# LEMURS

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# LEMURS
## ECOLOGY AND ADAPTATION

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This volume is dedicated to Mme. Berthe Rakotosamimanana (Madame Berthe), who passed away in Antananarivo, Madagascar, in 2005. Mme. Berthe's energy, wisdom, and leadership contributed immensely to primatological research and to our knowledge of the wonderful lemurs of Madagascar

# PREFACE

When we first went to the Red Island to begin our respective studies of ring-tailed lemur ecology (nearly twenty years ago), we were both struck by the sheer wildness of Madagascar. A land of great contrasts, one could travel the major highway that bisects the continent, and go from devastated vistas directly linked to human-induced changes, to intact forests where one could encounter a fantastic array of organisms. At that time there were only a handful of researchers who had met the challenges of fieldwork there, but over the past fifteen years there has been a virtual renaissance of studies focusing on Madagascar's unique plants and animals (see volumes by Kappeler and Ganzhorn, 1993; Rakotosamimanana et al., 1999; Goodman and Benstead, 2003; Jolly et al., 2006).

The lemurs of Madagascar remain the primate ambassadors of adaptive radiation. True to Darwin, they exhibit a wonderful example of the interplay between geographic isolation and speciation. Having evolved in complete isolation from other primates—lemur evolution dates back to the Eocene epoch (55–37 million years ago) and possibly even earlier (Martin, 1972, 2000; Mittermeier et al., 1994; Yoder et al., 2003)—the amazing variety of lemurs that we know today arose from either one or several separate waves of migration (see Yoder et al., 2003; Tattersall, 2004; Karanth et al., 2005; Tattersall, this volume). Once they arrived on Madagascar, these ancestral forms spread geographically into numerous niches to become a remarkable array of lemur species. As of this writing (2006) there are between 49 and 63 extant lemur species, depending upon which taxonomic source is consulted (Groves, 2001; Jungers et al., 2002; Moreira, 2005; Mittermeier et al., 2006), but there are also at least 16 species of subfossil lemurs, most of which have only gone extinct within the last 2000 years (see, for example, Karanth et al., 2005; Godfrey et al., this volume). Furthermore, there are new lemur taxa still being discovered. Given such a wealth of species, both living and extinct, it is not surprising that Madagascar attracts researchers from all over the world.

Madagascar's lemurs are also enterprising primates. From both a climatic and a geographical perspective, Madagascar has provided numerous challenges to its inhabitants. Lemurs make a living in a variety of habitats, from exotic spiny forests to seasonal dry forests, diminishing rain forests, limestone forests, and even high-altitude terrain, eking out an existence in habitats with poor soils, low and very seasonal plant productivity, and often unpredictable and sometimes devastating climates (Wright, 1999). Like their fellow island hoppers in Australia, this has resulted in a diverse and unusual number of traits, including female dominance, sexual monomorphism, seasonal fat storage, and strict seasonal breeding (Jolly, 1984; Wright, 1999 and this volume; Curtis, this volume, Fietz and Dausmann, this volume).

With such a wealth of lemur research during the last fifteen years, the major purpose of this volume is to provide a single source for information from many of these new studies. This volume brings together information on newly studied taxa as well as summaries from long-term data on well-known lemur species from a number of sites. Information found in this volume provides us with answers to questions concerning life-history traits, adaptations to extreme seasonality, and natural disasters. It also brings up new information on the ecology and adaptations of the recently extinct subfossil lemurs, which has emerged from both new excavations and technological advances in primate paleontology. From these collected readings we hope to provide new insight into the study of lemur origins, and the ecology and adaptation of both extant and recently extinct species. In a larger context, the information contained in this book will expand our knowledge of primate ecology and allow us further insight into mammalian adaptations to unusual and often harsh environmental conditions that arise from both natural and anthropogenic factors.

We begin literally at the beginning, with Tattersall's (Chapter 1) overview of lemur evolution based on recent fossil, molecular, and ecological evidence. One of the biggest questions regarding lemur evolution is how did lemur ancestors arrive in Madagascar? Current evidence indicates that all of Madagascar's extant and extinct terrestrial mammalian species arrived via an overwater route that may have included ephemeral land bridges or "steppingstones" formed by geological forces in the seafloor. We move from prehistory to history in the chapter by Jolly and Sussman (Chapter 2), where we are introduced to the world of lemur studies in a lively recounting of the history of lemur research in Madagascar and a look at future prospects for conservation in Madagascar. Godfrey et al. (Chapter 3) then enliven the fossil record by using skeletal evidence from the extinct lemurs to suggest possible patterns of their social behavior, biology, and life history.

Given the unique phylogenetic status of the Malagasy lemurs, understanding their basic as well as unusual adaptations is key. Cuozzo and Yamashita (Chapter 4) provide an in-depth overview of what we currently understand regarding lemur dentition. Putting this discussion in a strongly ecological context, they discuss how the external environment leaves an imprint on lemur dentitions, either through adaptations to the physical requirements of specific environments or through environmental effects during the lifetime of the animal. Fietz and Dausmann (Chapter 5) discuss one of the most unusual primate adaptations to Madagascar's marked seasonal climate changes, that of hibernation in *Cheirogaleus medius*. The authors contrast the mechanisms of hibernation in this species, a tropical hibernator, with those of temperate climate hibernators in terms of physiological changes in body mass, internal temperature, and energy efficiency. They explain this unusual behavioral pattern as a response to low ambient temperature as well as food and water shortages during the cool, dry season in western Madagascar.

Freed (Chapter 6) notes that in most communities, different species of diurnal lemurs barely tolerate, displace, or chase one another; yet amicable polyspecific associations are common among members of crowned lemurs and Sanford's lemurs. He then explores these patterns and discusses why such an unusual association occurs.

Several lemur species have been described as cathemeral, and Curtis presents information on cueing mechanisms, adaptive significance, and the evolution of this unusual activity pattern in *Eulemur*, *Hapalemur*, and *Varecia* (Chapter 7). Hypotheses related to the development of cathemerality, which involve such variables as differences in canopy cover, predator avoidance, and offsetting food competition, are presented, as Curtis stresses that there is no single explanation for the evolution of cathemerality. Sterling and McCreless (Chapter 8) discuss the behavior and adaptations of Madagascar's most unusual-looking lemur, indeed one of the most unique primates, the aye-aye. The ecology and biology of this primate are likewise unique and in nearly every aspect, this species stands outside what is even the norm for lemurs.

During the past 15 years a wealth of new lemur studies have greatly enhanced our understanding of lemur taxonomy and ecology, making distinctive connections between ecological factors and patterns of social organization and behavior. Johnson (Chapter 9) presents an overview of the taxonomy and behavioral ecology of the brown lemur complex (*Eulemur fulvus* spp.), and explains recent taxonomic changes and genetic differences between species and subspecies. He clarifies the question of hybrids, subspecies, and species differentiation, and highlights ecological distinctions in this geographically widespread array of lemurs. Radespiel (Chapter 10) provides us with comparative information on both intra- and interspecific differences in mouse lemurs (*Microcebus*) covering ecological, physiological, reproductive, and social variables, some of these correlating with Madagascar's marked climatic seasonality. Radespiel also posits a model for ancestral mouse lemur social organization and sociality, which may in fact reflect the ancestral lemur, or even the ancestral primate condition. The way in which climate and environmental variables have likely shaped social organization and sociality are addressed in Overdorff and Tecot's chapter on red-bellied lemurs (Chapter 11). They discuss how ecological pressures in the habitat of *Eulemur rubriventer*, and resource defense by both sexes, may have led to the evolution of pair bonding in this species. Gould (Chapter 12) provides an in-depth update of what is currently known of the ring-tailed lemur's geographic distribution, variation in habitat and population density, diet and feeding ecology, and life-history variables, illustrating the remarkable adaptability of this species. Gould stresses that future research in non-gallery forest habitats is needed in order for us to fully comprehend this highly adaptable lemur. Vasey (Chapter 13) synthesizes both theoretical and empirical studies, and using her extensive fieldwork on wild *Varecia rubra*, the red ruffed lemur, she tests a number of hypotheses that link large body size to particular foraging and social patterns and reproductive costs.

Recent studies of the behavioral ecology of many lemur species have provided us with a much clearer picture of their diversity, and their behavioral and morphological adaptations. Irwin (Chapter 14) provides a summary of the ecology and behavior of the beautiful eastern sifakas. These species have only recently been studied in any depth, and Irwin summarizes what is currently known, revealing a striking level of variability in terms of home range, diet, and social structure. Thalmann (Chapter 15) provides important new information on aspects of behavior and ecology of two sympatric nocturnal lemurs, *Avahi occidentalis* and *Lepilemur edwardsi*. He notes striking differences in their feeding ecology, activity, and behavioral patterns, highlighting alternative solutions to similar ecological stresses experienced by the two lemur species. Powzyk and Mowry (Chapter 16) focus on ecological research on the indri (*Indri indri*) at three sites in different decades: Mantadia and Betampona in the 1990s and 2000, and Analamazaotra in the 1970s. They discuss distinctions between indri and other lemur species with respect to gut and dental anatomy, and point out intraspecific differences in diet between habitats and study sites. In light of *Indri indri* being the largest prosimian folivore, Powzyk and Mowry suggest that they be considered "energetic minimizers" and that their unique territorial calls may have evolved because calling requires less energy than scent-marking given their large home ranges. Tan (Chapter 17) presents an overview of *Hapalemur* ecology, with a focus on the unusual diet of this genus, the only primates to specialize on bamboo. She touches on new research focusing on physical properties of *Hapalemur* food items, and masticatory adaptations that have evolved in the genus to allow for the processing of bamboo. Tan also points out that we know little about the ability of *Hapalemur* to cope with and avoid cyanide in their bamboo intake, and she suggests directions for future research in this area.

Madagascar is a place of changes. We know that in many respects the particular patterns of Madagascar's climate play a critical role in understanding lemur adaptations. Anthropogenic change is also a part of Madagascar's landscape and lemurs have long faced additional stresses from human-induced changes. Many of the authors address how lemurs respond to such stressors. For example, a serious drought in 1991–1992 affected *Lemur catta* populations at both Berenty and Beza Mahafaly research sites, and Gould (Chapter 12) discusses how these populations recovered within a few years. Godfrey, Jungers, and Schwartz (Chapter 3) address how human impact through habitat destruction, introduction of domestic animals, and direct hunting led to the extinction of the giant lemurs, while Irwin (Chapter 14) highlights important conservation issues for the endangered eastern sifakas, for example, noting that in his own study on *Propithecus diadema*, fragmented habitats may alter diet composition in ways that may have both serious reproductive and social (i.e., competitive) effects. Cuozzo and Yamashita (Chapter 4) report that dental health may be compromised when lemurs begin to include foods of human origin.

Natural disasters and climate extremes are part of the climatic unpredictability of Madagascar, as discussed by Wright (Chapter 18). She notes that the Malagasy lemurs have a number of biological and behavioral responses to periods of food scarcity that may be responses to such unpredictability. Droughts and cyclones can seriously affect already fragile lemur populations, and likely have for thousands or millions of years. In this context Ratsimbazafy (Chapter 19) discusses the feeding and foraging strategies employed by a group of *Varecia variegata editorium* (black-and-white ruffed lemurs) at the Manombo rainforest site after a devastating cyclone hit southeastern Madagascar in 1997. Even though half of their preferred food trees were killed, many *Varecia* at this site survived and remained highly frugivorous, which Ratsimbazafy attributes to their use of two exotic plant species. He stresses that such diet flexibility prevented subsequent starvation in these lemurs after the cyclone hit. Monitoring health and understanding disease transmission in wild lemur populations is also critical with respect to future conservation efforts. Junge and Sauther (Chapter 20) explain how the relatively recent arrival of humans and domestic animals in Madagascar has had an important impact on pathogen transmission in lemur populations, and how introduced diseases can have serious detrimental effects on endemic lemur populations residing both in remote regions as well as in habitats undergoing rapid anthropogenic change.

Many populations of Madagascar's lemurs are threatened by anthropogenic and climatic factors, despite the fact that all lemur species are listed in the Convention on International Trade in Endangered Species (CITES). In just the past decade, several new species have been discovered (see for example Kappeler et al., 2005; Thalmann and Geissmann, 2005) bringing the number of extant species and subspecies to far more than previously thought.

The 2005 IUCN Red List assessment considers that 63% of today's lemur species are threatened with extinction, and 11 of these are considered Critically Endangered (Mittermeier et al., 2006). Anthropogenic effects such as habitat destruction (primarily for cattle grazing and crops), charcoal production, and hunting are still major threats to lemur population survival. A mere 3% of Madagascar's area is actually protected (Mittermeier et al., 2006), but Madagascar's president, Marc Ravalomanana, announced in 2003 that he plans to triple the amount of protected land in the next 5 years (Mittermeier et al., 2006; and see Jolly and Sussman, this volume, for a more detailed explanation). Hopefully this plan will be successful, and will allow for far greater protection for Madagascar's unique fauna and flora.

It is important that lemur conservation and scientific research go hand in hand, as one has a crucial influence on the other. New research conducted on well-known species as well as on newly discovered species, or species and populations for which little was previously known, can aid conservation strategies and programs, as such studies can clarify or contribute to diverse issues such as genetics, disease ecology, habitat change, hormone ecology, life-history and population ecology. Morphological and paleontological studies can also help us to understand the evolutionary history and adaptation of the lemurs, and give us greater perspective on past and present environments, and the multitude of ways that extinct and extant lemurs have coped with and adapted to the unique habitats found on the Red Island. In this volume, we present some of the recent and insightful research conducted on these topics, and at the same time, we look forward to an even further blossoming of future research on the remarkable lemurs of Madagascar.

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Lisa Gould and Michelle Sauther
Victoria, British Columbia and Boulder, Colorado, 2006

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SECTION ONE

# Lemur Origins, History of Ecological Studies on Lemurs, and the Ecology of the Recently Extinct (Subfossil) Lemurs

CHAPTER ONE

# Origin of the Malagasy Strepsirhine Primates

*Ian Tattersall*

The great island of Madagascar has a long insular history, having split from Africa some 120 million years (myr) ago and from India around 88 myr ago (see below). The length of its isolation has much to do with its extraordinary biotic uniqueness. Madagascar's endemic primates, the lemurs, are the most spectacularly diversified element of a highly unusual fauna that displays an adaptive variety surpassing that of any comparable primate group, especially if the recently extinct "subfossil" forms are taken into account. But although from a geographical perspective the strepsirhine primates of Madagascar represent a contained unit, there are many reasons why it is hardly possible, still less desirable, to discuss their origins separately from the larger biogeographic tapestry within which they are woven. This is particularly true given the current total lack in Madagascar of a terrestrial Tertiary fossil record that might give a direct indication of the ancestral stock(s) from which today's major groups of Malagasy strepsirhine primates emerged. At least for the Paleocene and Eocene, the fossil records of Africa and Asia are only marginally better, with the result that inferences about the primate colonization of Madagascar have largely to be made from indirect—even highly indirect—evidence. For these reasons I begin this survey well before the initial emergence of the strepsirhines, with a brief overview of Madagascar's geological and geographical histories.

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## THE ISOLATION OF MADAGASCAR

Madagascar is separated from the southeastern African coast by the 350- to 750-mile-wide Mozambique Channel, and with a surface area of 230,000 square miles it is the world's largest oceanic island (Greenland, New Guinea, and Borneo are all larger, but are connected to the adjacent mainlands at times of lowered sea level). This isolation has evidently had a strong effect on the composition of Madagascar's fauna which, when compared to those of the continents and even to other very large islands, shows an unusual combination of low diversity at high taxonomic levels with high within-family diversity. Clearly the waters surrounding Madagascar have acted as a powerful faunal filter, albeit a slightly porous one.

The fragment of continental crust we know today as Madagascar once lay deep within the ancient supercontinent of Gondwana, with India to its east. But by the time that Gondwana began actively to fragment in the middle Jurassic, about 160 myr ago, the western edge of the island was already underwater and Madagascar, still attached to Antarctica in the south and to India in the east, began to move south-southeast away from Africa along a slip-strike fault, the modern remnant of which in the Mozambique Channel seafloor is called the Davie Fracture Zone (see review by Wells, 2003). This movement had ceased by the middle Cretaceous, about 125 myr ago, leaving Madagascar in roughly its present position vis-à-vis Africa (Coffin and Rabinowitz, 1988). It is not certain whether at this point Madagascar still retained a land connection to Africa and Antarctica via India (contrast Krause, 2003, with Smith et al., 1984). India parted company with Madagascar in the late Cretaceous, about 88 myr ago (Storey, 1995; Storey et al., 1997), definitively completing the island's isolation well before the beginning of the Age of Mammals at around 65 myr ago.

Although the current record of Cretaceous mammals in Madagascar consists of little more than a small handful of teeth, a remarkably wide range of taxa is represented. Among them are the world's oldest tribosphenic mammal, *Ambondro mahabo* (Flynn et al., 1999) from the middle Cretaceous, and the earliest marsupial, from the latest Cretaceous (Krause, 2001). The balance of late Cretaceous specimens includes a multituberculate and two gondwanatheres (Krause, 2000, 2003). But as impressive as this variety may be compared to the size of the collection, no modern placental groups are represented; and it is clear that none of Madagascar's modern mammalian groups (or any plausible precursor) is represented among Mesozoic fossils discovered so far, and that none can be shown to represent a Gondwanan remnant. Instead, it appears that all must be descended from ancestral forms that somehow contrived to cross a substantial water barrier (Krause et al., 1997). Terrestrial mammals are notoriously poor overwater dispersers (Lawlor, 1986), and the only even remotely plausible mechanism for getting them to Madagascar is by rafting on tangled mats of vegetation such as those that are swept out to sea by the floodwaters of African rivers.

Today's terrestrial Malagasy mammals belong to four orders: Primates, Lipotyphla (broadly, Insectivora), Carnivora, and Rodentia, all of which also occur on the African and Asian continents. A fifth order, the enigmatic and endemic Bibymalagasia (MacPhee, 1994), was also represented on Madagascar until recently, as was Artiodactyla in the form of pygmy hippopotamuses. However, large-bodied semiaquatic forms like the (probably quite recently arrived) hippopotamuses disperse by different rules from the strictly terrestrial forms, and the same is true for the volant Chiroptera. Among the strictly terrestrial groups, the ancestral primates (see below) and lipotyphlans probably arrived early in the Tertiary period, while the ancestral carnivores and rodents most plausibly reached Madagascar early in the Miocene epoch (see reviews by Tattersall, in press a and b). The general feeling at present is that the other Malagasy mammal groups are most likely monophyletic (see, for example, Goodman et al., 2003; Jansa and Carleton, 2003; Olson and Goodman, 2003; Yoder, 2003; Yoder and Flynn, 2003), and this is probably also true for the primates (e.g., Yoder and Yang, 2004, but see discussion below). If such is the case, then a minimum of five colonization events is still necessary to explain Madagascar's endemic terrestrial mammal diversity. Crossings were possibly concentrated into two periods of time, the early Tertiary and the early Miocene, which makes it necessary to look again at Madagascar's historical biogeography.

To say that Madagascar has been stable in its position relative to Africa since well before the beginning of the Age of Mammals is not to say that the geography of Madagascar and its surrounding crust has necessarily remained static throughout the Tertiary. Despite the fact that today most of the Mozambique Channel is of oceanic depth, it is possible that parts of its seafloor were raised in the past. Thus, McCall (1997) has argued that uplift along the Davie Fracture Zone in the period between about 45 and 26 myr ago resulted in its partial subaerial exposure, with subsequent tensional conditions returning the topographic highs. This scenario is based on core samples reported by Leclaire et al. (1989) and Bassias (1992) suggesting that subaerial sediments were deposited along the ancient fault line during late Eocene and Oligocene times. deWit and Masters (2004) have recently raised this possibility once more, and have also suggested a potential late Cretaceous or early Tertiary migration route along the set of fracture zones, known as the Antarctic–Africa Corridor, that lie between Antarctica and Africa/Madagascar. They have also proposed an alternative migration route from India, along the Deccan hotspot corridor to Madagascar's north and east. The latter suggestion evokes the notion of a potential Chagos/Laccadive filter connection between India and Madagascar that was recently mooted by Marivaux et al. (2001), echoing an earlier suggestion by Gingerich (1975).

The fact that Madagascar's modern mammalian fauna is so unlike Africa's (or Asia's) certainly suggests that the water barrier around the island has existed continuously throughout the Tertiary. Indeed, Krause (2003) has rejected the possibility of a landbridge at least partly because of the "extreme dissimilarity" of the African and Malagasy faunas This difference undeniably shows that crossings were rare, and therefore extremely difficult, but it is possible to read this evidence another way. As far as we know, no strictly terrestrial mammal has contrived to cross the water barrier surrounding Madagascar for at least the last 15–20 myr or so. In that case, it seems necessary at least to ask whether, under current geographical conditions, *any* crossing at all is possible for such inefficient overwater dispersers as placentals of this kind. And should this prove to be the case, the ephemeral existence of island-chain "steppingstones" at points during the Tertiary would clearly have been absolutely essential for the transfer to Madagascar of any terrestrial mammals at all. On the other hand, in the absence of a Tertiary terrestrial fossil record in Madagascar we have no way of knowing how many groups of mammals might have crossed the water barrier during this period without managing to establish themselves permanently on the island. If Madagascar's modern faunal composition is biased by selective extinction the implication is, again, that the barrier was more permeable in the past than it appears now, presumably also as a result of ephemeral land connections. It is because of such considerations that future clarification of the mode of primate colonization of Madagascar, and its source, is as likely to come from geological studies of the surrounding seafloor as it is from an enlarging fossil record, or from improved systematic knowledge of the island's endemic mammals and their closest continental relatives.

## MADAGASCAR'S PRIMATES

By far the most renowned and diverse group of Madagascar's mammals is its primates, the lemurs. There is general agreement that the lemurs, including the recently extinct "subfossil" forms, should be classified into seven families: Cheirogaleidae, the dwarf lemurs, with five living genera; Lemuridae, the "true" lemurs and their close relatives, with five genera (one extinct); Lepilemuridae, with two genera (one extinct); Indriidae, with three living genera; Archaeolemuridae, with two genera (both extinct); Palaeopropithecidae, with four genera (all extinct); and Daubentoniidae, the aye-ayes, with a single living genus and species. Depending on whose classification one accepts, the living lemurs alone may embrace well over 40 species, and an astonishing total of up to (and possibly exceeding) 72 primate taxa if subspecies are included. Thus, even excluding the recently extinct lemurs from the count, Madagascar ranks third-highest on the list of high-primate-diversity countries worldwide, even though it is less than a tenth the size of the world leader, Brazil (Mittermeier et al., 1994).

This amazing diversity is potentially due to a combination of several factors (see Tattersall, 1982). First, while paling in comparison to the huge area of Brazil, Madagascar is nonetheless extremely large: at 1600 km long, and with a surface area of almost 600,000 km$^2$ it is the world's biggest oceanic island. When first colonized by humans, the island was largely if not entirely forested, providing primate-friendly habitats in virtually all but the most open areas and the most extreme montane environments. Second, due to both its geographical position and its varied topography, Madagascar offers a huge range of forest habitats. Lying almost entirely within the southern tropical zone, Madagascar lies in the path of the easterly trade winds. Its narrow eastern coastal plain is paralleled by a steep and rugged escarpment which captures the moisture borne by those winds, and as a result is naturally clothed by luxuriant rainforest. Madagascar's raised central plateau is deeply dissected, and offers a large range of microenvironments. Toward the west it gradually yields to drier and more seasonal coastal plains where forest cover varies from riverine gallery forests to dry brush and scrub habitats. Madagascar's northern and southern extremities are very dry indeed, the far south supporting the unique "spiny forest" where plant endemism is as high as 98% at the species level. Altogether, this unique island offers primates and other mammals a diversity of ecological settings that is unmatched in any comparable area elsewhere.

All of Madagascar's primate families are completely endemic to the island, and merely on the basis of systematic diversity it is clear that primate evolution there has taken an independent course for a very long time. But in the absence of a Tertiary fossil record, exactly how long is debatable. Because of the overall distinctiveness of the Malagasy primate fauna, it has generally been assumed that the lemurs form a monophyletic group. At the same time, the suborder Strepsirhini to which the Malagasy primates belong is not unique to Madagascar, since there is no question that it also contains the African galagos (Galagidae) and the Afro-Asian pottos and lorisis (Lorisidae). All living strepsirhines share a suite of features that includes the package of characteristics, primitively typical of macrosmatic mammals, that includes retention of a rhinarium and a fully functional vomeronasal organ. Additionally, all strepsirhines lack bony posterior closure of the less than fully frontated orbits, and share possession of an unfused mandibular symphysis, a relatively small brain-to-body size ratio, and extremities bearing divergent first digits. There are flat nails on all digits except the second pedal, which bears a "toilet" or "grooming" claw. The most prominent hard-tissue synapomorphy of the group is the presence of a procumbent toothcomb in the lower jaw. This unusual structure (unique in its morphological details if not in its existence) consists of four teeth in the indriids, archaeolemurids, and palaeopropithecids, and of six teeth in all the other lemurs except for the highly derived *Daubentonia*, in which it is autapomorphically replaced by a single pair of constantly growing anterior teeth.

Until recently, there was no ancient fossil record of toothcomb-bearing primates anywhere in the world before the African early Miocene, by which time a substantial fossil record has long shown that both modern Afro-Asian strepsirhine families were already well established (Simpson, 1967). Recently, however, an earlier strepsirhine record has begun to emerge, both in Asia (Marivaux et al., 2001) and in Africa (Seiffert et al., 2003; Martin, 2003).

## THE TERTIARY FOSSIL RECORD OUTSIDE MADAGASCAR

The earliest fossil primate that undisputably bears a toothcomb is *Karanisia clarki*, described from a small sample of isolated teeth and jaw fragments by Seiffert et al. (2003). These specimens, which include a canine crown indicating the presence of a toothcomb, come from late middle Eocene (probably ca. 40 myr old) sediments of the Birket Qarun Formation, in the Egyptian Fayum. *Karanisia* is interpreted by its describers as dentally not only lorisiform but lorisid, possibly representing a sister genus to the living West African genus *Arctocebus*. Two teeth from the same stratigraphic were assigned to the galagid genus *Saharagalago misrensis*. Seiffert and his coauthors believe that these Fayum fossils establish the divergence of the two living non-Malagasy strepsirhine families by the mid-to-late Eocene.

Marivaux et al. (2001) allocated several isolated teeth from the Bugti Hills of Pakistan to the new species *Bugtilemur mathesoni*, in which a lower canine is said to confirm the presence of a toothcomb. Marivaux et al. assigned these very tiny early Oligocene (ca. 30 myr old) fossils to the Malagasy family Cheirogaleidae on the basis of cheektooth morphology, suggesting transfer via a putative sweepstakes/filter route involving a Chagos/Laccadive paleoridge system. Within Cheirogaleidae, Marivaux and colleagues most closely compared the molars of *Bugtilemur* to those of *Cheirogaleus*, and morphologically the resemblance is indeed remarkable. However, the living Malagasy genus is much larger in body size than the fossil one is, and it has a much longer and slenderer toothcomb than *Bugtilemur* apparently had.

The molar morphology of *Bugtilemur* is particularly interesting given that it has been argued that the cheirogaleid lemurs may in fact be more closely related to the Afro-Asian strepsirhines than to the other Malagasy lemurs (e.g., Szalay and Katz, 1973; Schwartz and Tattersall, 1985). In 1970 Charles-Dominique and Martin drew attention to the suite of behavioral similarities uniting the cheirogaleids and lorisoids. Charles-Dominique and Martin were content to regard these similarities as ancestral retentions; but Szalay and Katz (1973) proposed that many characters shared between lorisoids and cheirogaleids are in fact derived, and that in consequence the cheirogaleids and lorisoids are more closely related to each other than the cheirogaleids are to the other lemurs. Cartmill (1975) later added other features to the list of apparent cheirogaleid–lorisid synapomorphies. And a few years later Schwartz and Tattersall (1985) pointed to evidence from molar morphology that also supports this association. In addition, these authors found morphological justification for regarding the entire balance of the Malagasy primate fauna, including the aye-aye, as a monophyletic unit.

The paraphyly that these observations suggested had radical implications for lemur biogeography and origins. For if the cheirogaleids are in fact lorisoids, then there are only two biogeographical possibilities. The first of these is that the cheirogaleids are descended from an African (or conceivably Indian) ancestor that invaded Madagascar separately from the ancestor of the remaining lemur fauna (i.e., that there were two strepsirhine colonizations of Madagascar, the later one subsequent to the apparently Eocene or earlier divergence of the lorisiform and lemuriform groups in Africa). The second possibility is that, from a single African or Asian common ancestor, the lemurs diversified on Madagascar to the family level we now recognize and that today's Afro-Asian lorisoids are descended from a cheirogaleid ancestor that recolonized Africa (or conceivably India) from Madagascar, probably before the late Eocene. The pattern of ocean currents makes a Madagascar–Africa crossing considerably more probable than the reverse trip; but if the modern Afro-Asian families had already emerged by the late Eocene, as Seiffert et al. (2003) suggest, then the cheirogaleid back-crossing must have been an early one indeed. At the same time, however, a very early back-crossing of this kind might also be consonant with the presence of a cheirogaleid-like *Bugtilemur* in the early Oligocene of Pakistan, although Marivaux et al. (2001) prefer a dispersal event between Madagascar and Greater India.

A few years ago, before the finds in the Fayum and the Bugti Hills, any discussion of lemur origins would have begun with a look at the Eocene adapiform primates of Eurasia. This group formed part of the great Eocene radiation of early euprimates "primates of modern aspect," and produced a profusion of genera and species among which number some of the best-documented fossil primate species known. In the very vague sense of an evolutionary "grade" the adapiforms (possibly themselves paraphyletic in laxer definitions) seem generally to have resembled today's strepsirhine primates; and indeed, some recent primate classifications have included Adapiformes as an extinct infraorder of the suborder Strepsirhini (e.g., Delson et al., 2000). Within Adapiformes, signs of lemuriform ancestry have been particularly sought within the family Adapidae (first and still best known from Europe), despite the fact that all known adapiforms, including the adapids, primitively lack the principal strepsirhine synapomorphy, the toothcomb. Adapids also typically possess four premolars in each quadrant of the jaw as opposed to the three or two of lemurs, and show a fused mandibular symphysis. Intriguingly, though, a presumed adapid hindbody skeleton from Germany's middle Eocene Messel site does quite clearly show a grooming claw on the second digit of the foot (von Koenigswald, 1979); and adapids are well documented to have very lemurlike auditory bullae.

Impressed by these complex basicranial resemblances, Gregory (1920) argued that close molar similarities between the European Eocene adapid *Adapis* and the living Malagasy *Lepilemur* were of ancient derivation and provided a sort of evolutionary link between *Adapis* and the other modern strepsirhines. Gingerich (1975) later suggested that the closest molar resemblances were to be found between *Adapis* and *Hapalemur*, suggesting that *Adapis* had given rise to the other lemurs via a form that at least dentally resembled *Hapalemur*. Schwartz and Tattersall (1979) proposed the alternative notion that the dental morphologies of *Hapalemur*, *Lepilemur*, and *Adapis* were derived, thus indicating that the fossil taxon somehow nests *within* the strepsirhine clade, rather than lying at its origin. They later noted (Schwartz and Tattersall, 1985) that the indriid lemurs, in particular, shared a whole suite of dental and mandibular characters with adapids, whereas some of the dental characters of the cheirogaleid+lorisid+galagid group recalled those of some Eocene non-adapid adapiforms such as *Anchomomys* and *Periconodon*. However, Beard et al. (1988) observed that a wrist structure in which the os centrale overlaps the capitate to contact the hamate is unique to lemurs, to the exclusion of *Adapis*.

The paleontological argument over both the origin of the lemurs and the existence of potential lemur relatives in the Eocene is bedevilled by slender Paleocene and Eocene fossil records in the possible source areas of Africa and India. *Altiatlasius* from the early Eocene of Morocco is pretty indeterminate, while *Djebelemur* from the early Eocene of Tunisia is plausibly adapid but shows no particular affinity with any lemur. In the late Eocene of the Egyptian Fayum, the sketchily known genera *Aframonius* (Simons et al., 1995; Simons and Miller, 1997) and *Wadilemur* (Simons, 1997), plus an apparent representative of the European genus *Anchomomys* (Simons, 1997), show that adapiforms (though not adapids) may have survived there not only after the strepsirhines had originated, but also after the two modern lorisoid families had differentiated.

In Arabia, the poorly known *Omanodon* and *Shizarodon* from Oman indicate not much more than that adapiforms were present there in the early Oligocene. In the Indian region the two sivaladapid adapiforms *Indraloris* and *Sivaladapis* survived into the late Miocene, as recently as 8 myr ago (Gingerich and Sahni, 1984), and the possibly adapid genus *Panobius* has been described on the basis of a couple of teeth from early-to-middle Eocene deposits in Pakistan (Russell and Gingerich, 1987). However, *Sivaladapis* conspicuously lacks a toothcomb and otherwise bears no close resemblances to any lemur. Several other Asian fossil forms are also classified in the family Sivaladapidae, including the Eocene Chinese forms *Guanxilemur*, *Rencunius*, and *Hoanghonius*. The Eocene Chinese genus *Adapoides* may in contrast be a true adapid, as may *Wailekia* from Thailand. All in all, however, these various forms do little more at present than suggest that both adapids and other adapiforms were abundant in forests throughout the Old World tropics for much of both the Paleogene and the Neogene, at least back to about 55 myr ago. They do not shed any direct light on the origin of the Malagasy lemurs, and indeed the presence of *Aframonius* and the others in the Fayum, more or less contemporaneously with *Karanisia* and *Saharagalago*, implies that if the direct strepsirhine ancestor was an early member of the African adapid radiation it was very ancient, possibly even predating the early Eocene. This is in line with molecular phylogenies that suggest a much earlier initial diversification of the lemuriforms than of the lorisoids (see below).

## MOLECULAR STUDIES

In recent years, approaches to lemur systematics have been dominated by molecular comparisons that have mostly yielded findings that support the monophyly of the entire lemur fauna. Anne Yoder and her colleagues (e.g., Yoder et al., 1996; Yoder, 2003; Yoder and Yang, 2004) have particularly vociferously rejected the notion that there is a special affinity between the cheirogaleids and the lorisoids. Most of this work has consisted of comparative studies of the mitochondrial cytochrome *b* gene, but lately certain nuclear elements have been added to the mix. Yoder and co-workers find that the basal split among the strepsirhine primates is between lorisiforms on the one hand, and lemuriforms including Cheirogaleidae on the other. Within Lemuriformes, they find that the basal split is between Daubentoniidae and all the rest.

Numerous lower-level problems of relationship among the species and genera of lemurs have been clarified by the molecular studies undertaken so far; but the rather fast-evolving mitochondrial genome is generally considered unreliable for assessing ancient splits, and DelPero et al. (2001) have found among the lemurs that while the 12S rRNA mitochondrial gene is useful for gauging within-family affinities, relationships among families separated by large genetic distances (<12% divergence) defy consistent resolution. This is most clearly the case among lorisids, galagids, daubentoniids and the apparent lemurid/indriid clade.

A recent study by Roos et al. (2004) that combined cytochrome *b* results with an analysis of nuclear short interspersed elements in a variety of strepsirhines situated the cheirogaleids within the lemuriform radiation, with a basal split between the aye-aye and all the others. This is another pointer toward the conclusion that the deeply entrenched notion of lemur monophyly may well be accurate—even though it suggests enormous levels of convergence and primitive retention respectively between and within the lorisoids and cheirogaleids. For the time being, definitive demonstration perhaps still awaits; but the evidence of historical biogeography, together with the fact that the other groups of Malagasy terrestrial mammals also appear most likely to be monophyletic, suggests that the external probabilities are on the side of lemur monophyly as well.

A further ramification of molecular studies is the estimation of divergence dates for the various higher taxa recognized (e.g., Yoder et al., 1996; Porter et al., 1997; Yoder and Yang, 2004). The most recent estimated date for the basal split among a monophyletic lemuriform group is 47 Ma (Porter et al., 1997), and Yoder has lately raised her estimate from >54 Ma (Yoder et al., 1996) to 62–65 Ma (Yoder and Yang, 2004), based on a variety of both mitochondrial and nuclear gene loci. Calibration was from the fossil record, with all the consequent uncertainties enumerated by Grauer and Martin (2004). Still, current molecular and morphological estimates of the divergence time seem to be in (very) approximate agreement. For if the lemurs are in fact monophyletic, the ancestral strepsirhine having given rise very early in the Tertiary (and most probably in Africa) to the ancestor of the Malagasy group on the one hand, and to the ancestor of the lorisids/galagids on the other; and if the lorisids and galagids had indeed differentiated by the mid-to-late Eocene (ca. 41–37 Ma) as *Karanisia* and *Saharagalago* seem to indicate, then some stretching of the molecular time scale would seem to be plausible. This is especially the case given the sheer scale of the diversification that has taken place among the lemurs subsequent to the time of their common ancestor, and it is supported by molecular comparisons that suggest that much of this diversification took place at an early stage—earlier than that of the living lorisoids (see, e.g., Yoder and Yang, 2004).

## ECOLOGY

The lifeways (not to mention the identities) of the earliest primates have been much debated. But the fossil record has long shown that the basic package of prosimian/strepsirhine adaptations was in place by the early Eocene, about 55 myr ago; and if the earliest primate colonizers of Madagascar significantly predated this time, the strepsirhine bauplan would have been present substantially before. Early theories of euprimate origins (e.g., Jones, 1916; Smith, 1924) held that it was adoption of arboreality itself that was the key to the fixation of such primate features as grasping hands, binocular vision, and brain enlargement. However, since many other arboreal mammals do very well without such characteristics, this explanation is at the very least incomplete. Cartmill (e.g., 1972) added visual predation to the mix, with the implication that early primates had been at least mainly insectivorous. In contrast, Sussman and Raven (1978) noted that euprimate diversification followed closely on the heels of the radiation of flowering plants, and proposed that it was the "windfall" resources of abundant fruits and flowers that had provided early primates with the opportunity to radiate. Based on a field study of the "prosimian-like" neotropical marsupial *Caluromys*, Rasmussen (1990) integrated these two notions by concluding that the primate ancestor had been a visual predator that foraged in the fine terminal branches of the angiosperm canopy for a "combined windfall" of fruits and flowers and the insects attracted by them. Most authorities would currently accept this hypothesis.

Modern strepsirhine body sizes vary enormously, and within this large range *Bugtilemur* and the Fayum lorisoids vary from tiny to small. The majority of Eocene adapiform primates were larger than this, most of them also exceeding their omomyoid contemporaries in body size. Interestingly, this places the Fayum strepsirhines in the general size range of the modern lorisoids, while the adapiforms are more comparable to the midrange of Malagasy lemurs. As to locomotion, the Fayum lorisoids are known only from cranial material, but the adapiforms show a variety of locomotor types that apparently ranged from rather loris-like slow arboreal quadrupedalism in *Adapis* (Dagosto, 1983), to more active quadrupedalism in forms like *Pronyticebus* (Szalay and Dagosto, 1988) and thigh-powered leaping in *Smilodectes* (Covert, 1986). Smallish orbit sizes in almost all adapiforms point to diurnal activity, and molar form and wear suggest a preponderance of frugivory among many members of this group although some adapiforms, among them *Adapis* and *Leptadapis*, possess sharply crested molars that are suggestive of folivory (Covert, 1986).

It is, then, possible to view the radiation of adapiforms in the Eocene as a sort of early euprimate parallel of today's radiation of diurnal lemuriforms in Madagascar. If the modern lorisoid families had indeed diverged by the late Eocene, the Fayum genera (which derive from deposits that were laid down in moist lowland tropical forest conditions) were presumably fairly close ecological equivalents of their living counterparts. Interestingly, heterothermy, a potential facilitating factor in any rafting scenario, is absent in the few lorisoids so far studied (Mzilikazi et al., 2004), so that its presence in certain cheirogaleids seems most likely to be a specialization acquired in Madagascar rather than a dispersal advantage possessed by the original colonizers. The many adapiform genera are simply too diverse to suggest any ecological thread more precise than a preference for the canopies of tropical or semitropical forests. If the ancestral strepsirhine was a very early adapiform, it is thus difficult to surmise its exact ecological preferences; adapids were probably mostly frugivorous, but *Adapis*, the adapiform most frequently compared to lemurs, had the molar morphology of a folivore. On a comparative basis there is thus little to suggest the precise ecological niche or niches of Madagascar's founding primate. The problem is, of course, only exacerbated by the fact that *Daubentonia*, the probable outgroup of the diverse remaining Malagasy primate fauna, is so highly autapomorphic. And, in a fauna with such conspicuous diversity at low taxonomic levels, what may also be surprising is the typically rather eurytopic signal that emerges from field studies of living lemur species. Without doubt, this generalist tendency has been with euprimates from the very start, and we would do well to emphasize the role of geography/normal population variation above that of adaptation as determinant of the current genus- and species-level diversity of lemurs.

## CONCLUSION

The lemur fauna of Madagascar is totally endemic at the family level, and it may well also be endemic at the infraordinal level, as moderately to strongly supported by recent molecular studies. These studies lean to the conclusion that that the lemurs are indeed monophyletic, derived from a single tropical forest canopy-dwelling common ancestor (whose precise ecological preferences are hard to determine, given the diversity of adaptations displayed by both its living descendants and its presumed fossil relatives) that somehow contrived to colonize Madagascar at some point very early in the Tertiary. Molecular estimates for the basal split among the Malagasy lemurs point to a Paleocene (even early Paleocene) age for this common ancestor (Yoder and Yang, 2004): an age consistent with the remarkably ancient late Cretaceous (ca. 77 myr) date for the origin of Primates derived from various molecular data sets by Springer et al. (2003). These dates are, however, so far unsupported (though not contradicted) by the scrappy fossil record, which is also unhelpful in determining the age of the basal strepsirhine. The presence of apparent lorisids and galagids in the Fayum at ca. 40 myr ago provides a minimum fossil date for the existence of Strepsirhini, but one that is presumably highly underestimated. At the same time, the discovery of more or less contemporaneous adapids and strepsirhines in the late Eocene of the Fayum has tended to marginalize the primarily Eocene adapids as a potential source of Strepsirhini. Further, the absence of toothcombed strepsirhines in the fairly abundant European (and the more limited Asian) Eocene fossil records may suggest that this group is of African derivation, and that it spread to Asia only a substantial time after its origin. It seems likely that only improvement in the currently lamentably restricted Paleocene and Eocene fossil records of Africa (and the discovery of any Tertiary primate record at all in Madagascar) will help shed direct light on the origin of the strepsirhine primates in general and the Malagasy lemurs in particular.

Madagascar has been isolated by a very substantial water barrier since even before the very ancient Springer et al. (2003) molecular date for primate origins. The inescapable conclusion is that the ancestors of the island's four endemic terrestrial mammal orders must have arrived there via an overwater sweepstakes route in spite of the very high probabilities against such a crossing. No terrestrial mammal (other than *Homo sapiens* and its dependents) has, as far as we know, contrived to make this crossing at any time in the last 15 myr or so. This raises the possibility that under current geographic conditions the barrier is absolutely impermeable to such notoriously poor dispersers. If such is the case, it is necessary to inquire whether in fact the geology and topography of the ocean floor surrounding Madagascar has indeed been stable back into the farthest reaches of the Tertiary. The assumption of stability has been called into question recently by a variety of authors (McCall, 1997; Marivaux et al., 2001; deWit and Masters, 2004), who between them have evoked potential "steppingstone" routes both toward and from Africa and India. Clearly, the ocean surrounding Madagascar has acted as a powerful filter to potential mammal invaders of the island; but equally evidently the barrier has not been a totally unbreachable one, at least at certain times during the Tertiary. And it is for this reason that fuller knowledge of the geology of the seafloor surrounding Madagascar will be necessary before we can properly test hypotheses about the mechanisms of Madagascar's colonization by terrestrial mammals, including primates.

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