evolution of lorises and lemurs', written by Charles-Dominique and Martin [34] in 1970. Based on their pioneering field studies of *Galago demidoff* and *Microcebus murinus* [35], these two authors pointed out that the pervasive behavioral, ecological and morphological similarities shared by cheirogaleids and lorises are best interpreted as primitive retentions from a common ancestor. If their hypothesis is true, then the lemurid morphology commonly used as a morphotype for primitive prosimians is wrong, and there is no reason to believe that lemurid-like morphology found in the Eocene is anywhere near the ancestry of strepsirhines. Charles-Dominique and Martin [34, p. 259] concluded: 'The Eocene fossil Notharctidae, widely regarded as direct relatives of the Malagasy lemurs, probably came from a separate stock roughly contemporaneous with the hypothetical lemur/loris stock' (fig. 1).

Szalay and Katz [9] took issue with the conclusion of Charles-Dominique and Martin that the similarities shared by cheirogaleids and lorisids were primitive. They wrote [9, p. 90] that ‘adapid-lemuroid ties are one of the most convincing among groups separated by such a time gap as between the Eocene and Recent’ and that the two groups are ‘astonishingly similar’. As late as 1987, Szalay et al. [28, p. 96] proclaimed that ‘the uniformity of such special strepsirhine complexes as the basicranial morphology along with cranial and postcranial similarities’ allowed one to make a precise phylogenetic tie between Eocene adapoids and modern lemurids.

In reality, strepsirhine uniformity does not exist; the historical debates over the phylogenetic relationships of cheirogaleids, aye-ayes, and adapoids is evidence enough for that. Coming to grips with the real diversity of prosimians forces old views of the Eocene ancestry of strepsirhines to break down. Simply because something has been considered ‘lemur-like’ does not qualify it as an ancestral strepsirhine. Basal radiations of all the major primate taxa must have shared many primitive features. The search for the true strepsirhine ancestor must be more rigorous.

Eocene Candidates for Strepsirhine Ancestry

Are Eocene Adapoids Primitive Strepsirhines?

If Charles-Dominique and Martin [34] were correct about the ancestral strepsirhine, then nearly all known adapoids can be eliminated as lying near the ancestry of Strepsirhini. If small size, nocturnality, quadrupedal scrambling and leaping, and generalized omnivory are primitive for strepsirhines [34], then all notharctines and adapines, and most cercamoniines, are too specialized to be near the ancestry of strepsirhines. If the basicranial similarities shared by cheirogaleids and lorisoids are primitive for strepsirhines [23, 24] then no Eocene primates known by crania lie near the ancestry of strepsirhines.

The vertically implanted, spatulate incisors of adapoids also argue against an adapoid origin for strepsirhines. Procumbent, pointed lower incisors are probably primitive for euprimates, as supported by the fact that pointed, procumbent lower incisors are shared by strepsirhines, tarsiers, omomyids, and by outgroups such as plesiadapiforms, tree shrews, and many insectivore and proteuthere families. It seems reasonable to conclude that the strepsirhine dental comb derives from primitive, jutting, pointed incisors, rather than from vertical, spatulate ones. Why the strepsirhine tongue and sublingua should closely resemble those of tree shrews [36] is difficult to explain if strepsirhines originated from an ancestor with vertically placed, spatulate incisors.

Relying mainly on *Notharctus* and *Adapis*, Wortman [37] and Stehlin [32] reasoned very early that adapoids were too specialized to have given rise to lemurs, citing adapoid specializations of the incisors, canines, and basicranium. However, not until after the paper by Charles-Dominique and Martin [34] did the hypothesis of adapoid origins for strepsirhines come under closer scrutiny. Cartmill and Kay [38] sought possible synapomorphies to link strepsirhines to adapoids, and found none. Other authors also questioned the idea that adapoids were Eocene strepsirhines when they found dental and cranial specializations shared by adapoids and anthropoids to the exclusion of strepsirhines [25, 26, 39, 40]. True strepsirhines have broad gaps between their upper, central incisors allowing for physical continuity between rhinarium and

vomeronasal organ; this midline interincisal distance in notharctines was found to be narrower than those of strepsirhines (and within the platyrrhine range) while adapines overlapped only the narrowest of strepsirhines (*Propithecus* and some lorises [27]). Morphological features of the talus hypothetically linking adapoids and true strepsirhines have been described [41, 42], but polarity of these features remains uncertain, and it is not clear why the talar traits should be weighed more heavily than dental or cranial evidence even if they are specializations rather than ancestral conditions.

Given this background, it is useful to review briefly individual adapoid taxa that may be relevant to strepsirhine origins. The known diversity of adapoids increases at a steady pace. Several clades and lineages dating back to the base of the Eocene are classified as 'adapoid', but the relationships among lineages are unclear, and therefore, each must be addressed individually. A classification of all prosimian genera mentioned in the text appears in table 2.

Possible Strepsirhine Ancestors among Adapoids

Adapis parisiensis. A strepsirhine dental comb or scraper has never been found on an Eocene primate jaw. Convergent acquisition of somewhat different dental combs has been documented among unrelated early Tertiary mammals [43]. Several peculiar arrangements of the anterior teeth of Eocene prosimians have been identified as possible precursors or derivatives of a true tooth comb [44-46]. Gingerich [44, 47] emphasized that the lower canines of *Adapis parisiensis* were incorporated into a single functional unit with the lower incisors, as relatively low-crowned teeth with a flattened, anterior occlusal edge. He considered this alignment to be 'an initial step required by the functional reorganization of the canines into a unit with the incisors, as is later seen in the dental scraper of Lemuriformes' [44, p. 176]. Gingerich also cited morphological similarities between the folivory-adapted molars of extant *Haplemur* and *Lepilemur* on the one hand, and those of *Adapis* on the other [48], that suggested possible phylogenetic ties between *Adapis* and the origin of the Malagasy clade. This hypothesis has been criticized by later researchers [25, 38, 49].

Pronycticebus. Among the hundreds of known Eocene primates, none has received more attention as a possible loriform than *Pronycticebus gaudryi*. The famous skull of this species was originally described as having possible affinities with lorises [50]. Le Gros Clark's [24] careful study pushed *Pronycticebus* away from loroids towards lemuroids. Interestingly, Le Gros Clark foreshadowed the much later papers by Charles-Dominique and Martin [34] and Yoder [23] by concluding that the basicranial features of *Pronycticebus* represented 'a specialization which could hardly have given rise to the (in many respects) *more primitive loriform type*' [24; italics added]. Simons [51] pushed *P. gaudryi* back in the direction of loroids, while Szalay [52] pushed it away again. A crushed skull and postcranial skeleton attributed to a new species of *Pronycticebus* [53], found at the site of Geiseltal, Germany, may belong instead to *Caenopithecus* [54]. The Geiseltal skeleton was not evaluated with respect to its possible affiliations with true strepsirhines [53]. Given the presently available evidence, neither *Pronycticebus gaudryi* nor *Adapis parisiensis* can be viewed as lying especially close to the origin of true strepsirhines.

Anchomomyini. The best 'adapoid' candidates for true strepsirhine ancestry are probably some members of the European (and possibly North African) tribe Anchomomyini. Although classified within the subfamily Cercamoniinae, the anchomomyins are a distinctive group whose relationships remain uncertain. The anchomo-

Table 2. A classification of prosimian genera mentioned in the text

Order Primates	
Suborder <i>incertae sedis</i>	Infraorder Lorisiformes
Superfamily <i>incertae sedis</i>	Superfamily Lorisoidae
Family <i>incertae sedis</i>	Family Lorisidae
<i>Altiatlasius</i>	Subfamily <i>incertae sedis</i>
<i>Azibius</i>	<i>Progalago</i>
Superfamily Adapoidea ¹	<i>Mioeoticus</i>
Family Notharctidae	Subfamily Galaginae
Subfamily Notharctinae	<i>Galago</i>
<i>Notharctus</i>	? <i>Komba</i> ³
Subfamily Cercamoniinae	Subfamily Lorisiinae
<i>Aframomys</i>	<i>Loris</i>
<i>Caenopithecus</i>	<i>Nycticebus</i>
<i>Pronycticebus</i>	<i>Nycticeboides</i>
? <i>Djebelemur</i> ²	<i>Perodicticus</i>
Tribe Anchomomyini	<i>Arctocebus</i>
<i>Anchomomys</i>	Infraorder Lemuriformes
? <i>Omanodon</i> ²	Family Cheirogaleidae
? <i>Shizaradon</i> ²	<i>Cheirogaleus</i>
Subfamily Sivaladapinae	<i>Mirza</i>
<i>Sivaladapis</i>	<i>Microcebus</i>
<i>Indraloris</i>	Family Lemuridae
Family Adapidae	<i>Lemur</i>
Subfamily Adapinae	Family Indridae
<i>Adapis</i>	<i>Propithecus</i>
Suborder Strepsirhini	Family Daubentoniidae
Infraorder <i>incertae sedis</i>	<i>Daubentonia</i>
Superfamily Plesioipithecoidea	Suborder Tarsiiformes
Family Plesioipithecoidea	Family Omomyiidae
<i>Plesioipithecus</i>	Subfamily Microchoerinae
	<i>Necrolemur</i>
	Family Tarsiidae
	<i>Afrotarsius</i>
	<i>Tarsius</i>

¹ The subordinal or infraordinal classification of adapoids remains controversial. Among the subordinal choices are Strepsirhini Pocock, 1918; or if one is not convinced of strepsirhine affinities, the infraorder Adapiformes Szalay and Delson, 1979, may be raised to subordinal rank; or if one favors special affiliation with anthropoids, one may use Neopithecini Wortman, 1904 [206].

² The classification of these three genera of small-bodied primates from the Paleogene of North Africa is uncertain (see text).

³ The galagine status of *Komba* should be considered hypothetical.

myins are the only known adapoids that reasonably approach the conception of a primitive strepsirhine as developed by Charles-Dominique and Martin [34]. They are small-bodied forms with molars similar to those of cheirogaleids [33, 47, 55–57]. The preserved sockets of the anterior teeth suggest there was no tooth comb.

No crania are yet known of *Anchomomys*, but recently, an assemblage of postcrania from Middle Eocene deposits of the Spanish Pyrenees have been collected that represent a new species that weighed about 120 g [58]. The Spanish *Anchomomys*

exhibits the sloping talo-fibular joint that is found in large-bodied adapoids and in true strepsirhines [41]. This Spanish sample of postcrania is potentially the most exciting data set from the northern continents for addressing questions of an adapoid ancestry of strepsirhines.

Possible Ancestry among Omomyids

Schmid [45] discovered that the lower incisors of the microchoerine omomyid, *Necrolemur antiquus*, bear fine striations in the enamel caused by grooming hair. These striations are similar to those that occur on the teeth of the modern strepsirhine dental comb, which suggested to Schmid that omomyids may be related to strepsirhines [59]. The idea of an omomyid-strepsirhine clade – or even a more precise omomyid-lorisiform clade [60] – has found support mainly in the work of Schwartz [6]. Features shared by lorisids and omomyids (or actually, a subset of omomyids, because some genera are transferred by Schwartz to other families) that are used in support of the hypothesized clade are the elongate and narrow trochlear facet of the astragalus, the reduction of molar paraconids, and the procumbent, pointed lower incisors [6]. However, the link between omomyids and tarsiers is so strong [31, 61–65], that all known omomyids can be classified comfortably in Tarsiiformes. A tarsiiform origin for strepsirhines would be a surprise.

Biogeography of Strepsirhine Origins

The search for lorisiform or strepsirhine ancestors among adapoids and omomyids of the northern continents has been dictated by the limitations of the fossil record. In the absence of an Eocene fossil record for Africa, paleontologists naturally look for the ancestry of modern groups among the taxa that are represented in the fossil record. On biogeographic grounds, however, there are reasons to believe that the northern primate groups are not directly relevant to true strepsirhine ancestry. Given the strepsirhine distribution in Madagascar and Africa, with only one subfamily containing two extant genera in Asia, it makes sense to look for the origin of true strepsirhines in the early Tertiary of Africa. Fortunately, new Paleocene, Eocene and Oligocene primates are being discovered by active field projects in Egypt, Tunisia, Algeria, Morocco and Oman. African alternatives to the northern omomyids and adapoids are available finally for comparative study.

Fossil Prosimians of the African Eocene

Despite the low number of prosimian fossils that have been found in the early Tertiary of Africa (table 3), the higher taxonomic diversity represented by the rare finds exceeds that of any other continent during the Eocene, with representatives of cercamoniine and anchomomyin-like adapoids [57, 66, 67], omomyids and tarsiids [68–70], plesiopithecids which are possibly true strepsirhines [46, 71], and, finally, a mouse-lemur-sized primate with cheirogaleid-like cheek teeth [Simons, pers. commun.]. Africa was clearly a center of prosimian diversification during the early Tertiary.

The earliest of the African prosimians is *Altiatlasius*, known from about ten isolated teeth found in Paleocene deposits of Morocco [72]. *Altiatlasius* is probably the earliest known true primate (excluding Plesiadaptiformes) and at least in its teeth, it is

Table 3. Prosimians^a of the Paleocene to Oligocene of Africa^b

Locality and species	Described fossil material
Adrar Mgorn 1, Morocco <i>Altiatlasius koulchii</i>	ten isolated teeth
Chambi, Tunisia <i>Djebelemur martinezi</i> ? primate, unnamed	lower jaw with P ₃ -M ₃ and isolated uppers one lower molar
Gour Lazib, Algeria <i>Azibius trerki</i>	one lower jaw with three teeth
Thaytiniti, Oman Omomyidae? sp. nov.	two isolated molars
Taqah, Oman <i>Omanodon minor</i> <i>Shizaradon dhofarensis</i>	several isolated teeth one lower molar
Fayum, Egypt, quarry L-41 <i>Plesiopithecus teras</i> <i>Aframonioides diedes</i> New small-bodied taxon	cranium and 3 lower jaws several lower jaws several lower jaws
Fayum, Egypt, quarry E Omomyidae, unnamed	a few isolated teeth
Fayum, Egypt, quarry M ? Lorisoid or plesiopithecoid, unnamed <i>Afrotarsius chatrathi</i>	one isolated tooth one lower jaw with parts of 5 teeth

^a Note that several of these taxa have been identified as anthropoids rather than prosimians (*Djebelemur*, *Omanodon*, *Shizaradon* [73]).

^b Full references for the data in this table are presented elsewhere [74].

also one of the structurally most primitive or generalized. No evidence suggests that *Altiatlasius* is specifically lorisiform. Still, *Altiatlasius* does offer support to the idea that primates initially differentiated in Africa.

Small-Bodied Strepsirhine Candidates

Among the newly found prosimians of the African Paleogene is a very enigmatic assemblage of small-bodied forms that have been classified already by various authors as anthropoids, adapoids, and cheirogaleids. This group includes *Omanodon* and *Shizaradon* of Oman [57], *Djebelemur* of Tunisia [66], and a new, undescribed primate from Egypt. These primates are known only by isolated cheek teeth, and in the case of *Djebelemur*, one lower jaw. *Djebelemur* shows similarities to cercamoniine adapoids [66] and to early anthropoids [73], and has not really been mentioned in the context of strepsirhine origins. In contrast, *Omanodon* and *Shizaradon* have been investigated closely for possible relationships to strepsirhines, particularly cheirogaleids. An excellent, detailed study of the Omani genera by Gheerbrant and colleagues [57] concluded that these two Omani genera are related most closely to European anchomomyins, although similarities to cheirogaleids were also highlighted. The Omani teeth are also similar to those of a new primate known by several specimens from quarry L-41 of the Fayum, Egypt, heretofore important as the site of Eocene anthropoid primates [74]. The age of quarry L-41 is probably late Eocene [75].



Fig. 2. Cranium and unas-sociated mandible of *Plesioptithecus teras* from quarry L-41, Fayum, Egypt. The cranium has been distorted by crushing. Among the distinctive characteristics are the relatively short, deep rostrum and the enlarged upper canine, the enlarged orbit indicating nocturnality, and the heavy nuchal cresting. Along with the upper molar shape, these features give the skull a decidedly loris-like appearance. Reproduced from *Evolutionary Anthropology*.

The new primate is roughly the size of a mouse lemur, which it also resembles in dental structure. It will serve as an interesting point of comparison with the Omani primates, with anchomomyins, and with true strepsirhines. These recent finds from Tunisia, Oman, and Egypt are exciting, but also frustrating, because not enough is known of the animals to judge what the mixed pattern of similarities really mean [57, 73].

Plesioptithecus. The anterior dentition and cranium (fig. 2) are known for *Plesioptithecus teras*, another prosimian from the Fayum's quarry L-41 [71, 76]. This species has been interpreted as a close relative of strepsirhines which shows several features that are specifically loris-like [46]. Additional preparation of the delicate cranial specimen allows a more detailed evaluation of its taxonomic status than was previously possible.

In the initial description of the skull, strepsirhine and lorisiform-like characters were listed [46]. These included the projecting, compressed lower canine (or incisor?) that resembles the teeth of a true strepsirhine tooth comb; the buccolingually compressed upper canine; the lacrimal foramen positioned at the orbital margin; the obliquely oriented molar trigonids with paraconids reduced to a shelf; and the reduced size of the upper and lower third molars. These features are not viewed as evidence specifically allying *Plesioptithecus* with Lorisiformes because the retention of four premolars, and the relatively short P_2 crown, eliminate *Plesioptithecus* from being within the lorisiform clade. In addition, apparent specializations of the anterior, tusk-like teeth remove *Plesioptithecus* from lying directly in the ancestry of extant strepsirhines.

Among strepsirhines, *Plesioptithecus* shows special resemblances to lorisids in the heavily built cranium, short and deep muzzle, and greatly enlarged orbits. The initially reported mastoid inflation [46] cannot be sustained now that the cranium has

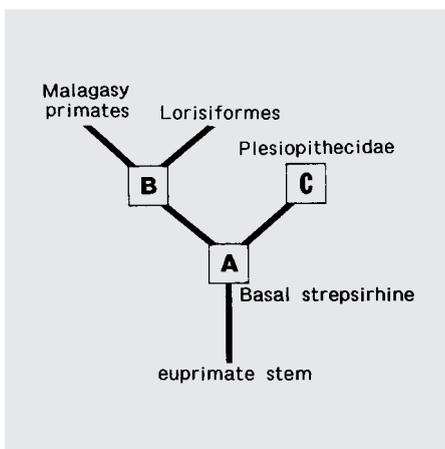


Fig. 3. Hypothesized phylogenetic relationships of *Plesiopithecus*. Node A represents an ancestral true strepsirhine, characterized by the following morphological specializations: elongate, procumbent lower canine; flattened, blade-like upper canine; oblique trigonids with paracristid reduced to a shelf; P_2 about the same size or only slightly taller than P_3 (while P_1 is retained from the euprimate ancestor). Node B represents the common ancestor of extant Malagasy primates and Lorisiformes, characterized by the following specializations: loss of the first premolar; tall, sub-caniniform P_2 . Node C represents specializations of *Plesiopithecus*, which include: loss of lower incisors (or one pair of incisors and canine?), enlargement of upper and lower canines.

been better prepared. Although the bone of the mastoid region is thick and heavy, there is no certain evidence that the region was notably inflated with pneumatic spaces. The few loris-like features of the cranium of *Plesiopithecus* are not strong enough to link this genus specifically to lorisiform primates, especially given the presence of a P_1 in some specimens and the specializations of the enlarged canine and loss of lower incisors. The loris-like cranial features are best viewed as primitive attributes retained by modern lorisines but subsequently lost by most other strepsirhine taxa. This inference, combined with the conclusions of Charles-Dominique and Martin about ancestral strepsirhines [34], suggests an interesting combination of primitive features: a generalized, nocturnal, relatively small-bodied primate with a proportionally robust, short-faced, low-vaulted cranium.

Our interpretation of *Plesiopithecus* is that it is an early strepsirhine, showing unique specializations of the incisors and canines (fig. 3). The isolated tooth from the early Oligocene of the Fayum described as a lorisoid molar [69], may be plesiopithecoid instead. The somewhat loris-like features of the cranium of *Plesiopithecus* could be primitive for Strepsirhini, an hypothesis that has implications for the interpretation of Miocene crania from East Africa.

Summary of Paleogene Record

Some of the major points of the foregoing review are the following. Uncritically viewing 'lemur-like' or 'primitive' primates of the Eocene as belonging to the strepsirhine clade cannot be justified. Strepsirhines are a distinctive, specialized primate clade of uncertain ancestry. The African Eocene is now producing credible strepsirhine candidates. Several small-bodied forms resemble cheirogaleids and European *Anchomomys*, but all are too poorly known for confident phylogenetic resolution. *Plesiopithecus* may be a true strepsirhine, an hypothesis based mainly on dental features. Assuming that this is correct, *Plesiopithecus* suggests that a large-eyed, robust cranium with a loris-like attributes may be primitive for strepsirhines.

The Lorisoid Fossil Record

Miocene of East Africa

Late Eocene and early Oligocene sites of North Africa are followed by a long gap in the African fossil record. The next appearance of strepsirhine primates is in the early Miocene of East Africa, where members of the family Lorisidae have been found. The Miocene lorisids occur too late in the fossil record to provide direct information about the origin of the family. Potentially, what they may provide is information about the early taxonomic divergence between the subfamilies Lorisinae and Galaginae, as well as insight into the adaptive divergence into slow-climbing and leaping specialties. Interest in these issues has dominated the study of the early Miocene lorisids.

The earliest fossil lorisids are from sedimentary and volcanic deposits associated with two ancient volcanoes, Tinderet and Kisingiri, located in northern Kenya, east of Lake Victoria. Fossil mammals have been found at several fossil-bearing sites in this region, with Rusinga Island of the Kisingiri system and Songhor of the Tinderet system being the most important sites for lorisids. The lorisids at Songhor are part of a mammalian assemblage that resembles faunas of modern tropical rain forests [77]. The Rusinga Island beds that yield lorisids represent riparian woodland, as indicated by paleosols [78] and by the associated fauna, which includes apes (*Proconsul*, *Dendropithecus*), flying squirrels (Anomaluridae), forest elephant shrews (*Miorhynchocyon*) and chevrotains (Tragulidae), among others [79, 80]. The Tinderet sites are the oldest at approximately 19 Ma, while the Kisingiri sites are slightly younger, dating from 17 to 18 Ma [81–83].

Lorisoid fossils are also found at two early Miocene sites in Uganda (Moroto, Napak) associated with volcanic activity 300 km north of the Kenyan sites [84]. Younger lorisoid fossils occur at the middle Miocene sites of Maboko Island in Lake Victoria, and Ft. Ternan near the older Tinderet sites [85, 86]. Details on the occurrence of fossils at each of the East African sites can be found elsewhere [85–88]. Isolated galagine teeth have recently been found at a geographically outlying site, an early Upper Miocene locality of cave breccias in northern Namibia [89].

The first fossil lorisids were found by Hopwood in 1931, but these were not described until 35 years later [87]. The first described fossil lorisid was the type mandible of *Progalago dora* [90]. A long-standing debate was initiated with this first description because MacInnes allocated his new fossil to the subfamily Galaginae. The correct subfamily affiliation of *Progalago* still remains in question; one of the most important historical threads in the study of the Miocene lorisoids has been debate over subfamilial allocation of material. Additional fossil material of *Progalago* was found in subsequent years, including specimens used to diagnose two smaller species, *P. robustus* and *P. minor* [91], species later placed in a new genus *Komba* [87]. Among the more interesting new fossils was an endocast with fragments of the basicranium adhering, including the auditory bullae. At this point, all three recognized species were considered to be galagines.

In 1954, the cranium of a lorisid (fig. 4) was found on Rusinga Island and described by Le Gros Clark [92]. Among the notable features of this cranium are the large orbits indicating nocturnality [93], and the configuration of the anterior tooth sockets. The incisor alveoli are very small and are widely separated from each other, a trait seen today among species with a tooth comb in the lower dentition. Le Gros Clark

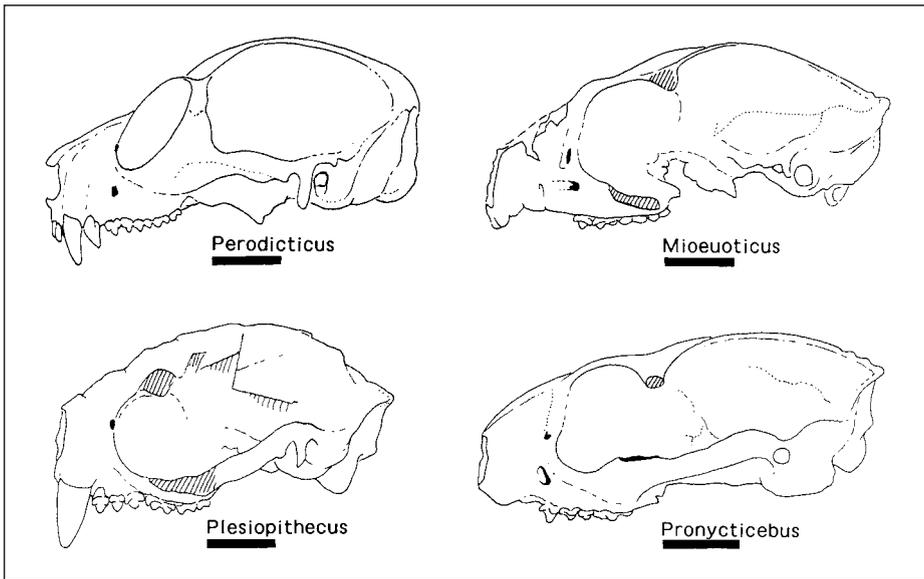


Fig. 4. Crania of extant *Perodicticus* and three fossil primates illustrating shared aspects of shape that resemble lorises, such as the short, deep rostrum; the relatively flat cranial base; the enlarged orbits; the low, heavily buttressed vault; and the prominent nuchal cresting. The fossils are the following: a skull attributed to *Mioeuoticus*, an early Miocene loroid from Rusinga Island, Kenya (modified from [92]); *Plesiopithecus*, a late Eocene strepsirhine from Fayum, Egypt; and *Pronycticebus*, a middle Eocene adapoid from Memerlein, France (modified from [93]). Bar scale = 1 cm.

[92, p. 5] hinted that the fossil may be loroid, but he emphasized that the specimen ‘shows an interesting assemblage of morphological characters not found in combination in any of the Recent loroidform genera’. Lacking a mandible that was comparable to the holotypes of species of *Progalago*, Le Gros Clark deferred from naming a new taxon.

The Rusinga skull was followed by discovery of a facial cranium from Napak, Uganda, which Leakey [94] named *Mioeuoticus bishopi* and placed in Galaginae. A thorough revision of the Miocene loroids was published soon afterwards by Simpson [87], who erected the new genus, *Komba*, for the two smaller species, now *Komba robusta* and *K. minor*. He was skeptical of the generic distinctiveness of Leakey’s Napak face, synonymizing it with *Progalago*, and suggested that the Rusinga cranium might also belong in *Progalago*. Simpson named a new species, *P. songhorensis* for some material previously put in *P. doriae*. Simpson differed from Le Gros Clark and Thomas [91] in concluding that the anterior tooth sockets preserved on some of the lower jaws indicated a fully modern tooth comb, a conclusion later substantiated by Walker [95]. Finally, Simpson also mistakenly identified a new genus and species, *Propotto leakeyi*, as a loroid, when in fact, it was later determined to be a bat [95]. Simpson did not believe that the Miocene forms could be allocated to either of the modern subfamilies, Loroidinae or Galaginae.

The cranium from Rusinga and the face from Napak became the focus of important discussion. Szalay and Katz speculated that the Rusinga cranium represented a phylogenetically intermediate stage between early Tertiary cheirogaleids and modern lorises in order to bolster their theory of a cheirogaleid-lorisid clade [9]. Walker's evaluation of the Rusinga cranium and the Napak face suggested that both specimens were lorises rather than galagines, based on lorisine features such as an uninflated auditory bulla [96]. Because of similarities to the Napak face, Walker classified the Rusinga cranium as *Mioeuticus* sp. nov. An additional lorisine maxillary specimen was identified from the Middle Miocene site of Ft. Ternan, but also not named [85]. The allocation of the faces to an allegedly lorisine-like genus, *Mioeuticus*, is central to many of the conclusions that have been reached about Miocene lorises. We will therefore review some of the cranial data in more detail.

Le Gros Clark [92] described a mosaic pattern of resemblances between the Rusinga skull and extant lorises. The fossil resembled lorises rather than galagines in its abbreviated face. It resembled Asian rather than African lorises in its uninflated bulla and less convex mastoid. A feature of the fossil that resembled galagos more closely than any lorisine was the small foramen lacerum. Features that Le Gros Clark interpreted as primitive, but that are absent from all extant lorises, included the heavy nuchal cresting, relatively large palate and nasal aperture, and the ectotympanic that was relatively independent ventrally without extensive fusion to the lateral part of the petrosal (most closely approximated among extant species in *G. crassicaudatus*).

In contrast to Le Gros Clark's interpretation, Walker found the Rusinga cranium to have 'an unmistakable lorisine stamp', listing six features: strongly constructed cranium, raised temporal ridges, orbits directed upwards, weakly inflated bulla and mastoid, internal nares broad, and only slight basicranial flexion [96]. Walker concluded that the Rusinga skull might represent the ancestral African lorisine, or even an ancestor of African and Asian lorises combined.

The Postcranium Debates

After Simpson's review [87], postcranial fragments of lorises were found in the collections from Napak, Uganda, and from Songhor, Kenya [97]. Walker [97], who undertook the study of these bones, encountered a major problem that has yet to be resolved to everyone's satisfaction: how to allocate isolated postcranial elements to species. The six species diagnosed on the basis of dentitions ranged in a graded size series from small forms similar in size to *Galago demidoff* up to ones larger than *Galago crassicaudatus*. The gaps between successive species in the size sequence were not enough to lend great confidence to all postcranial allocations. Walker chose to assign all the postcrania to either *Progalago* or *Komba* [96, 97]. His morphological comparisons revealed galagine-like structure of the fossils, especially in the femur. For example, the head of all specimens was cylindrical, the shaft was very straight, and the distal end was anteroposteriorly deep but narrow with a raised patellar groove [98, 99]. Walker also interpreted the calcaneus as having a synovial joint with the navicular, a facet found in galagines but not in lorises or cheirogaleids. The most important difference between the fossils and modern galagos was that the calcanei (allocated to *P. doriae*, *K. robusta*, *K. minor*) were relatively short, in contrast to the elongated calcaneus found in the living forms [95, 97]. The Miocene postcrania were unambiguous in indicating active, leaping animals, certainly more similar to galagines than to lorises: although the dental and cranial remains show quite eclectic resem-

blances to different galagines and lorises (Simpson, 1967), all the postcranial elements are clearly from animals that had a vertical clinging and leaping locomotion like that of modern galagos [97, p. 254].

Walker was the first researcher to examine in detail both the cranial fossils and the postcranial evidence pertaining to the Miocene lorises. His analyses yielded four galagine species, two each in the genera *Progalago* and *Komba*, and three lorine species, two in *Mioeuoticus* and one in an unspecified genus [85, 95, 97]. The putative galagines were known by postcrania and dental remains but no crania (except the basi-cranial fragments clinging to the Rusinga endocast), while the lorises were known by crania but no postcrania.

Meanwhile, Szalay [100] examined postcranial elements from the East African assemblage and concluded that the foot of the Miocene forms was not like that of modern galagines. He could not find the calcaneonavicular joint reported by Walker; this joint was later identified as one part of two separated anterior calcaneal facets for the plantar surface of the talar head and neck [101]. Szalay interpreted any one of the three different sizes of calcanei to be similar to those of cheirogaleids, and therefore 'ideal to pass for a structural ancestor for the calcaneum of lorises and galagos'. This echoed Szalay's earlier interpretation of the cranium as a connecting link between ancestral cheirogaleids and modern lorises [9].

Having recognized the importance of postcrania for interpreting the Miocene loriseid material, Gebo [101] conducted a detailed study that included comparisons of foot morphology and locomotor behavior among extant lorises, galagines and cheirogaleids. Gebo found that the smallest foot bones, assigned to *Komba minor*, indicated a leaping animal, but not specialized to the extent found in *Galago*. Similarly, foot bones allocated to *Progalago songhorensis* also indicated a leaping and quadrupedal animal, 'reminiscent of a smaller version of *G. crassicaudatus*' but with less calcaneal elongation. In contrast, a calcaneus (KNM-SO 1364) assigned by size to *K. robustus* was quite different, with a downward and medially sloping heel that suggested greater emphasis on intrinsic foot muscles, which in turn suggested climbing. Proportions of this bone resembled those of *Cheirogaleus* rather than the more actively leaping *Mirza* or *Microcebus*. In a later publication, Gebo [88] allocated this bone to the putative lorine, *Mioeuoticus bishopi*. Finally, Gebo identified a talus with an interesting assemblage of features, some found typically in lorises (flattened and wide talar head with a dorsal notch), some unique (large gap between anterior plantar facets), and some indicating leaping behavior (long, straight talar neck, and high talar body) [101]. Because of its lorine features, Gebo [101] initially suggested possible affiliation with *Mioeuoticus*, which was not otherwise known from the same locality (Koru). Later, Gebo [88] formally listed the specimen as belonging to *Mioeuoticus*. In summary, Gebo's study of the foot identified bones of four different species, all of them generalized and primitive with respect to the extreme lorine-galagine divergence seen among extant forms. Within the general 'cheirogaleid-like' assemblage, two leaned towards leaping specializations (attributed to *K. minor* and *P. songhorensis*) and two leaned towards climbing (attributed to *M. bishopi* and the Rusinga species of *Mioeuoticus*).

Gebo's foot study was followed by his more complete evaluation of the entire assemblage of known postcrania [88]. While some elements, such as the humerus, showed a mixture of loriseid-like and cheirogaleid-like structures, other elements were distinctly loriseid-like. In particular, the femurs from East Africa 'have clear galagine

affinities' [88], as reflected in their cylindrical heads, the straightness of the shaft, and the narrow and anteroposteriorly deep distal end. This result is especially interesting because femurs with these attributes were attributed to four different species (*K. minor*, *K. robusta*, *P. songhorensis* and *P. doriae*) some of which otherwise lack clear galagine features of the postcranium.

In the course of describing a new, Middle Miocene species of *Komba*, McCrossin reshuffled the postcranial allocations made by Walker and Gebo [88, 97, 101] to produce a list for *Progalago* containing only postcrania with 'lorisine-like' features [86]. McCrossin then used the modified postcranial list as evidence for lorisine affinities of *Progalago* [86] (clearly a tautological process). If one considers only the teeth and jaws, the only derived feature linking *Progalago* with lorisines is the mandibular corpus that deepens posteriorly [85, 96], a trait not seen in all extant lorisines but observed to evolve convergently among indrids and cebids. The unicusulate P₄ and square upper molars cited by McCrossin as additional evidence of lorisine affinities for *Progalago* are primitive features. (McCrossin used the bicuspid P₄ of *Komba* as evidence of galagine affinities [86].) McCrossin also overstated the significance of the 'lorisine-like' features identified and studied by Gebo [88, 101]. Gebo did not feel that climbing features were sufficient to establish membership in the true lorisine clade, only that 'a few foot bones do show specifically lorisine-like features which are functionally related to more frequent climbing activities, yet in overall morphology they still more closely resemble galagine foot bones. ... It is impossible to allocate material unambiguously to either the lorisine or galagine lineages' [88, p. 364].

Adaptive vs. Taxonomic Divergence

The description of the Rusinga Island cranium by Le Gros Clark [92] and the postcranial comparisons by Gebo [88, 101] share one notable conclusion: that the Miocene lorisoid material defies unambiguous placement in either Lorisinae or Galaginae. Both researchers emphasized the mosaic pattern of resemblances, and both identified primitive features not found among extant forms. Isolated features could be held up as hypothetical synapomorphies to substantiate one view or another, but given the lack of knowledge about polarity, the certain prevalence of homoplasy, and the absence of independent evidence for postcranial allocations, such moves are premature. A lorisine-galagine divergence as clean and broad as that observed among extant forms certainly did not exist among the known lorisids of the early Miocene, and a subtle dichotomy will be harder to substantiate. In some respects, such as calcaneal length [88, 100, 101], the Miocene specimens show morphology that could be interpreted as predating the lorisine-galagine split.

From an adaptive point of view, the known Miocene lorisids comprised a diverse fauna of variable body size, with diets probably falling along the insectivore-frugivore continuum judging from molar occlusal morphology, and with locomotor behavior characterized by generalized quadrupedalism, involving variable degrees of emphasis on leaping and climbing. The fauna contained no slow climbing lorisines, and no long-footed leaping specialists. The raw material for today's adaptive divergence was present, but today's extremes of specialization were not.

Even without a notable adaptive divergence, the taxonomic split between lorisines and galagines possibly could have occurred by the Miocene, and might be represented by fossils within the known fauna. Determining whether or not a true galagine or lorisine is present might be possible with better associated finds of crania, teeth and

postcrania. On the other hand, better associations might simply confirm the mosaic pattern of character state distribution, defying attempts by researchers to allocate isolated elements along lorisine-galagine lines. It remains unsettling that the three good craniofacial specimens all are allocated to the 'lorisine' *Mioeuoticus*, while most if not all of the more 'galagine' postcrania are attributed to *Progalago* or *Komba*. Is the idea of a somewhat loris-headed, generalized leaper and scrambler too preposterous? The sympatric ape-headed, monkey-bodied proconsuloids [102, 103], provide a thought-provoking analogy (fig. 5).

Miocene of Namibia

The material from Namibia is very sparse. Two upper molars have been recovered by Conroy from cave breccias at a locality called Harasib 3a, a site where mining debris from deep inside the caves has been dumped out onto a steep slope in the Otavi Mountains [89]. These teeth match modern galagines in detail (fig. 6). They represent a small-bodied galagine comparable to small individuals of the extant species, *Galago demidoff*. Unfortunately, the key diagnostic features of the extant members of Galaginae, such as molarized premolars, obviously cannot be addressed until further material is uncovered.

Plio-Pleistocene of Africa

More complete fossil material of galagines has been found at East African sites of Plio-Pleistocene age [3]. Teeth and jaws from the Shungura Formation of the Omo region of southern Ethiopia have been allocated to three species of *Galago* [104]. The most important of these is a medium-sized species named *G. howelli*, known from several teeth and jaws from Member B (ca. 3 Ma). Although the fossil resembles *G. alleni* in ways, Wesselman concluded that *G. howelli* may lie near the ancestry of the modern greater galagos, such as *G. crassicaudatus* [3, 104]. The two other galagos known from the Shungura Formation include a very small form similar to *G. demidoff* known by one tooth from Member B, and another small species represented by a fragment of a tooth from Member G (ca. 2 Ma) [104]. Other small Pliocene galagos have been found at Laetoli, Tanzania (*G. sadimanensis*) [105] and Olduvai Gorge, Kenya. A partial skeleton has been recovered of the Olduvai Gorge species, which reveals foot structure similar to those of extant species [7, 101, 106]. The fossil galagos of East Africa demonstrate that galagines had already invaded the semiarid brushlands of East Africa by the end of the Pliocene, when the sympatric primate fauna was characterized by open country species such as baboons and hominids [80]. The environmental and adaptive context of the galagine radiation has been thoroughly outlined by Masters [3].

Asia

The first fossil described from the Asian Siwaliks as a lorisid primate was *Indraloris lulli* [107]. The lorisid status of this primate was accepted by some authors [93, 108, 109], but eventually new fossil finds [110] proved that *Indraloris*, as well as other species initially classified in a procyonid genus and later named *Sivaladapis* [111, 112], were representatives of a late-surviving group of adapoids [113–115].

The first record of a true lorisid from Asia was therefore the report of *Nycticeboides simpsoni* [116]. This species represents a relatively small-bodied lorisine, known by several postcranial elements, a few badly fragmented cranial pieces, and

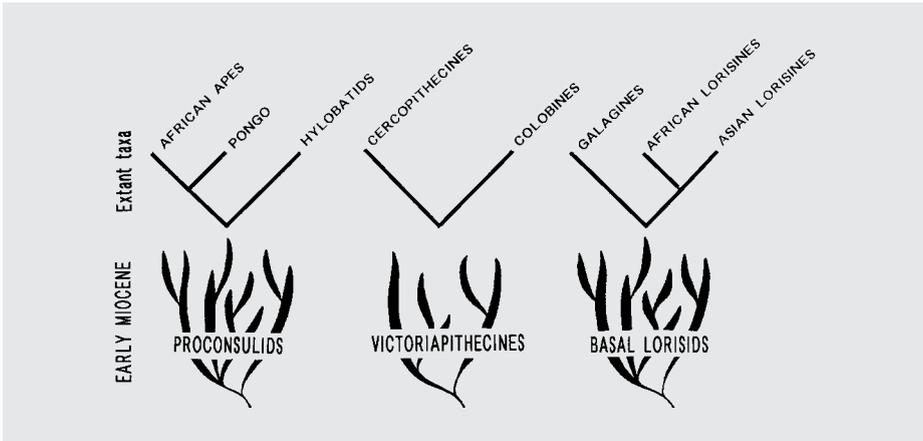


Fig. 5. Schematic diagram showing a basal, bushy radiation of apes (proconsulids) and Old World monkeys (victoriapithecines) in the early Miocene of Africa; in both cases, the early Miocene anthropoids predate the cladistic divergence among the major extant lineages. We propose that the same is true for most or all of the known lorises of the early Miocene; the somewhat galagine-like postcrania and somewhat lorisine-like crania that have been found in the early Miocene may represent the ancestral condition for the later clades of true galagines and lorises.



Fig. 6. Scanning electron micrograph stereopairs of an upper left molar from late Miocene cave breccias of Namibia [89]. The tooth is very similar to those of extant small species of *Galago*. Scale bar = 500 μm .

dental remains including a tooth comb [43, 88, 117]. *Nycticeboides* was found in the late Miocene deposits of the Siwalik Hills, Pakistan, and is approximately 8 Ma in age [116]. Analysis of the postcranial remains indicates a slow-climbing lorisine, certainly within the true lorisine clade. Orbital fragments of *Nycticeboides* suggest a narrow interorbital region and raised orbital margin similar to the condition found in extant Asian lorisines, rather than African ones [117]. The presence of lorisines in Asia by eight million years ago is not surprising, because by then the forest belt connecting African rainforests to Asian ones had broken up [118, 119].

Summary of Neogene Fossil Record

The fossil record unambiguously shows that lorisines and galagines had diverged from each other by the late Miocene. The fossil record is less clear concerning a possible lorisine-galagine split by the early Miocene. Several or all of the fossil lorisids known from the early Miocene may not belong on the modern lorisine or galagine lines, but rather, they may represent now extinct lineages of a basal lorisid radiation. The fossil record is simply inadequate at this time to help resolve the branching sequences among the extant lorisid lineages. To address this important evolutionary question, one must turn to a phylogenetic analysis based on the living species.

Phylogeny of Extant Lorisid Genera

The Problem

Very little attention has been paid to the higher level branching relationships among the extant lorisids. Although conventionally split into two distinct groups, a loris group and a galago group, there have been several indications that these may not be natural phylogenetic groups [14, 120]. Furthermore, debates occur among those researchers who accept a lorisine clade about the interrelationships of the two Asian and two African genera. The traditional view is to accept an Asian clade and an African clade, while some researchers [87, 121] have preferred instead a small-bodied clade (*Arctocebus* and *Loris*) contrasting with a large-bodied clade (*Nycticebus* and *Perodicticus*). Other suggested arrangements have *Nycticebus* and *Arctocebus* as a clade to the exclusion of *Loris* and *Perodicticus* [122–124], and finally *Perodicticus* as the outgroup to a clade of *Arctocebus*, *Nycticebus* and *Loris* [23]. The extant galagines certainly form a distinct clade when compared to the lorisines, but the internal relationships among galagines at the generic and specific levels remain controversial. In the absence of a definitive phylogeny of galagine groups, we conservatively retain all species in the genus *Galago* [1, 125]. Understanding the branching relationships among the extant lorisid genera (fig. 7) is important for generating any overall model of lorisid evolution, for assessing the relationships and significance of fossil lorisids, and for providing a suitable framework for comparative studies.

Morphological Data

At first glance, the lorisines seem to be a cohesive natural grouping with all four extant genera sharing some unique specializations. These include size reduction of the second manual digit, development of specialized vascular networks (retia mirabilia) as an adaptation for persistent grasping, reduction of the tail, and shared limb proportions [126, 127]. This assemblage of traits forms the basis for putting African and Asian

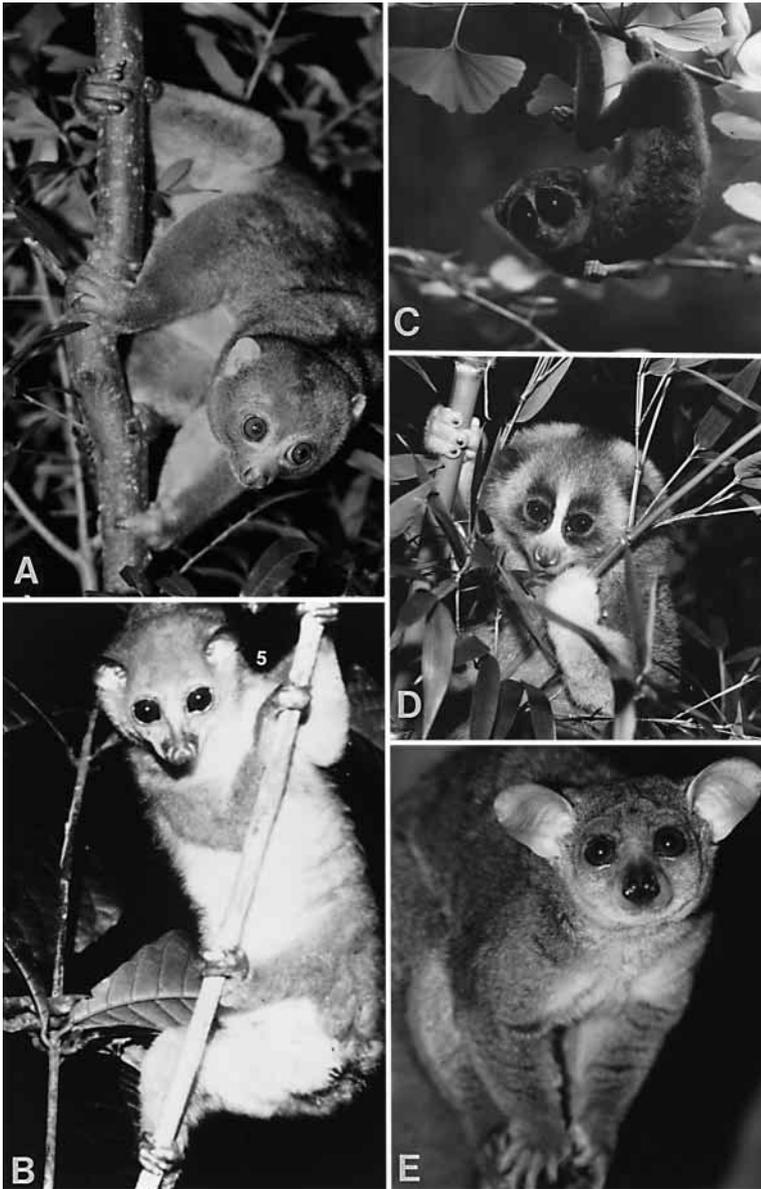


Fig. 7. A sample of the extant lorises, illustrating one species from each extant genus (some authors prefer to divide the *Galago* group into several genera). **A** *Perodicticus potto* (photo D. Haring). **B** *Arctocebus calabarensis* (photo S. Bearder). **C** *Loris tardigradus* (photo A. Rasmussen). **D** *Nycticebus cougang* (photo A. Rasmussen). **E** *Galago crassicaudatus* (photo D. Haring).

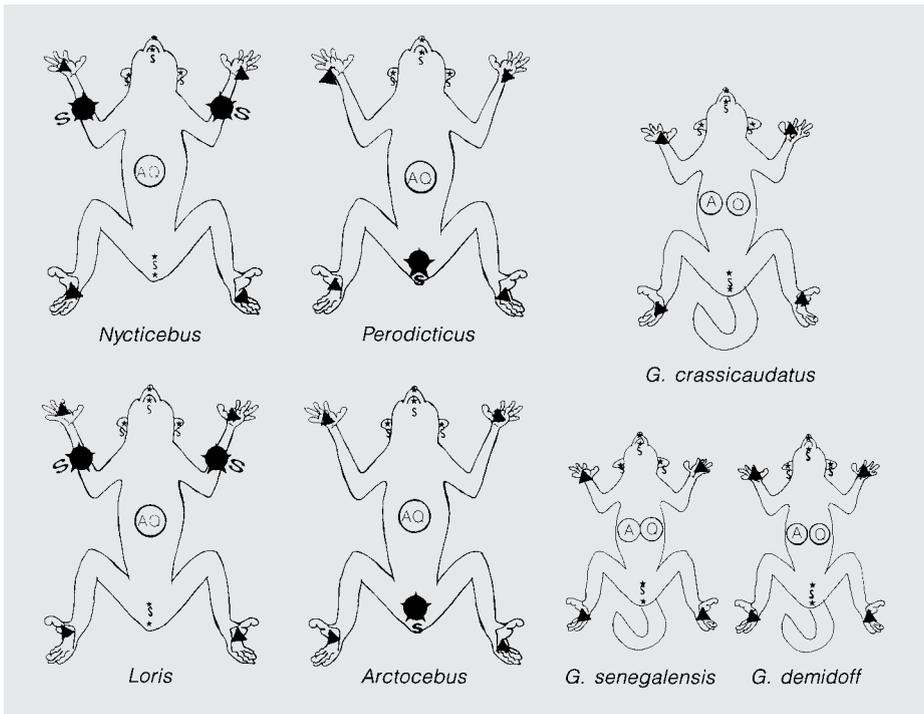


Fig. 8. Summary of the skin characters described by Montagna and colleagues (see text for references) of four lorises and three galagines. Small stars marked with 'S' indicate small sebaceous glands; large black symbols with 'S' indicate specialized, large scent glands; triangles are eccrine glands; A = Active hair follicles; Q = Quiescent hair follicles; A and Q together in a circle indicates that both types of follicles occur in hair groups synchronously, while separate circles indicate separate hair cycles.

slow climbers into a common clade that contrasts with the galagine clade. As these traits are all clearly related to slow-climbing mode of locomotion, it would be desirable to find nonlocomotor traits that confirm or refute the hypothesis of a lorise clade.

Several studies of lorise skin have been undertaken, especially by Montagna and colleagues [126, 128–132]. These comparative studies have been cited in discussions of lorise phylogeny, particularly because they revealed shared similarities between galagines and African lorises [133]. However, the comparative anatomical studies of Montagna and colleagues were not phylogenetic. In this section, we undertake a phylogenetic analysis of this important data set on lorise skin (fig. 8).

The epidermis of all seven lorises studied by Montagna and colleagues (*Galago demidoff*, *Galago senegalensis*, *Galago crassicaudatus*, *Perodicticus potto*, *Arctocebus calabarensis*, *Nycticebus coucang*, *Loris tardigradus*) is relatively thin, resembling the primitive condition for primates as found also in tree shrews [129–132, 134–137]. The epidermis of the two Asian lorises contains virtually no dendritic melanocytes, except in the scrotum, ears and perianal regions. In African lorises and galagines there is a superficial absence of dendritic melanocytes in these same areas, but these become evident upon treatment with alkaline phosphatase.

The pelage pattern of lorises also varies. *Arctocebus* and *Perodicticus* have hair arranged in clumps of 4–20, with small and large groups fitted together. In between these islands or clumps of hair is glabrous skin. One or two apocrine glands are attached to each hair group [129, 136]. Asian lorises also have hair groups of 4–20 follicles, and there is more than one apocrine gland per hair group. The apocrine glands of Asian lorises show high levels of phosphorylase activity, a condition different from that of African lorises. The hair of galagos grows in clumps of variable size (3–6 follicles in *G. demidoff* and *G. senegalensis*, and an average of 8 or 9, ranging up to 26 follicles, in *G. crassicaudatus*), but there is only one apocrine gland per hair group. This creates a growth pattern similar to those of mammals that have a period when the fur is shed, and indeed, galagos in the wild have been observed to go through a seasonal molting [L. Nash, pers. commun.]. Dwarf galagos differ from other lorises in having an absence of glycogen in their quiescent follicles, a similarity to tree shrews. The follicle end organs of galagos more closely resemble those of bovids than the ones found in lorises.

Probably the greatest differences distinguishing the skin of various lorises is the presence and distribution of scent glands. In *Perodicticus* and *Arctocebus*, scent glands are found in the anogenital region. This region is rich in apocrine and sebaceous glands, and has high levels of cholinesterase activity. The area is also highly innervated and contains numerous end organs rich in acetylcholinesterase [129, 136]. Though both male and female pottos have secretory glands in this region, the female has two additional glands which, when squeezed, emit a strong-smelling, keratinous, white fluid [130]. A similar structure is found in female *Arctocebus* and is most clearly seen during estrus [128]. *Arctocebus* has been reported to use its anogenital gland for allomarking in a process called ‘passing over’, whereas *Perodicticus* engages in genital scratching and marking [128].

The primary scent gland of the Asian lorises is a brachial gland. The structure of this gland is similar to the anogenital glands of the African lorises [134, 135]. When the arm is shaved over the brachial gland, a yellowish fluid is secreted that has a strong odor. Unlike the anogenital glands of the African lorises, these brachial glands have much phosphorylase activity [128, 135–137]. A behavior similar to the passing over of *Arctocebus* has been reported in both Asian genera, but it is not known if a scent is actually deposited [138].

The anogenital glands of galagos also contain cholinesterase, and do emit a strong odor, but they are nowhere as numerous or large as those seen in the African lorises [131, 137, 139]. *G. demidoff* lacks apocrine glands in this area. Much of the scent marking in galagos is done by chest-rubbing [140, 141]. The chest of at least some galagos is a region of enlarged sebaceous and apocrine glands [142–145]. The glands appear to be sexually dimorphic in size and secretions [143–145]. Galagos mark substrates with their lips, muzzles and cheeks, presumably using sebaceous and apocrine glands that are found there [142]. Face rubbing is lacking in Asian lorises [138] and *Arctocebus* [146] despite the presence of facial sebaceous and apocrine glands. Urine washing (rubbing the feet and hands together while urinating on them) is a prominent form of scent marking in galagos, cheirogaleids, and some platyrrhines, but is absent in the lorises except *Loris* [138, 147, 148].

The polarity of all the skin and glandular characters is hard to assess. Montagna and his colleagues consistently interpreted the skin of galagos to be primitive based on similarities they shared with other mammals, such as tree shrews and bovids. There-

Table 4. Taxon by character matrix for the skin of lorisids^a

	<i>Arcto.</i>	<i>Galago</i>	<i>Loris</i>	<i>Nycti.</i>	<i>Perod.</i>
1 Brachial glands present	no	no	yes	yes	no
2 Anogenital glands present	yes	yes	no	no	yes
3 Special exudative, keratinous, female anogenital gland	yes	no	no	no	yes
4 Hair groupings in small clumps with multiple glands	yes	no	yes	yes	yes
5 High phosphorylase activity of apocrine glands	no	no	yes	yes	no
6 Dendritic melanocytes evident without treatment	no	no	yes	yes	no

^a See text for data sources; the inferred primitive condition for each character is as follows: 1 = brachial glands absent; 2 = anogenital glands present; 3 = special exudative anogenital gland absent; 4 = hair groupings in large clumps with one gland each; 5 = low phosphorylase activity; 6 = dendritic melanocytes not visible.

fore, shared similarities between galagos and African lorises are not supportive of an African clade containing pottos and galagos. The two genera of Asian lorises are linked by their shared possession of several features that are plausibly interpreted as specializations: the presence of brachial glands, the presence of visible dendritic melanocytes in untreated specimens, and the high level of phosphorylase activity. The two African lorises are linked by their distinctive, exudous anogenital scent glands, and by the presence of the two additional glands found only in females of *Perodicticus* and *Arctocebus*. If the polarity assessments of Montagna and colleagues are correct, then African and Asian lorises together lack seasonal shedding of hair, and share the consistent presence of glycogen in quiescent follicles, and the presence of multiple apocrine glands in at least some hair groups. The first of these characters – absence of seasonal shedding – is conceivably primitive for primates, which would make the galago condition for this trait specialized. These data are summarized in table 4.

The skin data could be subjected to any number of different kinds of cladistic analyses. Given the ease and current popularity of such procedures, it might be useful to state the obvious, that the output from parsimony and other popular cladistic algorithms is dependent on the initial choice of characters, definition of character states, and assessment of character polarity, among other decisions made by the investigator. Parsimony procedures by themselves do not provide a statistical evaluation of phylogenetic branching sequences; they are merely a reordering of the given data from tabular form to more digestible dendritic form. Even the statistical approaches that have been devised for evaluating confidence in a tree [149–153], such as the bootstrap, are applied to data sets that almost always violate the statistical assumptions and are rarely interpreted strictly. Properly speaking, no ‘science’ occurs in a cladistic program; the science and the art is all contained in the input. Given these caveats, the results of a bootstrapped Wagner parsimony analysis using PHYLIP are presented in figure 9.

Apart from the skin data reviewed above, additional evidence that Asian lorises form a clade comes from cranial similarities found only in *Nycticebus* and *Loris* [23, 126, 154]. These include the greater extension of the ectotympanic into a tubular meatus, the more angled auditory bulla, the presence of an orbital ethmomaxillary fissure, the more tubular orbits with narrower interorbital distance, and the more reduced

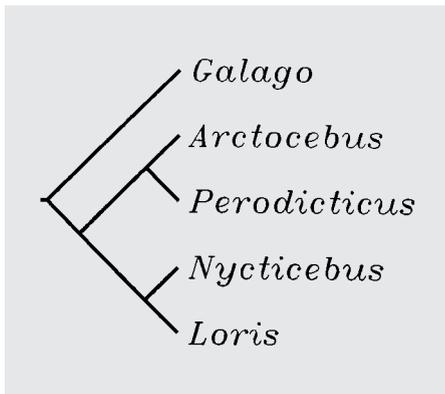


Fig. 9. Most parsimonious cladogram for the skin data of table 4 with all variables receiving equal weight. The lorisine node appeared in all 100 bootstrap replications, the Asian lorisine node also appeared in 100, while the *Arctocebus-Perodicticus* node appeared in only 82. This means that the African lorisine clade cannot be confidently resolved using repeated random sampling of the skin data. This is the same node that has been most difficult to resolve in previous studies. If the special exudative anogenital glands of female *Arctocebus* and *Perodicticus* are given more weight than some of the other skin characters, the African lorisine clade would be resolved with high confidence.

incisors. Establishing better osteological and dental features that help to define the extant clades is important for application to the fossil record, for which skin variables, reproductive biology, and molecular data are not available.

Molecular Evidence

The reconstruction of lorimid phylogeny has been the subject of several molecular and karyotypic studies. Among the earliest of these studies were ones that examined immunological distances among taxa [14, 120, 155]. In these studies, the strength of the antigenic reaction between two species is measured; the resulting antigenic distances are then clustered to generate branching trees interpreted as phylogenies. The immunological results of Goodman [120] showed a closer relationship (greater antigenic response) between *Nycticebus* and *Galago* than between *Nycticebus* and *Perodicticus*. *Loris* was linked closely with *Nycticebus*, supporting the idea of an Asian lorisine clade. The results of Goodman et al. [155] supported the hypothesis of an Asian lorisine clade, an African lorisine clade, and a bushbaby clade, but the relationships among the three clades remained unresolved. The results of Dene et al. [14] found the same three groupings as the earlier studies, and again, could not resolve how the three were related to each other, with different results being produced by different antisera. Dene et al. [14] followed the lamentable practice of immediately reshuffling *classifications* based on the outcome of a single phylogenetic study. Because they could not resolve a clean dichotomy, they raised each of their three hypothetical clades to family rank, Lorisidae, Galagidae and Perodicticidae! The key result of the immunodiffusion studies was that the lorisines (African and Asian) could not be shown to be an exclusive clade.

Concurrent with the immunological studies were a series of studies on the prosimian karyotype [122, 123, 156, 157]. In karyotypic analyses, the number and gross structure of chromosomes is evaluated in order to develop parsimonious phylogenetic hypotheses. De Boer examined the chromosomes of galagos, and concluded that *G. crassicaudatus* preserved the most primitive karyotype [122]. *G. senegalensis* and *G. alleni* shared several specialized traits that linked them to each other [122]. De Boer then compared the galago karyotypes to those of lorisines [123]. Based on his

assessment that *G. crassicaudatus* was primitive, de Boer found that *Perodicticus* and *Loris* were also relatively primitive, while *Nycticebus* and *Arctocebus* shared the loss of chromosomes. Egozcue also pointed out the similarities between *Nycticebus* and *Arctocebus* [156]. Researchers in the lab of Rumpler utilized chromosome banding to address the relationships among lorises [157]. They found that *Nycticebus* and *Loris* could be linked together relative to *Perodicticus*, but, unfortunately, *Arctocebus* was not included in the study. Finally, Rumpler et al. [17] examined members of several prosimian families together in a single phylogenetic analysis of chromosomal evolution. According to this analysis (minus *Arctocebus* again), different galago lineages differentiated from each other and from a common lorine trunk very early in the diversification of lorine chromosomes. The key results from the karyotypic studies are that a lorine and a galagine clade are supportable, that the galagos show greater karyotypic diversification than the lorines, and that the relationships within each of the two primary clades are not well resolved.

Several more recent studies have examined DNA sequences of a few lorine species. These types of studies obtain the nucleotide base sequences from selected sections of the DNA molecules, and then use the similarities and differences in base sequences to infer phylogeny, using parsimony or some other criterion. None of the studies on lorines has been complete enough taxonomically to address the issues of intergeneric relationships. One study included *Galago* and *Perodicticus* [158], while another included *Galago*, *Nycticebus* and *Loris* [23]. Future studies comparing all five genera will be of interest.

The studies of molecular evolution in lorines contribute to our knowledge of variation and character evolution among lorines, but obviously, no consensus has emerged over the details of the lorine genealogical tree. Too often, conflicts between molecular and anatomical studies are cast into the framework of a molecules versus morphology debate [159] that misses the point that all variable biological systems are subject to convergence, parallelism and reversal. Assessing polarity and phylogeny from a data set on either molecular or morphological data is a complex and uncertain procedure. In addition to the problems of homoplasy, each procedure is also subject to sampling error, faulty application of methodologies, and reliance upon questionable assumptions. In reference to apparent disparities between morphological and molecular studies, Larson [160, p. 374] observed:

'If the most parsimonious topology for the molecular data constitutes a suboptimal tree for the morphological data and vice versa, it is incorrect to conclude that the data sets conflict. We cannot reject the hypothesis that both sets are estimating with error the same phylogenetic topology.'

The molecular and morphological studies taken together favor the hypotheses of a galagine clade and lorine clade. Definition of clades within Galaginae remains an area requiring more research. The molecular studies have not converged on a consensus about the relationships among the four lorine genera. This ambiguity probably reflects a relatively ancient history of independent evolution following a relatively brief period of initial divergence. Parsimony analyses of molecular data often have trouble correctly resolving trees with short internal branches and long terminal branches [161–163], and so molecular results may continue to be ambiguous in the case of the lorine genera. In our interpretation, the brachial scent glands shared by Asian lorines and the specialized exudative anogenital glands shared by African lorines comprise strong phylogenetic evidence for Asian monophyly and African

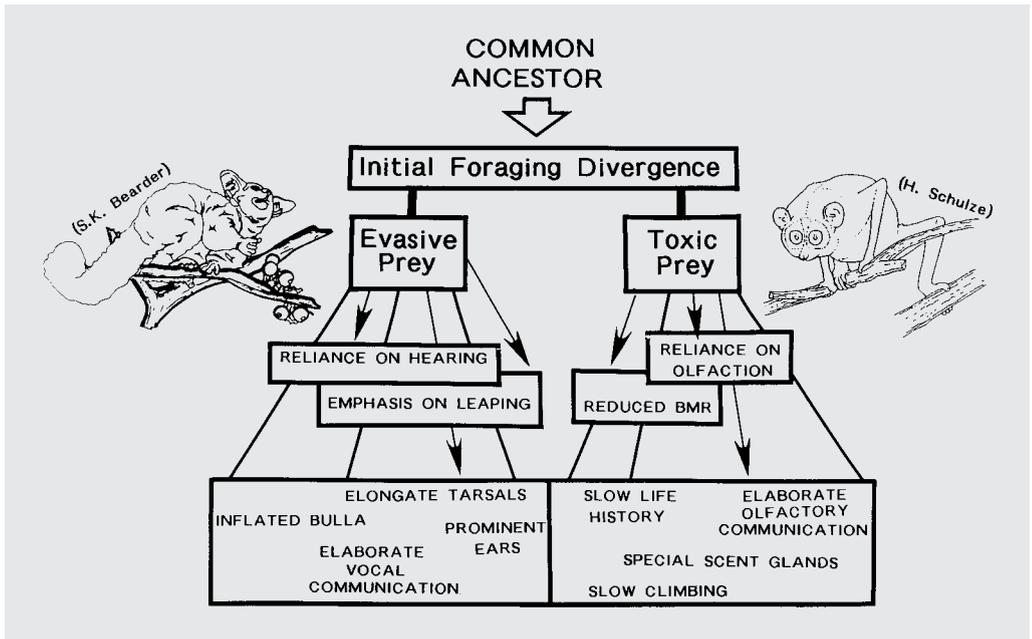


Fig. 10. Schematic flow chart to illustrate how an initial divergence in foraging adaptations between galagines (left) and lorises (right) may have led to a cascade of selective pressures that impacted nearly all aspects of galagine and lorine biology (see text for details).

monophyly despite ambiguity in other systems. Along with cranial features [154] and biogeographic pattern, we prefer figure 9 as a reasonable hypothesis about genus-level lorine phylogeny.

Adaptive Interpretation of the Lorine-Galagine Divergence

Phylogenetic trees are not an end in themselves; they allow much more interesting questions to be addressed about patterns of adaptation and evolutionary change. In this section, we review what is known about the correlations among different biological systems in lorines, and identify some key adaptive differences that may account for the specializations acquired along the galagine and lorine lineages. This logic follows the type of evolutionary modelling that has been applied in the case of primate origins [164, 165] or hominid origins [166].

Most of the distinctive differences between lorines and galagines may have followed from a relatively subtle divergence in foraging adaptations between ancestral forms of the two groups [138, 167]. According to this adaptive model, the ancestral galagines became increasingly specialized towards obtaining active prey for the arthropod component of their diet, while ancestral lorines became specialized for utilizing cryptic or toxic prey. This single adaptive shift could be responsible for a cascade of additional, divergent adaptations that followed (fig. 10).

The ecological rationale for specializing on active prey is that arthropods in this category (e.g. adult lepidopterans, nonpungent orthopterans) form a resource base of rich, nontoxic animals that tend to be easily detected by vision or hearing. Many of these prey items avoid predation by secondary defense mechanisms [168]; i.e. they utilize behavioral mechanisms such as fleeing after being detected by a predator. A primate that evolves leaping behavior with remote auditory sensing of prey might be expected to have greater success against this category of arthropods (as evolved in parallel by galagos and tarsiers). In contrast, the ecological rationale for specializing on cryptic or toxic prey is that arthropods in this category (e.g. larval lepidopterans, ants and termites, among others) are hyperabundant and easily obtained. The cost incurred by the predator is that many cryptic or slow arthropods are defended by toxic compounds, and these must be dealt with physiologically [169–172].

Note that this model does not require that the ancestral lorises and galagines be exclusively or even primarily faunivorous; only that the average animal portion of their diet be different. Data from the few field studies available suggest that lorises do include an unusually high proportion of toxic insects in their diets [146, 173–176]. More fieldwork is required on food choice among free-ranging lorises to further clarify this hypothesis.

The model suggests that the focus on different arthropod groups led to different foraging styles and locomotor adaptations. Galagines underwent intensified selection for detecting prey by hearing, and for pursuing prey by active leaping, thereby leading to selection for large external ears and hindlimb modifications such as the elongated tarsus. Lorises relied more upon smell and careful searching of substrates, thereby leading to enhanced olfactory systems and slow climbing. These sensory differences, in turn, led to a cascade of selective pressures that impacted social communication, with galagines orienting towards vocal communication and lorises emphasizing scent communication and elaborate scent glands.

The divergent specializations on nontoxic versus toxic prey may have impacted the basal metabolic rates of lorises and galagines. All lorises have basal rates lower than those predicted for animals of their size; however, the basal rates of lorises are particularly low, being less than 50% of expected values [177–179]. Other mammalian groups that specialize on toxic insect prey (anteaters, pangolins, armadillos, armadillos, numbats, echidnas, and some armadillos) exhibit notably reduced basal rates for animals of their body sizes [180]. The possible reasons for reduced basal rates as a physiological adaptation for detoxifying food are discussed elsewhere [167, 181]. Reduced metabolic rates may have had a significant impact on the locomotor styles of lorises, and on their reproductive rates. Lorises have greatly reduced reproductive rates and delayed life history schedules [167, 182] that have been unaccounted for by body size, sociality, ecological stability, or other variables aside from basal metabolic rate [138]. Whether or not a significant correlation exists between metabolic rate and life history pattern has become a controversial issue requiring more research [183, 184]. Thus, the evolutionary model outlined here suggests that a simple foraging dichotomy between ancestral galagines and lorises may have led to an accelerating synergy of selective pressures leading to two distinctive adaptive patterns found among the living lorises.

The early Miocene lorises are adaptively generalized enough to represent the kind of fauna from which the eventual lorisine and galagine specializations emerged. Judging from Miocene postcrania, the ancestral stock may have been more saltatorial

than slow-climbing. One might expect parallel evolution among lineages of a single subfamily because of the high degree of integration among selective pressures. This propensity for parallelism within subfamilies should be reflected by similar adaptations being obtained in slightly different fashion by lineages of significant antiquity. As the most ancient split within a single subfamily is probably that between African and Asian lorises, the greatest parallelism might be expected between these two groups. An example of parallel acquisition of a functionally similar system may be the evolution of additional, specialized scent glands in the African lorises (anogenital glands) and Asian lorises (brachial glands).

Evolution and Ecology in Modern Africa and Asia

Among the extant galagos, evolutionary biologists have spectacular examples of evolutionary radiations 'in progress'. Some galagine groups are represented by a diverse array of relatively young species and subspecies, many of which are only now being recognized. The current surge of interest on the topic of galago diversity [3, 185–188], and the rethinking of speciation mechanisms [189–192] and species concepts in primatology [193], are the subjects of other papers in this volume [194, 195]. These current studies are examples of how lorises continue to play an important role in topics of general interest in anthropology and evolutionary biology [196]. As just a few examples, African lorises have been the subjects of field studies that addressed questions of ecological partitioning [146], local resource competition [197–199], reproduction and life history in the context of r and K selection [200], the relationship between habitat structure, locomotion and foraging [201], and the implications of lorisid social systems for the origin and evolution of primate sociality [1, 146].

Unfortunately, fieldwork on Asian lorises has lagged behind that of the African taxa. The diversity of Asian lorises, like that of the African forms, may be currently underestimated. In southern India and Sri Lanka, populations of *Loris* – currently classified as a single species, *L. tardigradus* – are distributed in a variety of habitats and climates, and show great diversity in size, coloration and other morphological variables [126, 202]. Similarly, two or more species of *Nycticebus* are widely distributed on the mainland and islands of Southeast Asia [154, 203–205]. Whether the diversity is at the specific or subspecific level hardly matters in the context of getting reliable behavioral, ecological, morphological and molecular data from the full diversity of extant lorisid populations.

Acknowledgments

For access to casts and specimens of fossil primates we thank E.L. Simons, P.S. Chatrath, G.C. Conroy, and E. Gheerbrant. Conroy granted permission to use the previously unpublished photographs of the Namibian galagine fossils. We thank J. Masters for her thorough and expert review of the paper. Scanning electron micrographs were made by M. Veith. Line drawings in figure 10 are by S.K. Bearder and H. Schultz. Help in the preparation of the illustrations and the manuscript was provided by R. Speckman and A. Rasmussen. For informative lessons about ankles, reproduction, and the integumentary system, we thank D.L. Gebo, M.K. Izard, and D.N. Menton, respectively. The paper owes much to the collegial interaction we enjoyed with many colleagues at the Prosimian Conference in Chester, and we would like to thank the conference organizers: R.H. Crompton, N. Ellerton, A. Feistner, C. Harcourt, G.M. Reid, and J. Whitear.

References

- 1 Bearder SK: Lorises, bushbabies and tarsiers: Diverse societies in solitary foragers; in Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds): *Primate Societies*. Chicago, University of Chicago Press, 1987, pp 11–24.
- 2 Alterman L, Doyle GA, Izard MK (eds): *Creatures of the Dark: The Nocturnal Prosimians*, New York, Plenum Publishing, 1995.
- 3 Masters JC: Speciation in the greater galagos (Prosimii: Galaginae): Review and synthesis. *Biol J Linnean Soc* 1988;34:149–174.
- 4 Martin RD: *Primate Origins and Evolution: A Phylogenetic Reconstruction*. Princeton, Princeton University Press, 1990.
- 5 Gregory WK: On the classification and phylogeny of the Lemuroidea. *Bull Geol Soc Am* 1915;26: 426–446.
- 6 Schwartz JH: Primate systematics and a classification of the order; in Swindler DR, Erwin J (eds): *Comparative Primate Biology*, vol 1: Systematics, Evolution, and Anatomy. New York, Liss, 1986, pp. 1–41.
- 7 Szalay FS, Delson E: *Evolutionary History of the Primates*. New York. Academic Press, 1979.
- 8 Ankel-Simons F: Deciduous dentition of the aye aye, *Daubentonia madagascariensis*. *Am J Primatol* 1996; 39:87–97.
- 9 Szalay FS, Katz CC: Phylogeny of lemurs, galagos, and lorises. *Folia Primatol* 1973;19:88–103.
- 10 Hoffstetter R: Phylogeny and geographical deployment of the primates. *J Hum Evol* 1974;3:327–350.
- 11 Tattersall I, Schwartz J: Craniodental morphology and the systematics of Malagasy lemurs (Primates, Prosimii). *Anthrop Papers Am Mus Nat Hist* 1974;52:139–192.
- 12 Cartmill M: Strepsirhine basicranial structures and the affinities of the Cheirogaleidae; in Luckett WP, Szalay FS (eds): *Phylogeny of the Primates: A Multidisciplinary Approach*, New York, Plenum Press, 1975, pp 313–354.
- 13 Yoder AD: The applications and limitations on ontogenetic comparisons for phylogeny reconstruction: The case of the strepsirhine internal carotid artery. *J Hum Evol* 1992;23:183–196.
- 14 Dene HT, Goodman M, Prychodko: Immunodiffusion evidence on the phylogeny of primates; in Goodman M, Tashian R (eds): *Molecular Anthropology*. New York, Plenum Press, 1976, pp 171–195.
- 15 Dresser ME, Hamilton AE: Chromosomes of lemuriforms. A comparison of the karyotypes of *Cheirogaleus medius* and *Lemur fulvus fulvus*. *Cytogenet Cell Genet* 1979;24:160–167.
- 16 Rumpler Y, Couturier J, Warter S, Dutrillaux B: The karyotype of *Galago crassicaudatus* is ancestral for lorisiforms. *Folia Primatol* 1983;40:227–231.
- 17 Rumpler Y, Warter S, Ishak B, Dutrillaux B: Chromosomal evolution in prosimians. *Hum Evol* 1989;4: 151–170.
- 18 Dutrillaux B, Couturier J, Muleris M, Rumpler Y, Viégas-Pequignot E: Relations chromosomiques entre sous-ordres et infra-ordres et schéma évolutif général des primates. *Mammalia* 1986;50:108–121.
- 19 Koop BF, Tagle DA, Goodman M, Slightom JL: A molecular view of primate phylogeny and important systematic and evolutionary questions. *Mol Biol Evol* 1989;6:580–612.
- 20 Duffy LK, Luick J, Coppenhaver DH: Prosimian hemoglobins. V. The primary structures of the α -I, α -II and β -hemoglobin chains of *Hapalemur griseus*, with a note on the classification of *Microcebus*. *Comp Biochem Physiol* 1990;97:261–267.
- 21 Sarich VM, Cronin JE: Molecular systematics of the primates; in Goodman M, Tashian R (eds): *Molecular Anthropology*. New York, Plenum Press, 1976, pp 141–170.
- 22 Yoder A: *The Phylogenetic Affinities of the Cheirogaleidae: A Molecular and Morphological Analysis*; unpubl PhD diss, Duke University, 1992.
- 23 Yoder A: Relative position of the Cheirogaleidae in strepsirhine phylogeny: A comparison of morphological and molecular methods and results. *Am J Phys Anthropol* 1994;94:24–46.
- 24 LeGros Clark WE: On the skull structure of *ProNycticebus gaudryi*. *Proc Zool Soc Lond* 1934;1:19–27.
- 25 Rasmussen DT: Anthropoid origins: A possible solution to the Adapidae-Omomyidae paradox. *J Hum Evol* 1986;15:1–12.
- 26 Rasmussen DT: The different meaning of a tarsioid-anthropoid clade and a new model of anthropoid origins; in Fleagle JG, Kay RF (eds): *Anthropoid Origins*. New York, Plenum Press, 1994, pp 335–360.
- 27 Beard KC: The phylogenetic significance of strepsirhinism in Paleogene primates. *Int J Primatol* 1988;9: 83–96.
- 28 Szalay FS, Rosenberger AL, Dagosto M: Diagnosis and differentiation of the order Primates. *Yearbk Phys Anthropol* 1987;30:75–105.
- 29 Forsyth Major CI: On some characters of the skull in the lemurs and monkeys. *Proc Zool Soc Lond* 1901: 129–153.
- 30 Gregory WK: On the structure and relations of *Notharctus*, an American Eocene primate. *Mem Am Mus Nat Hist New Ser*, 1920;3:49–243.
- 31 Wortman IL: Studies of Eocene mammals in the Marsh collection. V. Peabody Mus Part II, Primates. *Art, XLI, Classification of the Primates*. *Am J Sci* 1903;13:399–414.
- 32 Stehlin HG: Die Säugetiere des schweizerischen Eocans. *Kritischer Katalog der Materialien, 7ter Theil, erste Hälfte Adapis*. *Abh Schweiz Pal Ges* 1912;38:1165–1298.

- 33 Stehlin HG: Die Säugetiere des schweizerischen Eocans. Kritischer Katalog der Materialien, 7ter Theil, Zweite Hälfte. Abh Schweiz Pal Ges 1916;41:1297–1552.
- 34 Charles-Dominique P, Martin RD: Evolution of lorises and lemurs. *Nature* 1970;227:257–260.
- 35 Charles-Dominique P, Martin RD: Behaviour and ecology of nocturnal prosimians. *Fortschr Verhaltensforsch* 1972;9:1–90.
- 36 Hofer HO, Castenholz A, Zöltzer H: The sublingua and tongue of *Tupaia* (Scandentia, Mammalia): A scanning electron microscope study. *Folia Primatol* 1993;60:185–194.
- 37 Wortman JL: Studies of Eocene Mammalia in the Marsh collection, Peabody Museum, Part II, Primates, Art II, Suborder Anthropoidea. *Am J Sci* 1904;17:23–33.
- 38 Cartmill M, Kay RF: Cranio-dental morphology, tarsier affinities, and primate suborders; in Chivers DG, Joysey KA (eds): *Recent Advances in Primatology*, vol 3: Evolution. London, Academic Press, 1978, pp 205–213.
- 39 Greenfield LO: Recent advances and suggestions for expansion of the field of human origins. *Pontif Akad Sci Scr Var* 1983;50:29–40.
- 40 Rasmussen DT: The phylogenetic position of *Mahgarita stevensi*: Protoanthropoid or lemuroid? *Int J Primatol* 1990;11:439–469.
- 41 Gebo DL: Anthropoid origins: The foot evidence. *J Hum Evolution* 1986;15:421–430.
- 42 Beard KC, Dagosto M, Gebo DL, Godinot M: Interrelationships among primate higher taxa. *Nature* 1988; 331:712–714.
- 43 Rose MD, Walker A, Jacobs LL: Function of the mandibular tooth comb in living and extinct mammals. *Nature* 1981;289:583–587.
- 44 Gingerich PD: Dentition of *Adapis parisiensis* and the evolution of the lemuriform primates; in Tattersall I, Sussman RW (eds): *Lemur Biology*. New York, Plenum Publishing, 1975, pp 65–80.
- 45 Schmid P: Die systematische Revision der europäischen Microchoeridae Lydekker, 1887 (Omomyiformes, Primates). Zürich, Juris Druck & Verlag, 1982, pp 1–85.
- 46 Simons EL, Rasmussen DT: A remarkable cranium of *Plesiopithecus teras* (Primates: Prosimii) from the Eocene of Egypt. *Proc Natl Acad Sci USA* 1994;91:9946–9950.
- 47 Gingerich PD: Radiation of Eocene Adapidae in Europe. *Géobios. Mém Spéc* 1977;1:165–182.
- 48 Schwartz JH, Tattersall I: The phylogenetic relationships of Adapidae (Primates: Lemuriformes). *Anthrop Papers Am Mus Nat Hist* 1979;55:271–283.
- 49 Maier W: Konstruktions morphologische Untersuchungen am Gebiss der rezenten Prosimiae (Primates). Verlag Waldmar Kramer, Frankfurt am Main, 1980.
- 50 Granddier G: Un nouveau lémurien fossile de France, le *Pronycticebus gaudryi*. *Bull Mus Hist Nat Paris* 1904;10:9–13.
- 51 Simons EL: A new Eocene primate genus, *Cantius*, and a revision of some allied European lemuroids. *Bull Br Mus Nat Hist Geol* 1962;7:1–36.
- 52 Szalay F: The European adapid primates *Agerina* and *Pronycticebus*. *Am Mus Novit* 1971;2466:1–19.
- 53 Thalmann U, Haubold H, Martin RD: *Pronycticebus neglectus*: An almost complete adapid primate specimen from the Geiseltal (GDR). *Palaeovertebrata* 1989;19:115–130.
- 54 Franzen JL: The Messel primates and anthropoid origins; in Fleagle JG, Kay RF (eds): *Anthropoid Origins*. New York, Plenum Press, 1994, pp 99–122.
- 55 Tattersall I, Schwartz JH: A revision of the European Eocene primate genus *Protoadapis* and some allied forms. *Am Mus Novitates* 1983;2762:1–16.
- 56 Godinot M: Les primates adapidés de Bouxwiller (Eocène Moyen, Alsace) et leur apport à la compréhension de la faune de Messel et à l'évolution des Anchomomyini. *Cour Forsch-Inst Senckenberg* 1988;107:383–407.
- 57 Gheerbrant E, Thomas H, Roger J, Sens S, Al-Sulaimani Z: Deux nouveaux primates dans l'Oligocène inférieur de Taqah (Sultanat d'Oman): Premiers Adapiformes (?Anchomomyini) de la Péninsule Arabique? *Palaeovertebrata* 1993;22:141–196.
- 58 Moya Sola S, Köhler M: Middle Bartonian locality with *Anchomomys* (Adapidae, Primates) in the Spanish Pyrenees: Preliminary report. *Folia Primatol* 1993;60:158–163.
- 59 Schmid P: Front dentition of the Omomyiformes (Primates). *Folia Primatol* 1983;40:1–10.
- 60 Robinson P: Paleontology and geology of the Badwater Creek area, Central Wyoming with a discussion of material from Utah. *Ann Carnegie Mus* 1968;39:307–326.
- 61 Simons EL, Russell DT: Notes on the cranial anatomy of *Necrolemur*. *Breviora Mus Comp Zool* 1960;127: 1–14.
- 62 Simons EL: Notes on Eocene tarsioids and a revision of some Necrolemurinae. *Bull Br Mus (Nat Hist) Geol* 1962;5:45–69.
- 63 Rosenberger AL: In favor of the necrolemur-tarsier hypothesis. *Folia Primatol* 1985;45:179–194.
- 64 Beard KC, Krishalka L, Stucky RK: First skulls of the early Eocene primate *Shoshonius cooperi* and the anthropoid-tarsier dichotomy. *Nature* 1991;349:64–67.
- 65 Beard KC, MacPhee RDE: Cranial anatomy of *Shoshonius* and the antiquity of Anthropoidea; in Fleagle JG, Kay RF (eds): *Anthropoid Origins*. New York, Plenum Press, 1994, pp 99–122.
- 66 Hartenberger J-L, Marandat B: A new genus and species of an early Eocene primate from North Africa. *Hum Evol* 1992;7:9–16.

- 67 Simons EL, Rasmussen DT, Gingerich PD: New cercamoniine adapoid from Fayum, Egypt. *J Hum Evol* 1995;29:577–589.
- 68 Simons EL, Bown TM: *Afrotarsius chatrathi*, first tarsiiform primate (?Tarsiidae) from Africa. *Nature* 1985; 313:475–477.
- 69 Simons EL, Bown TM, Rasmussen DT: Discovery of two additional prosimian primate families (Omomyidae, Lorisidae) in the African Oligocene. *J Hum Evol* 1986;15:431–437.
- 70 Thomas H, Roger J, Sen S, Al-Sulaimani Z: Découverte des plus anciens ‘Anthropoïdes’ du continent arabo-africain et d’un primate tarsiiforme dans l’Oligocène du Sultanat d’Oman. *CR Acad Sci Paris* 1988;306: 823–829.
- 71 Simons EL: Diversity in the early Tertiary anthropoidean radiation in Africa. *Proc Natl Acad Sci USA* 1992; 89:10743–10747.
- 72 Sigé B, Jaeger J-J, Sudre J, Vianey-Liaud M: *Altiallasius koulchii* n.gen. et sp., primate omomyidé du Paléocène supérieur du Maroc, et les origines des euprimates. *Palaeontographic [A]* 1990;214:31–56.
- 73 Godinot M: Les petits primates simiiiformes de Glib Zegdou (Éocène inférieur à moyen d’Algérie). *CR Acad Sci Paris* 1994;319:357–364.
- 74 Simons EL, Rasmussen DT: A whole new world of ancestors: Eocene anthropoideans from Africa. *Evol Anthropol* 1994;128–139.
- 75 Kappelman J, Simons EL, Swisher CC III: New age determinations for the Eocene-Oligocene boundary sediments in the Fayum depression, northern Egypt. *J Geol* 1992;100:647–667.
- 76 Simons EL, Rasmussen DT, Bown TM, Chatrath PD: The Eocene origin of anthropoid primates: Adaptation, evolution and diversity; in Fleagle JG, Kay RF (eds): *Anthropoid Origins*. New York, Plenum Press, 1994, pp 179–201.
- 77 Andrews P: Community evolution in forest habitats. *J Hum Evol* 1970;22:423–438.
- 78 Retallack, GJ, Bestland EA, Dugas DP: Miocene paleosols and habitats of *Proconsul* on Rusinga Island, Kenya. *J Hum Evol* 1995;29:53–91.
- 79 Evans J, Van Couvering J, Andrews P: Paleocology of Miocene sites in western Kenya. *J Hum Evol* 1981; 10:99–116.
- 80 Conroy GC: *Primate Evolution*. New York, Norton, 1990.
- 81 Bishop W: The later Tertiary in East Africa: Volcanics, sediments, and faunal inventory; in Bishop W, Clark JD (eds): *Background to Evolution in Africa*. Chicago, University of Chicago Press, 1967, pp 31–56.
- 82 Cooke HBS: Africa: The physical setting; in Maglio VJ, Cooke HBS (eds): *Evolution of African Mammals*. Cambridge, Harvard University Press, 1978, pp 17–45.
- 83 Drake RL, Van Couvering JA, Pickford M, Curtis GH, Harris JA: New chronology for the early Miocene mammalian faunas of Kisingiri, western Kenya. *J Geol Soc Lond* 1988;145:479–491.
- 84 Leakey LSB: A new lower Pliocene fossil primate from Kenya. *Ann Mag Nat Hist* 1962;4:689–696.
- 85 Walker AC: Prosimian primates; in Maglio VJ, Cooke HBS (eds): *Evolution of African Mammals*. Cambridge, Harvard University Press, 1978; pp. 90–99.
- 86 McCrossin ML: New species of bushbaby from the Middle Miocene of Maboko Island, Kenya. *Am J Phys Anthropol* 1992;89:215–233.
- 87 Simpson GG: The Tertiary lorisiform primates of Africa. *Symp Zool Soc Lon* 1967;45:165–193.
- 88 Gebo DL: Postcranial adaptation and evolution in Lorisidae. *Primates* 1989;30:347–367.
- 89 Conroy GC, Pickford M, Semet B, Mein P: Diamonds in the desert; the discovery of *Otavipithecus namibiensis*. *Evol Anthropol* 1993:46–52.
- 90 MacInnes DG: Notes on the East African Miocene primates. *J East Afr Uganda Nat Hist Soc Nairobi* 1943;17:141–181.
- 91 Le Gros Clark WE, Thomas DP: The Miocene lemuroids of East Africa. *Fossil Mammals Afr* 1952;5:1–20.
- 92 Le Gros Clark WE: A Miocene lemuroid skull from East Africa. *Fossil Mammals Afr* 1956;9:1–6.
- 93 Simons EL: *Primate Evolution*. New York, Macmillan, 1972.
- 94 Leakey LSB: Primates; in Bishop WW (ed): *The Mammalian Fauna and Geomorphological Relations of the Napak Volcanics, Karamoja*. *Rec Geol Surv Uganda*, 6–9, 1962.
- 95 Walker AC: New evidence from Uganda regarding the dentition of Miocene Lorisidae. *Uganda J* 1969;33: 90–91.
- 96 Walker AC: A review of the Miocene Lorisidae of East Africa; in Martin RD, Doyle GA, Walker AC (eds): *Prosimian Biology*. London, Duckworth, 1974, pp 435–437.
- 97 Walker AC: Post-cranial remains of the Miocene Lorisidae of East Africa. *Am J Phys Anthropol* 1970;33: 249–262.
- 98 McArdle JE: The functional morphology of the hip and thigh of the Lorisiformes. *Contrib Primatol* 1981; 17:1–132.
- 99 Anemone RL: The VCL hypothesis revisited: Patterns of femoral morphology among quadrupedal and saltatorial prosimian primates. *Am J Phys Anthropol* 1990;83:373–393.
- 100 Szalay FS: Systematics of the Omomyidae (Tarsiiformes, Primates): Taxonomy, phylogeny and adaptations. *Bull Am Mus Nat Hist* 1976;136:157–450.
- 101 Gebo DL: Miocene lorisids: The foot evidence. *Folia Primatol* 1986;47:217–225.
- 102 Rose MD: Locomotor anatomy of Miocene hominoids; in Gebo DL (ed): *Postcranial Adaptation in Nonhuman Primates*. Northern Illinois University Press, DeKalb, 1993, pp. 252–272.

- 103 Rose MD: Quadrupedalism in some Miocene catarrhines. *J Hum Evol* 1994;26:387–411.
- 104 Wesselman HB: The Omo micromammals. *Contrib Vert Evol* 1984;7:1–165.
- 105 Walker AC: Fossil Galaginae from Laetoli; in Leakey MD, Harris JM (eds): *Laetoli: A Pliocene Site in Northern Tanzania*. Oxford, Carendon Press, 1987, pp 88–90.
- 106 Simpson GG: Family Galagidae; in Leakey LSB (ed): *Olduvai Gorge, 1951–1961, vol 1: A Preliminary Report on the Geology and Fauna*. Cambridge, Cambridge University Press, 1965, pp 15–16.
- 107 Lewis GE: Preliminary notice of a new genus of lemuroid from the Siwaliks. *Am J Sci* 1933;26:134–138.
- 108 Tattersall I: A mandible of *Indraloris* (Primates: Lorisidae) from the Miocene of India. *Postilla* 1968;123:1–10.
- 109 Schwartz JH, Tattersall I, Eldredge N: Phylogeny and classification of the primates revisited. *Yrbk Phys Anthropol* 1978;21:95–133.
- 110 Sahne A, Khare SK: Fossil prosimians from the Siwaliks. *Bio Mem Lucknow* 1977;2:187–221.
- 111 Gingerich PD, Sahni A: *Indraloris* and *Sivaladapis*: Miocene adapid primates from the Siwaliks of India and Pakistan. *Nature* 1979;279:415–416.
- 112 Thomas H, Verma SN: Découverte d'un primate adapiforme (*Sivaladapinae* subf. nov.) dans le Miocène moyen des Siwaliks de la région de Ramnagar (Jammu et Cachemire, Inde). *CR Acad Sci Paris* 1919;289:833–836.
- 113 Wu R, Pan Y: New adapid primate from the Lufeng Miocene, Yunnan Province. *Acta Anthropol Sin* 1985;3:185–194.
- 114 Pan Y, Wu R: A new species of *Sinoadapis* from hominoid site, Lufeng. *Acta Anthropol Sin* 1986;5:39–50.
- 115 Pan Y: Small fossil primates from Lufeng, a latest Miocene site in Yunnan Province, China. *J Hum Evol* 1988;17:359–366.
- 116 Jacobs LL: Miocene lorisid primates from the Pakistan Siwaliks. *Nature* 1981;289:585–587.
- 117 MacPhee RDE, Jacobs LL: *Nycticeboides simpsonsi* and the morphology, adaptations, and relationships of Miocene Siwalik Lorisidae; in Flanagan KM, Lillegraven JA (eds): *Vertebrates, Phylogeny, and Philosophy*. *Contrib Geol, U Wyoming, Special Paper 3*, 1986, pp 131–161.
- 118 Bernor R: Geochronology and zoogeographic relationships of Miocene Hominoidea; in Ciochon R, Corrucini, R (eds): *New Interpretations of Ape and Human Ancestry*. New York, Plenum Press, 1983, pp 21–66.
- 119 Bernor R, Flynn L, Harrison T, Hussain S, Kelley J: *Dionysopithecus* from southern Pakistan and the biogeography of early Eurasian catarrhines. *J Hum Evol* 1988;17:339–358.
- 120 Goodman M: Deciphering primate phylogeny from macromolecular specificities. *Am J Phys Anthropol* 1967;26:255–276.
- 121 Schwartz JH, Tattersall I: Evolutionary relationships of living lemurs and lorises (Mammalia: Primates) and their potential affinities with European Eocene Adapidae. *Anthropol Papers Am Mus Nat Hist* 1985;60:1–100.
- 122 de Boer LEM: Cytotaxonomy of the Lorisidae (Primates: Prosimii). I. Chromosome studies and karyological relationships in the Galagidae. *Genetica* 1973;44:155–193.
- 123 de Boer LEM: Cytotaxonomy of the Lorisidae (Primates: Prosimii). II. Chromosome studies in the Lorisidae and karyological relationships within the superfamily. *Genetica* 1973;44:330–367.
- 124 Petter JJ, Petter Rousseaux A: Classification of the prosimians; in Doyle GA, Martin RD (eds): *The Study of Prosimian Behaviour*. New York, Academic Press, 1979, pp 1–44.
- 125 Nash LT, Bearder SK, Olson TR: Synopsis of *Galago* species characteristics. *Int J Primatol* 1989;10:57–80.
- 126 Hill WCO: *Primates: Comparative Anatomy and Taxonomy*. I. Strepsirhini. Edinburgh, Edinburgh University Press, 1953.
- 127 Ankel-Simons F: *A Survey of Living Primates and Their Anatomy*. New York, MacMillan, 1983.
- 128 Manley GH: Functions of the external genital glands of *Perodicticus* and *Arctocebus*; in Martin RD, Doyle GA, Walker AC (eds): *Prosimian Biology*. London, Duckworth, 1974, pp 313–329.
- 129 Montagna W, Ellis RA: The skin of primates. I. The skin of the potto (*Perodicticus potto*). *Am J Phys Anthropol* 1959;17:137–162.
- 130 Montagna W, Yun JS: The skin of primates. XIV. Further observations of *Perodicticus potto*. *Am J Phys Anthropol* 1962;20:441–449.
- 131 Montagna W, Yun JS: The skin of primates. VII. The skin of the great bushbaby (*Galago crassicaudatus*). *Am J Phys Anthropol* 1962;20:149–166.
- 132 Montagna W, Yun JS, Silver AF, Quevedo WC: The skin of primates. XIII. The skin of the tree shrew (*Tupaia glis*). *Am J Phys Anthropol* 1962;20:431–439.
- 133 Groves CP: *A Theory of Human and Primate Evolution*. Oxford, Clarendon Press, 1989.
- 134 Montagna W, Ellis RA: The skin of primates. II. The skin of the slender loris (*Loris tardigradus*). *Am J Phys Anthropol* 1960;18:19–44.
- 135 Montagna W, Yasuda K, Ellis RA: The skin of primates. III. The skin of the slow loris (*Nycticebus coucang*). *Am J Phys Anthropol* 1961;19:1–22.
- 136 Montagna W, Machida H, Perkins EM: The skin of primates. XXXIII. The skin of the angwantibo (*Arctocebus calabarensis*). *Am J Phys Anthropol* 1966;25:277–290.
- 137 Machida H, Perkins E, Giacometti L: The skin of primates. XXIX. The skin of the pygmy bushbaby (*Galago demidovii*). *Am J Phys Anthropol* 1966;24:199–204.

- 138 Rasmussen DT: Life History and Behavior of Slow Lorises and Slender Lorises: Implications for the Lorisine-Galagine Divergence; unpubl PhD thesis, Duke University, 1986.
- 139 Yasuda K, Aoki T, Montagna W: The skin of primates. IV. The skin of the lesser bushbaby (*Galago senegalensis*). *Am J Phys Anthropol* 1961;19:23–34.
- 140 Doyle GA, Bearder SK: A field study of the thick-tailed bushbaby *Galago crassicaudatus* (Primates: Lorisidae) in South Africa. *Natl Geol Soc Res Rep* 1970:117–123.
- 141 Doyle GA: The behaviour of the lesser bushbaby; in Doyle GA, Martin RD, Walker AC (eds): *Prosimian Biology*. London, Duckworth, 1974, pp 213–231.
- 142 Schilling A: Olfactory role of urine in territoriality of some nocturnal prosimians; in Doyle GA, Martin RD (eds): *The Study of Prosimian Behaviour*. New York, Academic Press, 1979, pp 461–542.
- 143 Dixson AF: Effects of testosterone on the sternal cutaneous glands and genitalia of the male greater galago (*Galago crassicaudatus crassicaudatus*). *Folia Primatol* 1976;26:207–213.
- 144 Katsir Z and Crewe RM: Chemical communication in *Galago crassicaudatus*: Investigation of the chest gland secretion. *S Afr J Zool* 1980;15:249–254.
- 145 Crewe RM, Burger BV, le Roux M, Katsir Z: Chemical constituents of the chest gland secretions of the thick-tailed galago (*Galago crassicaudatus*). *J Chem Ecol* 1979;5:861–868.
- 146 Charles-Dominique P: *Ecology and Behaviour of Nocturnal Primates*. Duckworth, London, 1977.
- 147 Andrew RJ, Klopman RB: Urine washing: comparative notes; in Martin RD, Doyle GA, Walker AC (eds): *Prosimian Biology*. London, Duckworth, 1974, pp 303–312.
- 148 Schulze H: Behaviour of captive *Loris tardigradus nordicus*: A qualitative description, including some information about morphological bases of behaviour; in Altermann L, Doyle GA, Izard K (eds): *Creatures of the Dark: The Nocturnal Prosimians*. New York, Plenum Publishing, 1995, pp 221–250.
- 149 Cavender JA: Tests of phylogenetic hypotheses under generalized models. *Math Biosci* 1981;54:217–229.
- 150 Templeton A: Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of humans and the apes. *Evolution* 1983;37:221–244.
- 151 Felsenstein J: Parsimony in systematics: Biological and statistical issues. *Ann Rev Ecol Syst* 1983;14:313–333.
- 152 Felsenstein J: Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 1985;39:783–791.
- 153 Corruccini RS: How certain are hominoid phylogenies? The role of confidence intervals in cladistics; in Corruccini RS, Ciochon RL (eds): *Integrative Paths to the Past: Paleoanthropological Advances in Honor of F. Clark Howell*. Englewood Cliffs, Prentice Hall, 1994, pp 167–183.
- 154 Groves CP: Systematics of the genus *Nycticebus*. *Proc 3rd Int Congr Primatol, Zurich, 1970*. 1971;1:44–53.
- 155 Goodman M, Farris W Jr, Moore W, Prychodko W, Poulik E, Sorenson M: Immunodiffusion systematics of the primates. II. Finds on *Tarsius*, Lorisidae and Tupaiidae; in Martin RD, Doyle GA, Walker AC (eds): *Prosimian Biology*. London, Duckworth, 1974, pp 881–890.
- 156 Egozcue J: Chromosomal evolution in prosimians; in Martin RD, Doyle GA, Walker AC (eds): *Prosimian Biology*. London, Duckworth, 1974, pp 857–863.
- 157 Rimpler Y, Warter S, Meier B, Preuschoft H, Dutrillaux B: Chromosomal phylogeny of three Lorisidae: *Loris tardigradus*, *Nycticebus coucang* and *Perodicticus potto*. *Folia Primatol* 1987;48:216–220.
- 158 Crovella S, Masters JC, Rimpler Y: Highly repeated DNA sequences as phylogenetic markers among the Galaginae. *Am J Primatol* 1993;32:177–185.
- 159 Cartmill M, Yoder A: Molecules and morphology in primate systematics: An introduction. *Am J Phys Anthropol* 1994;94:1.
- 160 Larson A: The comparison of morphological and molecular data in phylogenetic systematics; in Schierwater B, Streit B, Wagner GP, DeSalle R (eds): *Molecular Ecology and Evolution: Approaches and Applications*. Basel, Birkhäuser, 1994, pp 371–390.
- 161 Felsenstein J: Phylogenies from molecular sequences: Inference and reliability. *Ann Rev Genet* 1988;22:521–565.
- 162 Hillis DM, Huelsenbeck JP: Signal, noise, and reliability in molecular phylogenetic analysis. *J Hered* 1992;83:189–195.
- 163 Li WH, Zharkikh A: Statistical tests of DNA phylogenies. *Syst Biol* 1995;44:49–63.
- 164 Sussman RW: Primate origins and the evolution of angiosperms. *Am J Primatol* 1991;23:209–223.
- 165 Cartmill M: New views on primate origins. *Evol Anthropol* 1992;1:105–111.
- 166 Lovejoy CO: Modeling human origins: are we sexy because we're smart or smart because we're sexy?; in Rasmussen DT (ed): *The Origin and Evolution of Humans and Humanness*. Boston, Jones & Bartlett, 1993, pp 1–28.
- 167 Rasmussen DT, Izard MK: Scaling of growth and life history traits relative to body size, brain size and metabolic rate in lorises and galagos (Lorisidae, Primates). *Am J Phys Anthropol* 1988;75:357–367.
- 168 Lederhouse RC: Avoiding the hunt: primary defenses of lepidopteran caterpillars; in Evans DL, Schmidt JO (eds): *Insect Defenses: Adaptive Mechanisms and Strategies of Prey and Predators*. Albany, State University of New York Press, 1990, pp 175–189.
- 169 Schmidt JO: Ant venoms: A study of venom diversity; in Shankland DL, Hollinsworth RM, Smyth T Jr (eds): *Pesticide and Venom Neurotoxicity*. New York, Plenum Press, 1978, pp 247–263.

- 170 Deligne J, Quennedey A, Blum MS: The enemies and defense mechanisms of termites; in Hermann HR (ed): Social Insects. New York, Academic Press, 1981, vol 2, pp 1–76.
- 171 Guilford T: The evolution of aposematism; in Evans DL, Schmidt JO (eds): Insect Defenses: Adaptive Mechanisms and Strategies of Prey and Predators. Albany, State University of New York Press, 1990, pp 23–61.
- 172 Whitman DW, Blum MS, Alstop DW: Allomones: Chemicals for defense; in Evans DL, Schmidt JO (eds): Insect Defenses: Adaptive Mechanisms and Strategies of Prey and Predators. Albany, State University of New York Press, 1990, pp 289–351.
- 173 Jewell PA, Oates JF: Ecological observations on the loroid primates of African lowland forest. *Zool Afr* 1969;4:231–248.
- 174 Fooden J: Report on primates collected in western Thailand, January–April, 1967. *Fieldiana Zool* 1967;59: 1–62.
- 175 Fooden J: Primates obtained in peninsular Thailand, June–July, 1973, with notes on the distribution of continental Southeast Asian leaf-monkeys (*Presbytis*). *Primates* 1976;17:95–118.
- 176 Petter JJ, Hladik CM: Observations sur le domaine vital et la densité de population du loris tardigrade dans les forêts de Ceylan. *Mammalia* 1970;34:394–409.
- 177 Müller EF: Energy metabolism, thermoregulation and water budget in the slow loris (*Nycticebus coucang* Boddaert, 1758). *Comp Biochem Physiol* 1979;64A:109–119.
- 178 Müller EF, Jaksche H: Thermoregulation, oxygen consumption, heart rate and evaporative water loss in the thick-tailed bushbaby (*Galago crassicaudatus* Geoffroy, 1812). *Z Säugetierkunde* 1980:269–278.
- 179 Müller EF, Nieschalk U, Meier B: Thermoregulation in the slender loris (*Loris tardigradus*). *Folia Primatol* 1985;44:216–226.
- 180 McNab BT: Physiological convergence amongst ant-eating and termite-eating mammals. *J Zool Lond* 1984; 203:484–510.
- 181 McNab BT: Ecological and behavioral consequences of adaptation to various food resources; in Eisenberg JF, Kleiman DG (eds): Advances in the Study of Mammalian Behavior. Shippensburg, Special Publ American Society of Mammal, 1983, vol 7, pp 632–633.
- 182 Izard MK, Rasmussen DT: Reproduction in the slender loris (*Loris tardigradus malabaricus*). *Am J Primatol* 1985;8:153–165.
- 183 Harvey PH, Pagel MD, Rees JA: Mammalian metabolism and life histories. *Am Nat* 1991;137:556–566.
- 184 Kappeler PM: Life history variation among nocturnal prosimians; in Altermann L, Doyle GA, Izard K (eds): Creatures of the Dark: The Nocturnal Prosimians. New York, Plenum Publishing, 1995, pp 75–92.
- 185 Masters JC: Geographic distributions of karyotypes and morphotypes within the greater galagines. *Folia Primatol* 1986;46:127–141.
- 186 Masters J, Lubinsky D: Morphological clues to genetic species: Multivariate analysis of greater galago sibling species. *Am J Phys Anthropol* 1988;75:37–52.
- 187 Olson TR: Species diversity and zoogeography in the Galagidae. *Primate Report* 1986;14:213.
- 188 Bearder SK: Species diversity among galagos with special reference to mate recognition; in Alterman L, Doyle GA, Izard MK (eds): Creatures of the Dark: The Nocturnal Prosimians. New York, Plenum Publishing, 1996, pp 331–352.
- 189 Crompton RH: Mechanisms for speciation in *Galago* and *Tarsius*. *Human Evol* 1989;4(2):105–116.
- 190 Zimmerman E, Bearder SK, Doyle GA, Andersson AB: Variations in vocal patterns of Senegal and South African lesser bushbabies and their implications for taxonomic relationships. *Folia Primatol* 1985;51:87–105.
- 191 Zimmerman E: Differentiation of vocalisations in bushbabies (Galaginae, Prosimiae, Primates) and the significance for assessing phylogenetic relationships. *J Zool Syst Evol* 1990;28:217–239.
- 192 Masters JC: Loud calls of *Galago crassicaudatus* and *G. garnettii* and their relation to habitat structure. *Primates* 1991;32:153–167.
- 193 Masters JC: Primates and paradigms: Problems with the identification of genetic species; in Kimbel WH, Martin LB (eds): Species, Species Concepts, and Primate Evolution. New York, Plenum Press, 1993, pp 43–64.
- 194 Honess P: New primate species: Tanzania's forest islands and their conservation (abstract). *Folia Primatol* 1998;69(suppl 1): 394–395.
- 195 Masters JC: Speciation in the lesser galagos. *Folia Primatol* 1998;69(suppl 1):357–370.
- 196 Rasmussen DT: African and Asian prosimian field studies; in Spencer F (ed): History of Physical Anthropology. New York, Garland, 1997, pp 22–24.
- 197 Clark AB: Sex ratio and local resource competition in a prosimian primate. *Science* 1978;201:163–165.
- 198 Masters JC, Lumsden WHR, Young DA: Tertiary sex ratios in wild *Galago* populations. *J Zool* 1993;230: 659–663.
- 199 Masters JC, Centner MR, Caithness N: Sex ratios in galagos revisited. *S Afr J Sci* 1982;78:198–202.
- 200 Nash LT: Reproductive pattern in galagos (*Galago zanzebaricus*, *Galago garnettii*) in relation to climatic variability. *Am J Primatol* 1993;5:181–196.
- 201 Crompton RH: Habitat structure, foraging and locomotion in two species of *Galago*; in Rodman P, Cant J (eds): Adaptations for Foraging in Non-Human Primates. New York, Columbia University Press, 1984, pp 74–111.

- 202 Schulze H and Meier B: The subspecies of *Loris tardigradus* and their conservation status: A review; in Alterman L, Doyle GA, Izard MK (eds): *Creatures of the Dark: The Nocturnal Prosimians*. New York, Plenum Publishing, 1995, pp 193–210.
- 203 Fooden J: Eastern limit of distribution of the slow loris. *Int J Primatol* 1993;14:167–175.
- 204 Chen Z, Zhang Y, Shi L, Liu R, Wang Y: Studies on the chromosomes of genus *Nycticebus*. *Primates* 1993; 34:47–53.
- 205 Zhang Y, Chen Z, Shi L: Phylogeny of the slow lorises (genus *Nycticebus*): An approach using mitochondrial DNA restriction enzyme analysis. *Int J Primatol* 1993;14:167–175.
- 206 Simons EL, Rasmussen DT: The skull of *Catopithecus browni*, an early Tertiary catarrhine. *Am J Phys Anthropol* 1996;100:261–292.