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Lorisine Primate from the Late Miocene of Kenya

Martin Pickford*

* Collège de France, CNRS, UMR 7207, Case postale 38, 8, rue Buffon, 75005 Paris.
E-mail: pickford@mnhn.fr

Abstract

The origin of African Lorisidae has been the subject of debate for the past half century, so far without resolution. The matter is complicated by the fact that strepsirrhines (Lorisiformes = Lorisidae + Galagidae) are rare in the African fossil record, with large gaps between occurrences in the Early Oligocene Fayum (Egypt) deposits, the Early Miocene strata of East Africa and the Plio-Pleistocene of the same region. Likewise, the Asian fossil record of this group is spotty, with only a few specimens described from the Late Miocene of Pakistan.

In the search for evidence concerning the dichotomy between Lorisidae and Galagidae, authors have tended to focus on the Early Miocene fossils from Kenya and Uganda, which is the only region to have yielded a reasonable diversity of forms. Unfortunately, the history of study has been marred by the description and interpretation of non-primate material as strepsirrhines (Lorisiformes spurii)*. This contrasts with the genuine strepsirrhine* (Lorisiformes veri) *fossils from the same region which have thrown much light on the group, but which have not yet resolved the issue of the timing or the modality of the dichotomy between the two families. At present, among the described African fossil lorisiformes only the genus* Mioeuoticus *is accepted by some, but not all, authors (Harrison, 2010) as a Lorisidae (or Lorisinae), all the others generally being classed as Galagidae (or Galaginae) Walker (1987).*

It is thus of interest to put on record the discovery of a lorisid snout from the Late Miocene deposits of the Tugen Hills, Kenya, which is close in dimensions and some aspects of the cranial and dental morphology to Lorisidae from the Far East (Nycticebus, Nycticeboides) *and West Africa* (Arctocebus)*. The fossil does not particularly resemble any of the Early Miocene forms described from East Africa, and it is suggested that the lineage entered Africa during the Late Miocene at the same time that several other vertebrate groups spread into the continent from South-East Asia.*

Introduction

The Kenya Palaeontology Expedition collected the snout of a small primate during the 2010 field season (Fig. 1). The specimen was found at the base of the Lukeino Formation at Aragai, a site that has yielded abundant colobine monkeys and remains of the early bipedal hominid *Orrorin tugenensis*. Other sites in the formation have yielded tragulids, tragelaphine bovids, suids, palm civets, fruit bats and other mammals that are today associated with tropical forest.

There as been a long, drawn-out debate concerning the timing of the dichotomy between "lorises" and "bush babies" (Lorisidae and Galagidae, or Lorisinae and Galaginae depending on the authors) with almost no consensus emerging after half a century of endeavour. The Aragai strepsirrhine snout is closer to that of *Arctocebus* than to those of *Perodicticus* and *Pseudopotto*, and it is significantly different from all of the Galagidae. It therefore yields evidence that the family Lorisidae was present in Africa 6 million years, something that is not evident among the Early Miocene strepsirrhines from East Africa (hence the persistence of the debate) (Masters *et al.*, 2005, 2007).

In the search for evidence concerning the dichotomy between lorises and bush babies, some authors have included non-primate fossils in their samples (Gebo *et al.*, 1997; MaClatchy and Kityo, 2002; Walker, 1970) and this complicated the issue. Fossils that are unanimously attributed to Galagidae have been described from the Pliocene of Kenya and Tanzania (Walker, 1987). It is thus reasonably certain that these two families were present in East Africa during the Late Miocene, but claims for their presence in the Early Miocene of the same region are more tenuous. Pickford *et al.*, (2006) attributed some late Miocene fossils from Sheikh Abdallah, Egypt, to *Galago farafraensis* which indicate the existence of the family in the basal part of the Late Miocene some 10 million years ago, but lorisiform fossils from the Eo-Oligocene of the Fayum, Egypt (Seiffert *et al.*, 2003; Seiffert, 2007) are less convincingly members of either of the extant families. The aim of this contribution is thus to describe and interpret the Aragai snout, and to discuss its phylogenetic and palaeoenvironmental implications, in the awareness that in the future, more detailed comparisons will need to be made with fossil and extant lorisids from Asia in order to determine whether it is closer to any of those forms than it is to extant *Arctocebus* from Africa.

Material and Methods

The fossil described herein is a snout from the site of Aragai, Lukeino Formation, Kenya, aged ca 6 Ma. It is curated at the Orrorin Community Organisation, Baringo, Kenya. Comparisons were made with skulls of extant galagids (*Galago*) and lorisids (*Arctocebus*, *Perodicticus*, *Loris* and fossil *Nycticeboides*) (Jacobs, 1981, MacFee and Jacobs, 1986). The systematics and taxonomy of the Lorisiformes is not completely settled (Schwartz and Tattersal, 1985; Harrison, 2010) but there are broad features common to most recently published schemes. The post-cranial differences between lorises and bush babies are flagrant (Gebo,1986). Because of this, most authors are agreed about the separate family (or subfamily) status of the "lorises" and the "bush babies", although there is little agreement about the taxonomic rank that these two groups should have. Schwartz and Tattersall (1985) and Harrison (2010) treat them as separate families, Lorisidae and Galagidae, within Lorisoidea, whereas McCrossin (1992) considered Galaginae to be a subfamily of Lorisidae as did MacLatchy and Kityo (2002). Gebo *et al.*, (1997) employed Galagidae rather than Galaginae. In this contribution, I will employ the family ranks, Galagidae and Lorisidae, but use the ranked terms employed by the original authors when discussing their works. This complicates the issue but does respect the concept that the author had at the time of writing.

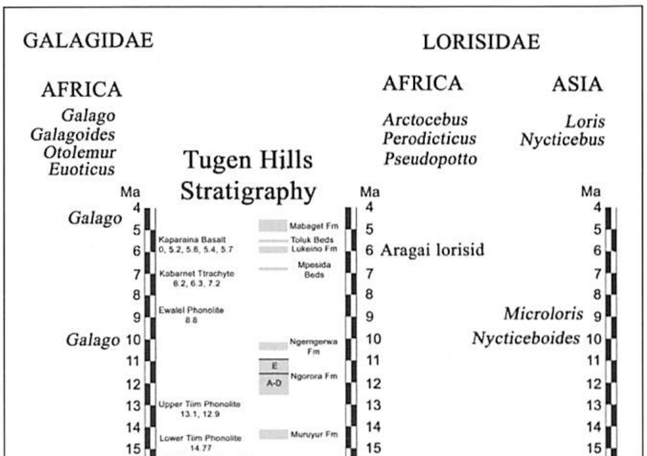

Fig.1. *Stratigraphy and geochronology of African and Asian lorisiforms. There are long gaps in the fossil record of both continents.*

Age

The Aragai lorisid snout is from the basal part of the Lukeino Formation (Fig. 1), the age of which is 6.1 Ma (Sawada *et al.*, 2002).

Description

Comparison of the Aragai snout with skulls of extant galagids and lorisids reveals that its affinities lie closer to West African *Arctocebus* than to *Perodicticus* or *Pseudopotto* and that it differs radically from *Galago*. The lachrymal foramen is close to the orbit, separated from it by a low ridge which is part of the raised circum-orbital margin. In front of the foramen there is an ovoid depression occupied by a second foramen anteriorly (Fig. 1). The nasal bones extend distally beyond the leading edges of the orbits. In palatal view, one can observe broken remnants of the right C/-M1/ and the left P3/-M2/ in poor condition. The leading edge of the orbit lies above the P4/.

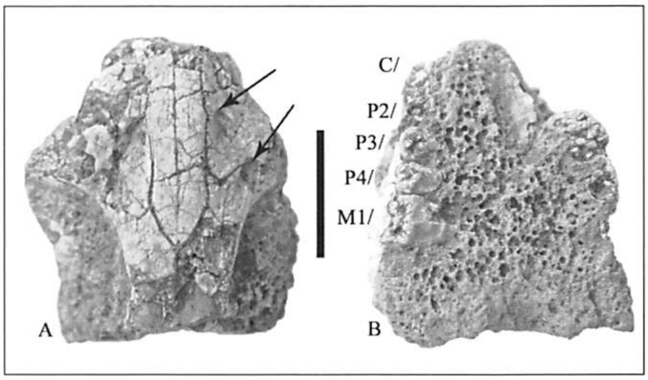

Fig. 2. *OCO 119'10, lorisid snout from Aragai, Lukeino Formation, Kenya (Late Miocene, ca 6 Ma) (scale bar 10 mm). A) dorsal view, B) palatal view. Arrows point to the lachrymal foramen and a second foramen at the anterior end of a shallow ovoid depression.*

The buccal cusps of all the cheek teeth are damaged, but it is possible to discern that the M1/ possessed two buccal cusps, and the P4/, P3/, P2/ and the canine probably only one. There is a short diastema between the canine and the P2/. The P2/ is a small tooth, not enlarged as in *Perodicticus* and it is in contact with the P3/, unlike *Perodicticus* which has a short gap between these two teeth. The P4/ has an anteriorly positioned protocone behind which is a capacious distal basin bordered by a sharp-edged cingulum. The M1/ has a prominent protocone (damaged in the specimen) behind which is an expansive distal basin bordered by the posthypocone crista and the sharp distal cingulum. The morphology of the P4/ and M1/ is distinct from the more bunodont pattern observed in *Perodicticus* and *Pseudopotto*, but is close to that expressed in *Arctocebus calabarensis*. Measurements are provided in Tab. 1.

Discussion

The Aragai fossil is of a lorisid close to but not identical to *Arctocebus calabarensis*. Further preparation of the specimen

Measurement	OCO 119'10	Perodicticus potto	Arctocebus calabarensis
C-P4/	10.0	13.7	8.4
M1/ l x b	3.1 x 4.3	4.2 x 5.5	3.0 x 4.2
Orbital separation	6.2	9.8	6.0
Palate breadth at M1/	9.7	11.6	8.3

Tab.1. *Measurements (in mm) of the snouts of the Aragai lorisid, Perodicticus and Arctocebus.*

will permit a more detailed study of the palatal area which is currently covered in a red phosphatic deposit typical of fossils from the site (Fig. 2). Detailed comparisons are yet to be made with Lorisidae from the Far East, both extant and fossil, but the upper molars do not have the enlarged and well separated hypocone that occurs in *Nycticeboides simpsoni* Jacobs, 1981. Nevertheless, the Aragai specimen is clearly more closely related to Lorisidae than it is to Galagidae. It is provisionally attributed to the genus *Arctocebus* (Tab. 2).

Lorisidae Gray, 1821	*Perodicticus* Bennett, 1831 *Arctocebus* Gray, 1863* *Pseudopotto* Schwartz, 1996 *Loris* Geoffroy, 1796 *Nycticebus* Geoffroy, 1812 ***Nycticeboides Jacobs, 1981*** ***Microloris Flynn & Morgan, 2005*** ***Mioeuoticus Leakey, 1962***
Galagidae Gray, 1825	*Galago* Geoffroy, 1796* *Galagoides* Smith, 1833 *Otolemur* Coquerel, 1859 *Euoticus* Gray, 1863 *Sciurocheirus* Gray, 1873 ***Komba* Simpson, 1967** ***Progalago* MacInnes, 1943**

*Tab.2. List of Cenozoic Lorisiform genera accepted by Harrison (2010). Genera in bold are extinct, in normal script are extant; * = extant genus with a fossil record.*

The origin of *Arctocebus* remains obscure, but it is here suggested that it may be a descendant of a lineage that entered Africa from the Far East, perhaps during the Late Miocene. Lorisids occur in the Late Miocene of Pakistan (Fig. 5) midway between their extant range in India and the Indonesian Archipelago on the one hand, and Africa on the other (Jacobs, 1981; Flynn and Morgan, 2005). What seems clear is that it is morpholgically closer to extant Asian Lorisidae than to any of the Early Miocene African Lorisiformes, including *Mioeuoticus*, the only extinct genus from the continent interpreted by some, but by no means all researchers, to belong to the Lorisidae (Harrison, 2010). Because of this, scholars have found it difficult to propose durable hypotheses for the origin of African lorisids, especially because their studies were based exclusively on the African Early Miocene fossils and ignored the Asian Miocene and extant lineages (Jacobs, 1981; MacFee and Jacobs, 1986, Flynn and Morgan, 2005).

Lorisiformes *spurii*

The attribution of non-primate fossils to Lorisiformes has complicated the study of lorisid and galagid origins. Simpson (1967), Walker (1970), Gebo *et al.*, (1997) and MacLatchy and Kityo (2002) discussed the phylogeny of the lorisiforms, basing their arguments either partly (in the case of the first two papers) or exclusively (in the case of the latter two papers) on non-primate fossils.

Simpson (1967) identified a mandible from Songhor, Kenya (ca 19 - 20 Ma) as a lorisiform, and named it *Propotto* on account of perceived close similarities to the potto (*Perodicticus*). However, the type specimen was soon shown to be that of a fruit bat (Walker, 1969).

A proximal humerus from Songhor (KNM SO 1028) was identified by Walker (1970, Fig. C) as cf. *Progalago dorae*, whereas Gebo (1989) claimed that the specimen was that of a procyonid. McCrossin (1992) in contrast, accepted its strepsirrhine status, but considered that its morphology linked it to Lorisidae rather than to Galagidae. Thus, if McCrossin (1992) is correct, then *Progalago* would be a lorisid rather than a galagid, contrary to the view of Walker (1970). The fossil resembles humeri of *Paranomalurus bishopi*, a non-volant anomaluroid rodent. The other proximal humerus described by Walker (1970, Fig. B) also belongs to *Paranomalurus*, but it is smaller than *P. bishopi* and probably represents *Paranomalurus walkeri* Lavocat, 1973. The distal humerus in the same figure is probably primate, in which case the illustration is a chimera.

A distal humerus (Fig. 3) and a proximal femur from Early Miocene (20-18 Ma) deposits at Napak, Uganda, were attributed to Lorisidae by Gebo *et al.*, (1997) and MacLatchy & Kityo (2002) and were used to infer locomotor repertoires, to estimate body weight, and to deduce aspects of lorisid and galagid behaviour, evolution and phylogeny. The two fossils (MUZM 30, distal humerus and BUMP 20, proximal femur) were interpreted by these authors to indicate the presence of two taxa of strepsirrines at Napak, which were reported to differ principally in size; small species estimated to weigh about 900 gm (Gebo *et al.*, 1997) and a second, larger species estimated to be «significantly larger than known Miocene and extant lorisoids» (MacLatchy and Kityo, 2002).

The anatomical features of the distal humerus of the "small" species were reported to suggest that "forelimb function resembled arboreal quadrupedal and cautious climbing primates, with several functional similarities to extant lorises» (Gebo *et al.*, 1997) whilst the femur, which was attributed to the "large" species, was interpreted to provide evidence for slow climbing (MacLatchy and Kityo, 2002). The femur mentioned by MacLatchy and Kityo (2002) has not yet been figured but it is identical to that of *Paranomalurus bishopi* (Fig. 4).

Comparisons of the distal humerus by Gebo *et al.*, (1997) with those of other Early Miocene galagids (Walker, 1970, 1974, 1978) and extant lorisids, formed the basis for his suggestion that the Napak distal humerus "helps to document the beginning of lorisid locomotor adaptation and evolution in the forelimb". MacLatchy and Kityo (2002)

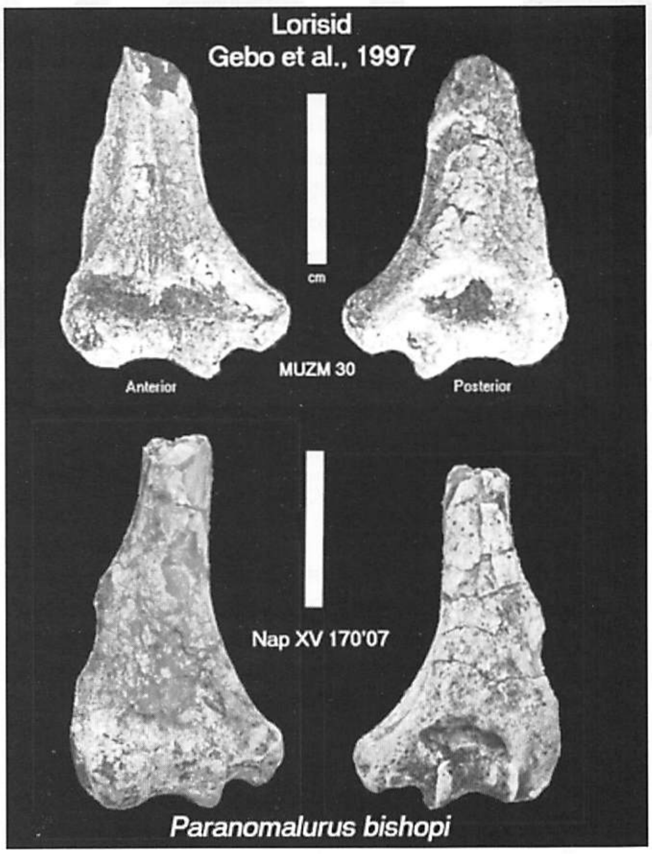

Fig. 3. *Comparison of the distal humerus of* Paranomalurus bishopi *(bottom frame) with a specimen attributed to Lorisidae by Gebo et al., (1997) (top frame). The two are identical in morphology and similar to each other in dimensions. It is concluded that both belong to the same species of arboreal rodent.*

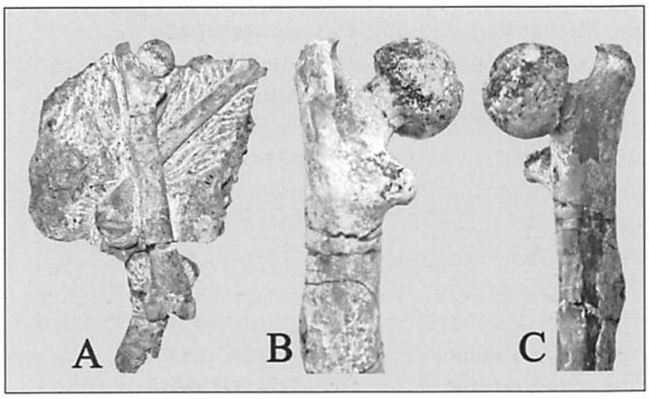

Fig. 4. *Nap XV 170'07, left femur of* Paranomalurus bishopi, *part of a complete skeleton. A) femur, tibia and other bones in the sediment block during extraction, B) posterior view of femur, C) anterior view of femur. The diameter of the femoral head is 10 mm.*

wrote that the "timing and nature of the divergence of the lorisoid clade into bushbabies and slow lorises is poorly documented by the fossil record" but that the question could now be addressed on the basis of the Napak fossil femur which "suggests that the adaptive divergence of the two lorisid lineages was well under way by the Early Miocene" (i.e. galagines and lorisines). Thus, in two successive papers, rodent fossils from the same species and the same site were interpreted to indicate two contrasting scenarios of the timing of the lorisid-galagid divergence, one well before the Early Miocene, one during the Early Miocene.

Paranomalurus was a non-volant anomalurid (flying squirrel) which has clear arboreal post-cranial adaptations which have converged on those of small arboreal primates, and it is this convergent evolution that underlies the confusion.

With the removal of these non-primate fossils from the hypodigms of East African fossil lorisiforms, there remains remarkably little evidence which might be used to interpret the dichotomy between lorisids and galagids (Gebo, 1986).

Lorisiformes *veri*

Early and Middle Miocene lorisiforms have been described from Kenya and Uganda on a number of occasions (Bishop, 1968; Gebo, 1986, 1989; Harrison, 2010; Leakey, 1962; Le Gros Clark, 1950; Le Gros Clark and Thomas, 1952; MacInnes, 1943; McCrossin, 1992; Phillips and Walker, 2000, 2002; Simpson, 1967; Walker, 1970, 1974, 1978). Late Miocene Galagidae have been reported from Egypt (Pickford *et al.*, 2006) and Plio-Pleistocene lorisiforms are known from Tanzania, Kenya and Ethiopia (Simpson, 1965; Walker, 1987; Wesselman, 1984).

There is still no consensus about the diversity of living lorisiforms. The list in Tab. 2 (Harrison, 2010) includes *Sciurocheirus* and *Galagoides*, but neither of these genera were considered valid by Schwartz and Tattersall (1985). Simpson (1967) wrote that, apart from *Propotto*, which he thought was close to *Perodicticus* (recall that *Propotto* is a fruit bat, Walker, 1969) "none of the other Miocene forms has clear and special resemblances to any Recent genus, let alone species" and despite improvement of the fossil sample since then, the same sentiment is equally valid today, with different authors attributing Early Miocene specimens to one or other family inconsistently. For example, Leakey (1962) thought that the Early Miocene lorisiform from Napak, Uganda, was a galagid (hence its name *Mioeuoticus*) but Harrison (2010) classified it in the Lorisidae. Walker (1970) classified *Progalago* in the Galaginae (within Lorisidae) but McCrossin (1992) considered that its morphology linked it to lorisids rather than to galagids.

Resolution of the family (or subfamily) affinities of the Early Miocene lorisiforms of East Africa requires a better fossil record from the Middle and Late Miocene. There is consensus that all the known Plio-Pleistocene lorisiforms from Africa are Galagidae (Walker, 1987; Harrison, 2010; Wesselman, 1984) and the family can be traced back as far as the Vallesian (10 Ma) of Egypt (Pickford *et al.*, 2006). The Aragai snout is the first loris-like primate to be described from the Neogene of Africa, and it indicates that the families Lorisidae and Galagidae were both present in the continent by the Late Miocene. Lorisidae have been described from the Late Miocene of Pakistan (Jacobs, 1981; MacFee and Jacobs, 1986; Flynn and Morgan, 2005) and they survive today in India and the Indonesian Archipelago (Lebrun, 2008; Szalay and Katz, 1973) but no Galagidae have ever been reported outside Africa.

Biogeography

In view of the difficulties that researchers have experienced concerning the affinities of the Early Miocene lorisiforms of Africa, it is perhaps more likely that galagids originated in (and were always confined to) Africa, while the lorisids evolved in South East Asia, and spread to Africa during the Late Miocene as part of a biogeographic event which implicated a variety of vertebrate lineages that entered Africa from the Far East during the Late Miocene and basal Pliocene.

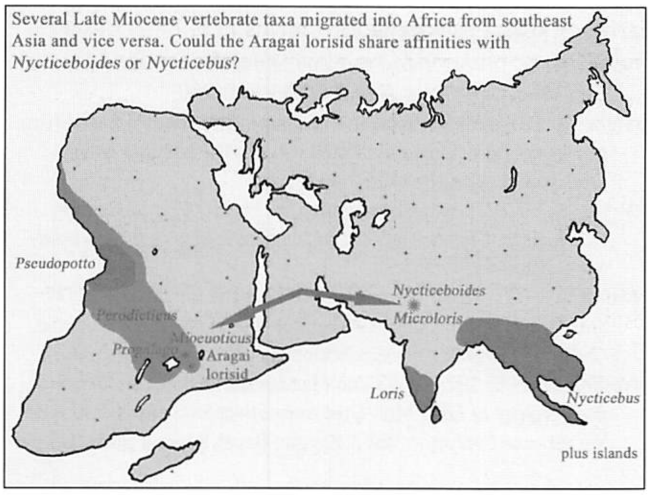

Fig. 5. *Biogeography and palaeobiogeography of Lorisiformes. Extant and fossil Galagidae are exclusively African, whereas Lorisidae occur in both Africa and the Far East. The question is "Did the lorises originate in the Far East, and then spread to Africa during the Late Miocene, or were they present in Africa during the Early Miocene?".*

Among the vertebrates that spread to Africa from the Far East were giant bunodont lutrines (*Sivaonyx*), agriotheres (*Agriotherium*), wolverines (*Plesiogulo*), canids (*Eucyon*), true hyaenas, hares (*Alilepus*), porcupines (*Hystrix*), camels (*Paracamelus*) and some suids (*Sivachoerus*, *Dasychoerus*) as well as the peafowl (*Pavo*) among others. The same biogeographic event included the red panda (*Ailurus*) the monkey (*Macaca*) and the tapir (*Tapirus*) which spread to Europe as far north as England, but with the exception of *Macaca* (which reached the Palaearctic parts of North Africa) did not enter Africa.

Palaeoenvironment

The discovery of a lorisid snout at Aragai, Lukeino Formation, Kenya, confirms the humid, tropical palaeoenvironment at the time of deposition, already deduced from the presence of other forest adapted taxa such as the tragulid (*Hyaemoschus*), abundant colobine monkeys, and fruit bats. The fossil leaves from the same formation indicate the presence of dry evergreen forest in the region 6 million years ago (Bamford *et al.*, in press). Extant *Arctocebus* appears to prefer leafy areas in clearings in secondary forest patches (Kingdon, 2004) as there are more lianas, vines and small branches low down near the ground than there are in fully mature tropical rain forest. Dry evergreen forest would thus be a suitable environment of *Arctocebus*.

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