Mechanisms of faunal origin and diversity in island environments: The case of Madagascar's mammals*

Ian Tattersall[1]

[1] *Division of Anthropology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA*
email: iant@amnh.org

ABSTRACT: Madagascar, some 400 km off the coast of southeastern Africa, is the world's largest oceanic island. It has been widely separated from its parent continent for some 120 Ma, and as a result it has a rather unusual faunal composition, with a relatively restricted number of major taxa but high diversity at lower taxonomic levels. This pattern is particularly evident among the island's terrestrial mammals, among which only the orders Primates, Rodentia, Carnivora and Insectivora are represented (and until recently the enigmatic Bibymalagasia and the Artiodactyla, in the form of semi-aquatic pygmy hippopotamuses). Terrestrial mammals are notoriously poor overwater dispersers, yet evidently the ancestors of all of Madagascar's mammals had to have crossed a wide oceanic barrier to get to the island. In this paper I review the fossil records and phylogenies of each of Madagascar's mammalian groups in an attempt to approximate the minimum number of crossings necessary to produce the island's current faunal composition, and examine the paleogeographic evidence for potential landbridge or "stepping-stone" connections with adjacent continents from the Mesozoic through the Cenozoic. Monophyletic origins for each major group and thus a smaller rather than larger number of crossings of the Mozambique Channel seem to be indicated, implying that this water barrier has acted as an extremely powerful filter. So much so, indeed, that it is still unclear whether any crossings at all would have been possible without some form of subaerial connection, however ephemeral, at times during the Tertiary. Clarification of the mechanisms of origin of Madagascar's terrestrial mammal fauna is thus as likely to come from studies of the surrounding seafloor geology as it is to emerge from examinations of the fossil record and systematics of the island's fauna itself.

Key-words: *Madagaskar, mammals, Biogeography, Primates, Rodentia, Carnivora, Insectivora.*

ΠΕΡΙΛΗΨΗ: Η Μαδαγασκάρη, περίπου 400 χλμ από την ακτή της νοτιοανατολικής Αφρικής, είναι το μεγαλύτερο ωκεάνιο νησί του κόσμου. Έχει χωριστεί ευρέως από την γειτονική του ήπειρο πριν από περίπου 120 εκατομ. χρ., και κατά συνέπεια έχει μια μάλλον ασυνήθιστη πανιδική σύνθεση, με έναν σχετικά περιορισμένο αριθμό σημαντικών ειδών αλλά υψηλής ποικιλότητας στα χαμηλότερα ταξονομικά επίπεδα. Αυτό είναι ιδιαίτερα εμφανές στα ηπειρωτικά θηλαστικά του νησιού, μεταξύ των οποίων μόνο τα πρωτεύοντα, τα τρωκτικά, τα σαρκοφάγα και τα εντομοφάγα αντιπροσωπεύονται (και μέχρι σήμερα τα αινιγματικά Bibymalagasia (Λεμούριοι) και τα Αρτιοδάκτυλα, υπό μορφή ημι-υδρόβιων νάνων ιπποποτάμων). Τα ηπειρωτικά θηλαστικά εμφανώς παρουσιάζουν περιορισμένη διασπορά στο νερό, παρόλα αυτά προφανώς οι πρόγονοι των θηλαστικών της Μαδαγασκάρης έπρεπε να έχουν διασχίσει ένα ευρύ ωκεάνιο εμπόδιο για να φτάσουν στο νησί. Σε αυτήν την εργασία πραγματοποιείται αναθεώρηση των απολιθωμένων αρχείων και των φυλογενέσεων κάθε ομάδας θηλαστικών της Μαδαγασκάρης σε μία προσπάθεια να προσεγγιστεί ο ελάχιστος αριθμός διασταυρώσεων απαραίτητων για τη δημιουργία της τρέχουσας πανιδικής σύνθεσης του νησιού, καθώς και έλεγχος των παλαιογεωγραφικών δεδομένων για την ύπαρξη γεφυρών σύνδεσης με τις παρακείμενες ηπείρους από το Μεσοζωικό έως τον Καινοζωικό. Μονοφυλετικές προελεύσεις για κάθε κύρια ομάδα και έτσι ένας μικρότερος παρά μεγαλύτερος αριθμός διασταυρώσεων μέσω του καναλιού της Μοζαμβίκης φαίνεται να υποδεικνύεται, υπονοώντας ότι αυτό το εμπόδιο ύδατος έχει ενεργήσει ως εξαιρετικά ισχυρό φίλτρο. Πράγματι, είναι ακόμα ασαφές εάν οι οποιεσδήποτε διασταυρώσεις θα ήταν δυνατές χωρίς κάποια μορφή εναέριας σύνδεσης, έστω και εφήμερης, κατά τη διάρκεια του Τριτογενούς. Η διευκρίνιση των μηχανισμών προέλευσης της ηπειρωτικής πανίδας θηλαστικών της Μαδαγασκάρης είναι πιθανό να προέλθει και από τις μελέτες της γεωλογίας του θαλάσσιου πυθμένα και όχι μόνο από τη μελέτη του απολιθωμένου αρχείου της πανίδας του νησιού.

Λέξεις-κλειδιά: *Μαδαγασκάρη, Θηλαστικά, Βιογεωγραφία, Πρωτεύοντα, Τρωκτικά, Σαρκοφάγα, Εντομοφάγα.*

INTRODUCTION

Madagascar is famous for its unusual and strongly endemic fauna that combines a relative dearth of major taxa with remarkable diversity at lower taxonomic levels. Only a few decades ago it was still possible to view Madagascar's extant vertebrate assemblage as a slimmed-down and locally-diversified remnant of an early African fauna; now it is clear that this vast island's faunal history was a good deal more complex than this model would suggest. And it also seems that there has been something eccentric about Madagascar's faunal composition from the very earliest days. Our colleague

---

* Μηχανισμοί πανιδικής προέλευσης και ποικιλότητας στα νησιωτικά περιβάλλοντα: Η περίπτωση των θηλαστικών της Μαγαδασκάρης.

Paul Sondaar, whose memory we are honoring in this volume, spent much of his productive career in the attempt to unravel the idiosyncracies of island faunas in various venues around the globe. And although, regrettably, he never turned his attention specifically to Madagascar Paul would, I think, have approved of the subject I have chosen to address here: the potential mechanisms of colonization of Madagascar by terrestrial mammals.

THE INSULAR HISTORY OF MADAGASCAR

Despite the high level of endemism among Madagascar's vertebrates, it has long been accepted that –somehow– this fauna is of essentially African origin. In early days, when Earth's geography was regarded as having been largely fixed from the remotest past, it seemed clear that the ancestral Malagasy mammals, at whatever time(s), had had to cross the daunting 350-1200 km-wide barrier formed by the Mozambique Channel that separates Madagascar from the African mainland. For despite the inherent implausibility of such a "sweepstakes" route, there was no evident alternative. It was noted that at flood season African rivers emptying into the Indian Ocean regularly carry large "rafts" of matted vegetation far out to sea, and that given sufficient time such a raft might very occasionally have drifted across the Channel (although against prevailing winds and currents) to deposit any luckily surviving terrestrial vertebrate "stowaways" on Madagascar's shores. With the advent of plate tectonics, it was speculated that the Mozambique Channel had gradually widened over the course of the Tertiary (e.g. McKenna, 1967), making earlier crossings over a narrower Channel more likely than later ones; and even when it became apparent that Madagascar had moved southward from a northerly attachment point on the east African coast (see review in Tattersall, 1982), this still would have been the case. This scenario of increasing isolation of Madagascar over the course of the Tertiary was particularly attractive to students of Madagascar's most famous indigenous inhabitants, its primates, because these latter appeared to be most closely related to fossil forms known from the Laurasian Eocene, at whch time the crossing would have been relatively easy.

Over the past couple of decades much has been learned from the surrounding seafloor and from trans-continental correlation about Madagascar's tectonogeographic history, and the paleogeographic situation has been greatly clarified although much remains to be learned (see review by Wells, 2003). Briefly, through much of the Mesozoic the rocks that today compose Madagascar's core were embedded deep within the ancient supercontinent of Pangaea, whose shoreline lay well over a thousand kilometers to the east, beyond India. By the time that Gondwana began to separate from the rest of Pangaea and itself to break up in the middle Jurassic, about 160 Ma, the island's western edge was already underwater. And Madagascar, still attached to India to its east and to Antarctica/Australia in the south, began to move south-southeast relative to Africa along a slip-strike fault whose modern remnant is known as the Davie Fracture Zone (or Ridge). By the middle Cretaceous, about 125 Ma, Indiagascar had ceased its southward movement and had come to rest in more or less its present position relative to Africa (Coffin & Rabinowitz, 1988). At this point, Madagascar may (Krause, 2003), or may not (Smith *et al.*, 1994) have maintained connections to Antarctica and Madagascar via India. India itself seems to have separated from Madagascar in the late Cretaceous, at about 88 Ma (Storey *et al.*, 1995, 1997), sundering the final connection of the island with other landmasses. Exceptionally rapid northeast movement of the Indian plate then ensured substantial separation of Madagascar from its nearest neighboring landmass within a very short space of time.

Flynn & Wyss (2003) detect increasing faunal endemism and provinciality through the later part of the Mesozoic in the fragments of Gondwana including Madagascar, although the discovery of gondwanatheres in the late Cretaceous of Madagascar itself suggested to Krause *et al.* (1997) that some lingering cosmopolitanism in the Gondwanan fauna might have been due to a land connection maintained through Antarctica. Whatever the details, however, it is clear that Madagascar has been as far from Africa as it is today since before the the beginning of the Age of Mammals at some 65 Ma. Although some (e.g. Tattersall, 1982) have been tempted to suggest that the roots of the modern mammalian radiation lie deeper in time than the fossil record currently suggests, there is no substantial current reason to suggest that Madagascar's present mammal groups established themselves on the island before the early Tertiary (see below), or that, as interestingly mooted by Gingerich (1975) (and echoed more recently by Marivaux *et al.* and Dewit & Masters, 2004), the ancestors of the island's primates arrived in the Oligocene (still by a sweepstakes route) from India.

The ancestors of today's Malagasy mammals must thus somehow have contrived to cross the wide water barrier of the Mozambique Channel (or something wider yet). Is it possible, though, that conditions might have existed in the past to make that crossing easier (or just to make the difference between impossibility and tiny probability)? McCall (1997) believes this may have been the case. Most of the Channel is over 1500 m deep, and even the largest posited sea-level lowerings over the course of the Cenozoic would have resulted in negligible reductions in its overall width. But McCall suggests that compressional forces resulting ultimately from India's collision with Asia initiated uplifting along the old Davie Fracture Zone that resulted in the subaerial exposure and erosion of a significant area of the floor of the Mozambique Channel in the period from about 45 to 26 Ma. He finds evidence for this in core samples, reported by Leclaire *et al.* (1989) and Bassias (1992), who suggest that a chain of topographic highs formed along the ancient fault line at this time, resulting in the deposition of subaerial sediments before tensional conditions and consequent subsidence were re-established with the activation of the east African rifting system. KRAUSE (2003) finds the geological evidence for such a land bridge or island series less than compelling, and points to the "extreme dissimilarity" of the African and Malagasy terrestrial faunas as evidence that crossings of the Channel were rare and therefore difficult. More recently yet, however, DEWIT & MASTERS (2004) have resurrected the possibility of episodic continental connections to Madagascar along the Davie Fracture Zone or the suite of similar structures that lie between Antarctica and Africa/ Madagascar (or even the "Deccan hotspot" route between Africa and India), and have pointed out that in certain respects Madagascar's fauna is more "cosmopolitan" than is usually admitted. They have thus returned landbridge/island-hopping possibilities to the mix. Given this high degree of uncertainty about the exact mode of origin of Madagascar's fauna what, if anything, do Madagascar's mammals themselves suggest was the case?

MADAGASCAR'S MAMMALS

The study of mammalian history in Madagascar is bedevilled by the absence of anything but very remote and very recent paleontological records. Only in the past decade or so has anything at all become known about early mammals in Madagascar, and even today what evidence exists is very slight, consisting as it does of a tiny handful of teeth and jaw fragments from sites of middle Jurassic and late Cretaceous age in the Mahajanga basin (FLYNN *et al.*, 1999; FLYNN & WYSS, 2003; KRAUSE, 2001, 2003). Astonishingly, though, this insubstantial record includes the world's oldest tribosphenic mammal, the middle Jurassic *Ambondro mahabo* (FLYNN *et al.*, 1999), considered by LUO *et al.* (2001) to support the notion of a Gondwanan origin for the tribosphenidans (marsupials, placentals and their close therian relatives). It also includes the single marsupial molar reported by KRAUSE (2001) from the latest Cretaceous, which likewise represents the earliest reliable record of its clade, securely dated Gondwanan marsupials being otherwise known only from Cenozoic sediments. Six other late Cretaceous mammalian teeth have also been found (KRAUSE, 2000, 2003). One of these represents a multituberculate and two others different gondwanatheres, yielding a remarkable diversity given the tiny size of the total collection.

Despite the fact that LUO *et al.* (2001) have taken the *A. mahabo* mandibular fragment to represent an "australophenidan" clade of trobosphenidans, endemic to Gondwana, that gave rise ultimately to the modern monotremes separately from the Laurasian-endemic "boreosphenidan" tribosphenidians from which the extant marsupials and placentals sprang, it seems largely premature to draw elaborate biogeographic conclusions from Madagascar's few and poorly known Mesozoic mammals. Still, one inference seems seems pretty firm, especially since most of the molecular claims for a very early radiation of mammals remain unsupported by the fossil record. This is that none of the modern mammal groups of Madagascar is closely related to any Mesozoic form known from the island. As far as can be told at present (from a very sketchy record), none of Madagascar's modern endemic mammals represents a Gondwanan remnant. Instead, all are almost certainly derived from forms which crossed a substantial marine barrier subsequent to Madagascar's origin as an island (KRAUSE *et al.*, 1997). Interestingly, this may also be true for most if not all other groups of Malagasy vertebrates (see FLYNN & WYSS, 2003; KRAUSE, 2003). At the present state of our knowledge, it seems highly probable that few if any components of Madagascar's Gondwanan fauna survived the worldwide crisis at the end of the Cretaceous.

While terrestrial sediments of Mesozoic age are quite widely exposed in the large sedimentary basins of western Madagascar, such rocks are virtually absent from the island's Tertiary record. Nearly all of the known Tertiary rocks that outcrop in Madagascar are marine in origin (e.g. BESAIRIE, 1973), and for this reason effectively nothing is directly known of Madagascar's Tertiary terrestrial faunas. In the late Quaternary, however, the picture changes dramatically. "Subfossil" mammalian, reptilian and avian assemblages, nearly all of them of Holocene age and containing numerous species that are now extinct, are now known from numerous sites in northern, western and southern Madagascar (e.g. MAHE & SOURDAT, 1972; TATTERSALL, 1982; SIMONS *et al.*, 1995; GODFREY & JUNGERS, 2003). Available radiocarbon dates indicate that the most ancient of these assemblages is some 26,000 years old (SIMONS *et al.*, 1995), and that the youngest dates to a mere 630 years ago (SIMONS, 1997).

The contexts from which the subfossils are derived lie mostly within karst caves, in ephemeral marsh systems, or in riverbank deposits, and the subfossils themselves can be regarded as representing a segment of the modern fauna that has become extinct due to the activities of human beings over the last two millennia since their initial colonization of Madagascar (STANDING, 1908; TATTERSALL, 1982). In general those forms that are only known as subfossils are the largest-bodied ones, those belonging to species which would have had the lowest reproductive turnovers and which would have been the most vulnerable as well as the most desirable to human hunters. Madagascar's subfossil mammals all belong to mammalian orders that are still represented by survivors on the island today, with the exception of a couple of species of pygmy hippopotamus and of the fossorial but otherwise enigmatic *Plesiorycteropus*, which has recently been placed in its own order, Bibymalagasia (MACPHEE, 1994).

Native mammalian orders that are currently represented in Madagascar are Primates, Insectivora (alternatively, Lipotyphla), Carnivora, Rodentia and Chiroptera. If one includes *Homo sapiens* in this category, all except the last are also represented by introduced species. Among the artiodactyls pygmy hippopotamuses, likely quite recent arrivals, may have survived into historic times; those certainly present as a result of human introduction include not only domesticated bovids and suids, but a few species of feral suids and cervids. A useful classification of all of Madagascar's surviving endemic mammals has recently been published by GOODMAN *et al.* (2003).

PRIMATES

By far the most renowned and diverse group of Madagascar's mammals is its primates, colloquially known together as the lemurs. It is generally agreed that the lemurs should be classified into seven families: Cheirogaleidae, the dwarf lemurs, with 5 genera; Lemuridae, the "true" lemurs and their close relatives, with five genera (one extinct); Lepilemuridae, with two genera (one extinct); Indriidae, with three genera; Archaeolemuridae, with two genera (both extinct); Palaeopropithecidae, with four genera (all extinct); and Daubentoniidae, the aye-ayes, with a single genus. Depending on whose classification one accepts, these seven families together contain over 50 species, and an astonishing total of up to (and possibly exceeding) 65 primate taxa if subspecies are included. Even if the recently extinct lemurs are excluded from the count, this places Madagascar third-highest on the list of high-primate-diversity countries worldwide, despite being 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 1,600 km long, and with a surface area of almost 600,000 km^2, it is the world's biggest oceanic island, and at the moment of its first colonization by humans it was largely if not entirely forested, providing primate-friendly habitats in all but the most extreme montane environments. Second, due both to its geographical position and to its varied topography, the island offers a huge range of forest habitats. Except for its southern tip, the elongated island of Madagascar lies entirely within the southern tropical zone, and in the path of the easterly trade winds. Its narrow eastern coastal plain is paralleled by a sharp and rugged escarpment which captures the moisture borne by those winds and as a result is clothed by luxuriant rain forest. The island's central plateau is deeply dissected and offers a large range of microenvironments. It gradually gives way, toward the west, to an extensive and much drier and more seasonal coastal plain where forest cover varies from riverine gallery forests to dry brush-and scrub habitats. The northern and southern ends of the island are generally very dry indeed, the southern area 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 in the world.

All of Madagascar's primate families are completely endemic to the island, and it is clear that primate evolution there has taken an independent course for a very long time. But because of the lack of a Tertiary fossil record, exactly how long is debatable. Most authors have assumed, initially at least simply because of the overall distinctiveness of the Malagasy primate fauna, that the lemurs form a monophyletic group. However, the primate suborder Strepsirhini to which they belong is not unique to Madagascar, since it also uncontestably contains the African galagos (Galagidae) and the Afro-Asian pottos and lorises (Lorisidae). All of today's strepsirhines share a suite of features that includes the primitive retention of a rhinarium, no bony posterior closure of the orbit, and relatively small brain-to-body size ratio; and their most prominent synapomorphy is the possession of a procumbent toothcomb in the lower jaw. Until recently there was no fossil record anywhere of toothcomb-bearing primates, at least before the African Miocene, by which time both modern Afro-Asian strepsirhine families were already well established (SIMPSON, 1967). Now, however, an earlier record has just begun to surface, both in Asia (MARIVAUX *et al.*, 2001) and in Africa (SEIFFERT *et al.*, 2003; MARTIN, 2003).

The earliest definitely toothcombed strepsirhine fossil is *Karanisia clarki*, described from some teeth and jaw fragments by SEIFFERT *et al.* (2003). These come from late middle Eocene (probably ca. 40 Ma) sediments of the Birket Qarun Formation, in the Fayum area of Egypt. One of the teeth concerned is a left canine crown with typical toothcomb morphology, and one of the mandible fragments clearly shows the characteristic laterally compressed and forwardly inclined canine and lateral incisor alveoli. *Karanisia* is interpreted by SEIFFERT *et al.* as dentally not only lorisiform but lorisid, possibly representing a sister genus to the living West African genus *Arctocebus.* From the same stratigraphic level, but represented only by one lower and one upper molar, the same authors named a second form, *Saharagalago misrensis*, the generic appellation being emblematic of its assigned galagid affinity. Between them, these fossils are said to establish that the two living non-Malagasy strepsirhine families had already diverged by the late Eocene. A couple of years earlier MARIVAUX *et al.* (2001) had described several isolated teeth from the Bugti Hills of Pakistan as belonging to the new species *Bugtilemur mathesoni*. They assigned these tiny early Oligocene (ca. 30 Ma) fossils to the Malagasy family Cheirogaleidae on the basis of cheektooth morphology, and suggested that a putative sweepstakes/ filter route via a Chagos/Laccadive paleoridge system might be evoked to explain this resemblance. The presence of a toothcomb in *Bugtilemur* is confirmed by a single lower canine which bears the basic hallmarks of this structure although its crown is rather short (even compared to its homologue in *Karanisia*) and a bit less procumbent than standard for the strepsirhine toothcomb. MARIVAUX and co-workers most closely compared the molars of *Bugtilemur* to those of *Cheirogaleus*, and morphologically the resemblance is remarkable. However, the living Malagasy genus is of much larger size than the fossil one, and has a longer and slenderer toothcomb than *Bugtilemur* apparently had.

Still, the molar morphology of *Bugtilemur* is of particular interest in light of the fact that it has been argued, though by a minority of workers, 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 & KATZ, 1973; SCHWARTZ & TATTERSALL, 1985). In 1970 CHARLES-DOMINIQUE & MARTIN called attention to the fact that a suite of behavioral similarities exists among the cheirogaleids and lorisoids, and particularly between species of *Microcebus* and *Galagoides*. Charles-Dominique and Martin were content to regard these similarities as ancestral retentions; but not long afterwards SZALAY & KATZ (1973) proposed that many of the morphological characters (particularly of the bony ear region) 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 latter are to the other lemurs. CARTMILL (1975) later added features of the medial orbital wall, and additional specializations of the carotid circulation, to the list of apparent cheirogaleid-lorisid synapomorphies. And SCHWARTZ & TATTERSALL (1985) found evidence from molar morphology that supports an association between the cheirogaleids and the lorisoids. In addition, they found reason to regard the entire balance of the Malagasy primate fauna, including the aye-aye, as a monophyletic unit.

The paraphyly that such observations suggest has radical implications for lemur bigeography and origins. For if the cheirogaleids are in fact lorisoids, then the possibilities are two: that the cheirogaleids are descended from an ancestor of African origin that invaded Madagascar independently of the ancestor of the remaining lemur fauna (i.e., that there were two strepsirhine colonizations of Madagascar subsequent to the divergence of the lorisiform and lemuriform groups in Africa); or that the lemurs diversified on Madagascar from a single common ancestor to the family level we now recognize, and that the Afro-Asian lorisoids are descended from a cheirogaleid ancestor that recolonized Africa from Madagascar. The pattern of ocean currents makes a Madagascar-Africa crossing considerably more probable than the reverse trip; but on the other hand, if the modern Afro-Asian families had already emerged by the late Eocene, as SEIFFERT *et al.* suggest, then the cheirogaleid back-crossing must have been a very early one indeed. At the same time, however, a very early back-crossing would 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.

In recent years molecular evidence has dominated discussion of lemur relationships, and most studies have found in favor of the monophyly of the entire lemur fauna. YODER and colleagues (e.g. YODER *et al.*, 1996; YODER, 2003; YODER & YANG, 2004) have been particularly energetic in rejecting the notion that there is a special affinity between the cheirogaleids and the lorisoids, mainly on the basis of comparative studies of the mitochondrial cytochrome b gene, but lately encompassing certain elements from the nuclear genome. Yoder and co-workers find that the basal split among the strepsirhines is between lorisiforms and lemuriforms including Cheirogaleidae; and that, indeed, the basal split among the lemuriforms is that between Daubentoniidae and all the others. Numerous lower-level problems of relationship among species and genera of lemurs do appear to have been clarified by the molecular studies undertaken so far; but the 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 assessing within-family affinities, the relationships among families that are separated by large genetic distances (>12% divergence) remain difficult to resolve consistently. This is 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 short interspersed elements in a variety of strepsirhines placed 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 turn out to 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, though, definitive demonstration still awaits.

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 & 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 & YANG, 2004), based on a variety of gene loci, mitochondrial and nuclear. Calibration was from the fossil record, with all the attendant uncertainties adumbrated by GRAUER & MARTIN (2004). If the lemurs are indeed monophyletic, with the ancestral strepsirhine having given rise 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 already differentiated by the late Eocene (ca. 41-37 Ma) as *Karanisia* and *Saharagalago* seem to indicate, then the stretching of the molecular timescale would seem to be plausible. This is especially the case given the sheer scale of the diversification that took place among the lemurs subsequent to the time when their common ancestor existed, particularly since current molecular estimates suggest that much of this diversification may well have taken place at an early stage (see, e.g., YODER & YANG, 2004). It is not easy to square this observation directly with the fact that adapiform euprimates ("primates of modern aspect," comparable to today's strepsirhines and plausibly sharing a common ancestry with them) are not known in Laurasia until the early Eocene, <55 Ma; but an early date of strepsirhine divergence would also support an African ancestry for the group.

LIPOTYPHLA (INSECTIVORA)

The insectivorans of Madagascar that are un-questionably native to the island consist of some 28 endemic species that are all grouped into the family Tenrecidae. In addition to these are found two species of shrews, both soricids of the genus *Suncus*. One of these, *S. murinus*, is definitely introduced to Madagascar, but the other, *S. madagascariensis*, presents more of a puzzle (GOODMAN *et al.*, 2003). Formerly allocated to the cosmopolitan Old World species *S. etruscus*, the Madagascar and Comoro populations of this form were elevated to separate species status only comparatively recently, by HUTTERER (1993). The systematics of *Suncus* remain somewhat in doubt; and while GOODMAN *et al.* (2003) provisionally regard these Malagasy and Comorian shrews as endemics, they remain poorly known and the possibility is very much alive that *S. madagascariensis* is in fact also a species introduced by humans. Whatever the case, it is clear that the ancestral *S. madagascariensis* arrived in Madagascar independently of, and much later than, the island's demonstrably endemic insectivorans. In Africa soricids are extremely diverse and speciose; and the fact that the Malagasy representatives of this family are not is, by itself, just as as suggestive of a short history on the island as is the close relationship of *S. madagascariensis* to mainland forms.

The remaining Malagasy tenrecids are generally divided into three subfamilies: Tenrecinae, the spiny tenrecs, with 5 species in four genera; the ecologically diverse Oryzorictinae, with 21 species in three genera; and the monospecific Geogalinae, with just the long-eared tenrec, *Geogale aurita*. GOODMAN *et al.* (2003) point out that the diversity of insectivorans in Madagascar is quite staggering, especially when the 28 species of Madagascar are compared with the seven of Borneo, an island (though not, it is true, an oceanic island) that is of rather greater size and that boasts a higher diversity of carnivorans and rodents. And although it may certainly be relevant in this connection that Borneo's mammalian richness at the ordinal level is double Madagascar's, this observation alone does appear to suggest that these Malagasy insectivorans and their precursors have been on the island a long time.

Until recently all authors assumed monophyly of Madagascar's tenrecs and, outside the island, the three species of African otter shews (Potamogalinae) have for long been considered the closest relatives of these insectivorans. However, OLSON & GOODMAN (2003) have recently included the potamogalines within Tenrecidae, opening up a Pandora's box of possibilities. This makes it especially unfortunate that considerable uncertainty currently exists as to the precise geometry of relationships within the Malagasy component of this enlarged concept of Tenrecidae (see discussion in OLSON & GOODMAN, 2003). To add to the confusion, although most authors currently agree that the tenrecids indeed belong within Insectivora (or Lipotyphla), it has been suggested on the basis of molecular findings that, together with the chrysochlorids (golden moles) the tenrecs are in fact derived from a clade of non-lipotyphlan African mammals (SPRINGER *et al.*, 1997, quoted in OLSON & GOODMAN, 2003), though this suggestion has been rejected on morphological grounds (see OLSON & GOODMAN, 2003). The most recent study, by OLSON (1999), did not not find a clear signal of monophyly in a phylogenetic analysis of 125 morphological characters that were recorded in all tenrec species. However, a number of mitochondrial and nuclear DNA markers, when compared among 26 tenrec species and to a wide variety of outgroup species, favored monophyly of Afro-Malagasy tenrecids in most analyses, with strong support for a unitary Malagasy clade (OLSON, 1999; OLSON & GOODMAN, 2003).

Besides being absent in Madagascar, the tenrec fossil record is sparse indeed in Africa. Some decades ago, BUTLER & HOPWOOD (1957) described three species of early tenrecids from the east African early Miocene: *Protenrec tricuspis, Erythrozootes chamerpes* and *Geogale aletris*. The last of these was assigned to the previously endemic Malagasy genus *Geogale* (it was later transferred to a new genus, *Parageogale*), and BUTLER (1969, 1978) subsequently argued that since the single Malagasy species *G. aurita* was too specialized to be a stem species, its own ancestor must have colonized the island separately from the ancestor(s) of the remaining Malagasy tenrecs. How many insectivoran invasions of Madagascar this hypothesis would imply depends on the exact geometry of relationships among the Malagasy tenrecs, an issue that is still in doubt. However, the status of *Parageogale* as a relative of the Malagasy *Geogale* —or even as a tenrecid— has been contested (PODUSCHKA & PODUSCHKA, 1985). OLSON & GOODMAN (2003) have summarized some of the complexities of tenrecid systematics, and have concluded that at our current state of knowledge the best-supported hypothesis is one of monophyly for Madagascar's insectivorans, "with a single colonization event followed by an extensive evolutionary radiation." (p. 1239). As yet there are no molecular estimates for the divergence time of the Malagasy and African tenrecids and the relevant fossil record is, as we have seen, sparse and fairly unhelpful on the matter. However, Tenrecidae does appear to have been established in the east African record by the early Miocene, and it is generally regarded as an ancient group that "very likely formed part of the Paleogene African fauna" (BUTLER, 1978: 63) although it does not appear to be represented in any of the Fayum localities. If any of Madagascar's terrestrial mammal groups besides the primates entered the island early in the Tertiary it is surely this one, though it cannot yet be demonstrated that this was the case.

CARNIVORA

There is a great deal of morphological and ecological diversity among the seven native (and endemic) carnivoran genera of Madagascar, and their history of classification within the superfamily Aeluroidea has been at least as varied. GREGORY & HELLMAN (1939), for example, divided them between two families, each of which is widely represented outside Madagascar: the fosa, *Cryptoprocta*, was placed in Felidae (the cats), and all the rest went into Viverridae (the civets). ALBIGNAC (1973) placed them all into Viverridae, dividing them into the three endemic subfamilies Fossinae, Galidiinae and Cryptoproctinae. WOZENCRAFT (1993) restored the two-family division, but with a difference: he put the genera *Galidia*, *Salanoia*, *Mungotictis* and *Galidictis* into the family Herpestidae (the mongooses, also widely distributed outside Madagascar), while *Fossa*, *Eupleres* and *Cryptoprocta* went into Viverridae. Each group constituted a distinct endemic subfamily of its cosmopolitan family. Subsequently, however, DNA sequencing by SLATTERY & O'BRIEN (1995) found that *Fossa* and *Galidia* (regrettably the only viverrid/herpestids in the study) formed a single clade relative to other carnivorans examined, a result that contrasted with chromosome analyses by COUTURIER *et al.* (1986) and RAZAFIMAHATATRA (1988) that had indicated a polyphyletic or at least a diphyletic origin of Malagasy carnivorans. To confuse the situation further, DNA hybridization (VERON & CATZEFLIS, 1993) and morphological (VERON, 1995) studies of *Cryptoprocta* by came up with conflicting results, the first study indicating herpestid affinities, and the second viverrid ones. VERON (1995) went so far as to suggest that as many as four independent colonizations of Madagascar might be necessary to explain carnivoran diversity in Madagascar today.

In developing a better understanding of Malagasy faunal origins the importance of clarifying this chaotic situation among the carnivorans is self-evident, and recent molecular studies reported by YODER *et al.* (2003) and YODER & FLYNN (2003) have greatly helped in this regard. These authors studied four unlinked DNA markers, mitochondrial and nuclear, in samples of all seven Malagasy carnivoran genera. In a maximum parsimony analysis all of the Malagasy forms consistently showed up as a single clade in contradistinction to a wide variety of non-Malagasy carnivorans. The closest outgroup of this clade was one consisting of African plus Asian Herpestidae. Within the Malagasy set, the "mongoose-like" forms *Galidia*, *Galidictis*,*Mungotictis* and*Salanoia* consistently grouped together, while *Fossa* and *Cryptoprocta* equally consistently showed up as basal to the Malagasy clade although their relative positions remained unresolved. The pretty clear conclusion from all of this was that the Malagasy carnivorans together constitute a coherent endemic subset of the wider cosmopolitan family Herpestidae, although certain relationships within the Malagasy subgroup remain to be satisfactorily determined. No special viverrid affinities were demonstrable on the basis of this data set.

This conclusion has clear implications for the biogeographic origins of the Malagasy carnivorans, notably that only a single crossing of the Mozambique Channel, by a primitive herpestid ancestor, is necessary to explain the presence of the morphologically diverse carnivorans existing on the island today. Bayesian analysis of the molecular data sets, with several independent calibrations from the fossil record, yielded a rather young age of about 18-24 Ma for the ancestral Malagasy carnivoran (YODER *et al.*, 2003), a much younger age than yielded by similar data sets for the lemur ancestor. This dating is consistent with the notion (MADDEN & VAN COUVERING, 1976; VAN COUVERING & HARRIS, 1991) that aeluroids first entered Africa during the Grande Coupure, an episode of dramatically lowered sea-levels at the debut of the Oligocene, about 34 million years ago (a notion that would, however, push the later Fayum faunas, usually considered Oligocene, back into the Eocene). More conventionally, it is clearly in line with the early Miocene age of *Kichechia,* the earliest recorded herpestid occurrence in Africa (MCKENNA & BELL, 1997). Taken together, and pending better knowledge of the African fossil record, the various lines of evidence and inference favor an age of about 24 Ma or (probably not much) less for the herpestid penetration of Madagascar.

RODENTIA

Currently, 22 species and nine genera of native (and endemic) Malagasy rodents are recognized. Following MAJOR's (1897) century-old review, authors continue to assign all the native Malagasy rodents to the single endemic subfamily Nesomyinae, now generally regarded as lying within the cosmopolitan family Muridae (e.g. MCKENNA & BELL, 1997). However, as JANSA & CARLETON (2003) have observed, the amount of morphological variety observed among these relatively few genera is nothing short of astonishing, and the common subfamilial allocation is due essentially to the notion that, because of their endemicity to Madagascar, these rodents form a single monophyletic grouping. In understanding the origin of this varied fauna a reliable phylogeny is thus indispensable; and in both the absence of a relevant Malagasy fossil record and the presence of considerable dispute over potential affinities between the living Malagasy rodents and putative African Miocene relatives (see LAVOCAT, 1973; CHALINE *et al.*, 1977; CARLETON & SCHMIDT, 1990; PETTER, 1990), any such phylogeny must necessarily derive from comparative studies of the Malagasy forms.

Morphological analyses of this kind have, however, reached varying conclusions as to the monophyly of the Nesomyinae (see MAJOR, 1897, ELLERMAN, 1941, 1949 and PETTER, 1990). It is thus fortunate that the two published molecular studies (DUBOIS *et al*., 1996; JANSA *et al*., 1999) agree in their broader implications, if not in their exact conclusions. DUBOIS *et al*. (1996) investigated mitochondrial 12S rRNA gene and DNA-DNA hybridization data sets to investigate nesomyine monophyly. They found that the two (morphologically very disparate) Malagasy genera *Nesomys* and *Macrotarsomys* formed a clade, with the African cricetomyine *Cricetomys* as its closest outlier. In the DNA hybridization analysis the Malagasy genus *Eliurus* was added, but the results still indicated Malagasy monophyly, with *Cricetomys* and its relative *Saccostomus* forming the neighboring clade. The study by JANSA *et al*. (1999) examined a wider variety of murids and other rodents, and compared them with a full sample of nesomyine taxa for the complete mitochondrial cytochrome b sequence. In this analysis several nodes remained unresolved, and two non-Malagasy genera, the dendromyine *Steatomys* and rhizomyine *Tachyoryctes*, found their way inside the Malagasy clade. Clearly, further genetic markers and analyses are needed before the matter of Nesomyine coherence and affinities can be cleared up; but, as JANSA & CARLETON (2003) remark, "although nesomyines are paraphyletic in [the JANSA *et al*.] phylogeny, they are not polyphyletic … and their origin on Madagascar can still be explained by a single immigration to the island." (p. 1262). In terms of specific findings, the molecular results also simplify the picture by rejecting suggestions (CORBET & HILL, 1991) of special affinity between the odd South African genus *Mystromys* and the nesomyines, placing the former firmly as a close relative of *Peromyscus*.

There is evidently a great deal still to learn about relationships among the nesomyines, but to this point their place as a natural grouping that forms the sister taxon to other murids seems fairly well supported. And although the morphological and ecological diversities observed within this assemblage of genera are admittedly extraordinary, a single invasion of Madagascar by an African murid ancestor appears on the present imperfect evidence to be sufficient to account for them. No molecular estimates of divergence time between the basal nesomyine and its nearest murid relative are currently available, but the sheer morphological and ecological if not systematic diversity of Madagascar's native rodents argues for an earlier rather than a later occupation of the island. However, the earliest appearance of murids (including cricetomyines) in the African fossil record comes in the early Miocene (LAVOCAT, 1973; MCKENNA & BELL, 1997), only phyomyid rodents being present in the Fayum fauna. Although the African mid-Tertiary is poorly sampled, this may suggest a limiting lower date of 24 Ma or so for the incursion into Madagascar of the nesomyine ancestor.

CHIROPTERA

Compared to other islands of comparable size Madagascar has a fairly impoverished bat fauna. This presumably results from its status as an oceanic island, an attribute that also appears to account for its very high rate of 60% bat endemism at the species level. The current count is of some 30 bat species in 16 genera, representing seven families of which only one (Myzopodidae) is endemic. EGER & MITCHELL (1996, 2003) report that six of Madagascar's bat families are shared with Africa and that 37% of its bat species also occur on the neighboring continent. Further, of the 18 endemic bat species, 10 have clear African affinities. In contrast, only three have Asian affinities, although the fruit bat *Pteropus* is shared with India and elsewhere in Asia but not at all with the African mainland (though its westward distribution extends as far as Zanzibar).

In general bats have been considered poor dispersers over water, so notions of island-hopping (over "steppingstones" that no longer exist) have periodically been introduced into considerations of the origin of Madagascar's bat fauna. The eastern African fossil record suggests that two living Malagasy genera, *Hipposideros* and *Taphozous*, were already present on the continent in the Miocene (KINGDON, 1974); and if the Davie Ridge had truly been exposed at that time, it could have served as a steppingstone for these volant mammals. However, the fact that even today Madagascar shares at least 11 species of bat with Africa suggests that while the Mozambique Channel is certainly a barrier to the transmission of flying mammal species it is a fairly permeable one. Certainly it has been a much less effective filter than the Indian Ocean has been for bats colonizing Madagascar from the east. Dispersal to Madagascar of volant mammals is clearly much easier to explain —and has occurred much more frequently— than the arrival of terrestrial forms.

CONCLUSIONS

The physical evidence is pretty convincing that Madagascar has lain far from Africa and other Gondwananan continents throughout the Age of Mammals. Equally, to the best of our knowledge today, none of the four terrestrial mammalian orders now native to Madagascar had differentiated before the island had become thus emplaced, so that the ancestors of today's Malagasy mammals must all somehow have crossed the substantial water barrier formed by the 350-1200 km-wide Mozambique Channel that lies between Madagascar and Africa. Terrestrial mammals are notoriously poor dispersers over wide stretches of water; but the greater fauna of Madagascar, too, is remarkable for combining a relative dearth of major taxa with high levels of both endemism and diversity at lower taxonomic levels. It is beyond the scope of this contribution to examine the biogeography of Madagascar's Mesozoic faunas; but in the light of current debates it is of interest to know whether or not Madagascar's present faunal composition can be satisfactorily explained on the basis of an essentially steady-state Cenozoic geography.

The presence of great diversity at species level among Madagascar's residents is readily explained by the absence of competition for ecological space from other major taxa. This is, for example, the reason conventionally advanced for the success of the wildly diversified "lower" primates of Madagascar, whose continental cousins appear to have been marginalized to nocturnal niches by the competitive success of the diurnal "higher" primates with which they have had to coexist since the Oligocene at least. But whence that low level of competition? Why does Madagascar possess representatives of far fewer mammalian orders than might be expected in a landmass of such large size? The traditional answer lies in the island's great physical isolation, which makes it overwhelmingly improbable that any terrestrial mammal should cross the oceanic barrier separating Madagascar from its nearest continental neighbor. After all, terrestrial mammals in general have succeeded in permanently colonizing remarkably few isolated islands (LAWLOR, 1986). In that case, however, why any terrestrial mammals at all in this supremely isolated place? The fact that Madagascar is home to any mammals of the Tertiary radiation at all is what makes the notion of now-foundered land bridges or "stepping stones" attractive. But then again, if such waypoints existed, why did more kinds of mammal not take advantage of them? Clearly Madagascar's isolation, whatever its exact nature, has exerted a very strong filtering effect. So do we simply see on Madagascar examples of the tenacious sorts of terrestrial mammals to which such oceanic filters are most porous? This may be partly the case; but even so there is no doubt that the makeup of the island's terrestrial mammal fauna is rather peculiar.

If Madagascar's terrestrial mammals belong to larger groups that disperse overwater particularly well (and their ancestors were certainly successful not only in crossing the ocean barrier but in establishing themselves once they had arrived on the island), perhaps they can themselves provide an internal test of the strength of the barrier. As we have seen, there has in the past been extensive disagreement over the monophyly of Madagascar's terrestrial mammal groups; as many as four independent arrivals have been suggested for the carnivorans, two (or perhaps more) for the primates (including one back-crossing), and two or more for the insectivorans and for the rodents. If such multiple arrivals were indeed the case, they would imply a higher permeability of the barrier for creatures such as these, at least periodically; on the other hand, radiation of each group from a single ancestor would suggest a consistently much lower permeability. Understanding the phylogenetic histories of these immigrant groups is thus critical; and as the as the discussion earlier makes plain, present evidence is tending quite strongly toward monophyly for each of them, thereby favoring the notion that the probability of any terrestrial mammal successfully translocating across the Mozambique Channel and leaving established descendants is indeed very low.

This is where calibration of the record becomes particularly important, for if there were a consistent low but real probability of crossing, then arrivals in Madagascar would have been random with regard to time (although it is arguable that probabilities of successful implantation would decrease as more prior groups became established). Unfortunately we have no relevant fossil record and only two molecular estimates of arrival date, though both of these (very early in the Tertiary for Primates; early Miocene for the carnivorans, a date also plausible for the rodents) are quite convincing in light of inferences from both current diversity and from phylogenetic relationships. YODER *et al.* (2003) point out that the window of time (45 to 26 Ma) quoted by MCCALL (1997) for the putative subaerial exposure of the Mozambique Channel seafloor along the Davie Fracture Zone falls in between the molecular date ranges, and does not coincide with either. They also conclude that since only four colonization events are needed to explain the presence in Madagascar of its entire current terrestrial mammal fauna (actually, a fifth would be necessary to explain the presence of Bibymalagasia, and a sixth, very recent, is needed to explain the presence of the pygmy hippopotamus – although a large semi-aquatic mammal may certainly be excluded from the central conundrum here) it is superfluous to posit any landbridge structures to explain the presence on Madagascar of its mammals.

Certainly, the need for stepping-stones diminishes with the (still substantial) number of ancestors required. But in answer to this argument it is still possible to make two observations. First, in the absence of a fossil record we cannot know how many other mammal lineages may (or may not) have contrived to cross the water barrier without establishing themselves in the long term; and second, we cannot be absolutely sure that the Mozambique Channel as we know it today is not absolutely impermeable to strictly terrestrial mammals such as those that now inhabit Madagascar. Certainly, as far as we know no strictly terrestrial mammals have managed to cross it in the last 15-20 million years. In the light of this, we cannot altogether ignore the possibility that some form of island-hopping, at least, has been necessary to transfer *any* strictly terrestrial mammals whatever, against all odds, across the Mozambique Channel from Africa. On present evidence it is possible to entertain the notion that the crossings might have been concentrated at two points in time: the early Tertiary (lemurs, tenrecs) and early Neogene or at least post-Grande Coupure (rodents, carvivores). This might be taken to imply the former existence of ephemeral land connections at these junctures. For all these reasons it is reasonable to expect that future advances in our understanding of how Madagascar's curious fauna originated may well lie as much in the realm of seafloor geology as in those of paleontology and systematics.

ACKNOWLEDGMENTS

I should like to thank Professor M. D. DERMITZAKIS, Dr HARA DRINIA, and the editors of *Annales Géologiques des Pays Helléniques* for this opportunity to salute the memory and career of our friend and colleague PAUL SONDAAR. And thanks also to KEN MOWBRAY, JOHN VAN COUVERING and SUSAN BELL for their help, and to JUDITH MASTERS for prompting me to tackle this intriguing subject.

REFERENCES

ALBIGNAC, R. (1973). Mammifères Carnivores. 36 of *Faune de Madagascar*, 1-206. Paris (ORSTOM/CNRS).

BASSIAS, Y. (1992). Petrological and geochemical investigations of rocks from the Davie Fracture Zone (Mozambique Channel) and some tectonic implications. *Jour. Afr. Earth Sci.*, 15, 321-339.

BESAIRIE, H. (1973). Précis de géologie malgache. *Ann. Géol. Madagascar*, 35, 1-142.

BUTLER, P. M. & A. T. HOPWOOD (1957). Insectivora and Chiroptera from the Miocene rocks of Kenya Colony. *Fossil Mammals of Africa*, 13, 1-35.

BUTLER, P. M. (1969). Insectivores and bats from the Miocene of East Africa: New material. *In:* LEAKEY, L. S. B. (*Ed.*) *Fossil Vertebrates of Africa*, 1, 1-38. New York (Academic Press).

BUTLER, P. M. (1978). Insectivora and Chiroptera. *In:* MAGLIO, V. J. & H. B. S. COOKE (*Eds*). *Evolution of African Mammals*, 56-68. Cambridge MA (Harvard University Press).

CARLETON, M. D. & D. F. SCHMIDT (1990). Systematic studies of Madagascar's endemic rodents (Muroidea: Nesomyinae): An annotated gazetteer of collecting localities of known forms. *Amer. Mus. Novitates*, 2987, 1-36.

CARTMILL, M. (1975). Strepsirhine basicranial structures and the affinities of the Cheirogaleidae. *In:* LUCKETT, W. P. & F. S. SZALAY (*Eds*). *Phylogeny of the primates: A multidisciplinary approach*, 333-354. New York (Plenum Press).

CHALINE, J., P. MEIN & F. PETTER (1977). Les grandes lignes d'une classification évolutive des Muroidea. *Mammalia*, 41, 245-252.

CHARLES-DOMINIQUE, P. & R. D. MARTIN (1970). Evolution of lorises and lemurs. *Nature*, 227, 257-260.

COFFIN, M. F. & P. RABINOWITZ (1987). Reconstruction of Madagascar and Africa: Evidence from the Davie Fracture Zone and the Western Somali Basin. *Jour. Geophys. Res.*, 92, 9385-9406.

CORBET, G. B. & J. B. HILL (1991). *A World List of Mammalian Species*, 3rd ed. 1-212. London (British Museum [Natural History]).

COUTURIER, J, R. E. RAZAFIMAHATRATRA, B. DUTRILLAUX, S. WARTER & Y. RUMPLER (1986). Chromosomal evolution in the Malagasy Carnivora. *Cytogenet. and Cell Genet.*, 41, 1-8.

DELPERO, M., J. C. MASTERS, P. CERVELLA, S. CROVELLA, G. ARDITO & Y. RUMPLER (2001). Phylogenetic relationships among the Malagasy lemuriforms (Primates, Strepsirrhini) as indicated by mitochondrial sequence data from the 12S rRNA gene. *Zool. Jour. Linn. Soc. Lond.*, 133, 83-103.

DEWIT, M. & J. MASTERS (2004). The geological history of Africa, India and Madagascar, and dispersal scenarios for vertebrates. *Folia Primatol.*, 75, 117.

DU BOIS, J.-Y., D. RAKOTONDRAVONY, C. HANNI, P. SOUROUILLE & F. M. CATZEFLIS (1996). Molecular evolutionary relationships of three genera of Nesomyinae, endemic rodent taxa from Madagascar. *Jour. Mammal. Evol.* 3, 239-259.

EGER, J. L. & L. MITCHELL (1996). Biogeography of the bats of Madagascar. *In:* LOURENCO, W. R. (*Ed*). *Biogéographie de Madagascar*, 321-328. Paris (ORSTOM).

ELLERMAN, J. R. (1941). Family Muridae. Vol. 2 of *The Families and Genera of Living Rodents*. 1-204. London (British Museum [Natural History]).

ELLERMAN, J. R. (1949). Appendix II: Notes on the rodents from Madagascar in the British Museum, and on a collection from the island obtained by Mr C. S. Webb. Vol 3 of *The Families and Genera of Living Rodents*. 1-96. London (British Museum [Natural History]).

FLYNN, J. J. & A. R. WYSS (2003). Mesozoic terrestrial vertebrate faunas: The early history of Madagascar's vertebrate diversity. *In:* GOODMAN, S. M. & J. P. BENSTEAD *(Eds)*. *The Natural History of Madagascar*, 34-40. Chicago (University of Chicago Press).

FLYNN, J. J., J. M. PARRISH, B. RAKOTOSAMIMANANA, W. F. SIMPSON & A. R. WYSS (1999). A Middle Jurassic mammal from Madagascar. *Nature*, 401, 57-60.

GINGERICH, P. D. (1975). Dentition of *Adapis parisiensis* and the evolution of lemuriform primates. *In:* TATTERSALL, I. & R. W. SUSSMAN (*Eds*). *Lemur Biology* 65-80. New York (Plenum Press).

GODFREY, L. R. & W. L. JUNGERS (2003). Subfossil lemurs. *In:* GOODMAN, S. M. & J. P. BENSTEAD (*Eds*). *The Natural History of Madagascar*, 1247-1252. Chicago (University of Chicago Press).

GOODMAN, S. M., J. U. GANZHORN & D. RAKOTONDRAVONY (2003). Introduction to the mammals. *In:* GOODMAN, S. M. & J. P. BENSTEAD (*Eds*). *The Natural History of Madagascar*, 1159-1186. Chicago (University of Chicago Press).

GRAUR, D. & W. MARTIN (2004). Reading the entrails of chickens: Molecular timescales of evolution and the illusion of precision. *TRENDS in Genet*, 20, 80-86.

GREGORY, W. K. & M. HELLMAN (1939). On the evolution and major classification of the civets (Viverridae) and allied fossil and Recent Carnivora. *Proc. Amer. Philos. Soc.*, 81, 309-392.

HUTTERER, R. (1993). Order Insectivora. *In:* WILSON, D. E. & D. M. REEDER (*Eds*). *Mammal Species of the World: A Taxonomic and Geographic Reference*, 69-130. Washington DC (Smithsonian Institution Press).

JANSA, S. A. & M. D. CARLETON (2003). Systematics and phylogenetics of Madagascar's native rodents. *In:* GOODMAN, S. M. & J. P. BENSTEAD (*Eds*). *The Natural History of Madagascar*, 1257-1265. Chicago (University of Chicago Press).

JANSA, S. A., S. M. GOODMAN & P. K. TUCKER (1999). Molecular phylogeny and biogeography of the native rodents of Madagascar (Muridae: Nesomyinae): A test of the single-origin hypothesis. *Cladistics*, 15, 253-270.

KINGDON, J. (1974). *Insectivores and Bats*. Vol 2 of *East African Mammals. An Atlas of Evolution in Africa*, 1-334. New York (Academic Press).

KRAUSE, D. W. (2000). New mammalian specimens from the late Cretaceous of Madagascar. *Jour. Vert. Paleo.* 20, 52A-53A.

KRAUSE, D. W. (2001). Fossil molar from a Madagascan marsupial. *Nature*, 412, 497-498.

KRAUSE, D. W. (2003). Late Cretaceous vertebrates of Madagascar: A window into Gondwanan biogeography at the end of the Age of Dinosaurs. *In:* GOODMAN, S. M. & J. P. BENSTEAD (*Eds*). *The Natural History of Madagascar*, 40-47. Chicago (University of Chicago Press).

KRAUSE, D. W., J. H. HARTMAN & N. A. WELLS (1997). Late

Cretaceous vertebrates from Madagascar: Implications for biotic change in deep time. *In:* GOODMAN, S. M. & B. D. PATTERSON (*Eds*). *Natural Change and Human Impact in Madagascar*, 3-43. Washington, DC (Smithsonian Institution Press).

LAVOCAT, R. (1973). Les rongeurs du Miocène d'Afrique Centrale I – Miocène inférieur. *Mém. Et Trav. Inst. Montpellier Haut-Etudes*, 1, 1-284.

LAWLOR, T. E. (1986). Comparative biogeography of mammals on islands. *Biol. Jour. Linn. Soc*, 28, 99-125.

LECLAIRE, L., Y. BASSIAS, M. CLOCCHIATTI & J. SEGOUFIN (1989). Le Ride de Davie dans le Canal de Mozambique: Approche stratigraphique et géodynamique. *C. R. Acad. Sci. Paris* Série II, 308, 1077-1082.

MACPHEE, R. (1994). Morphology, adaptations, and relationships of *Plesiorycteropus*, and a diagnosis of a new order of eutherian mammals. *Bull. Amer. Mus. Nat. Hist.*, 220, 1-214.

MADDEN, C. T. & VAN COUVERING, J. A. (1976). The Proboscidean Datum Event: Early Miocene migration from Africa. *Geol. Soc. Amer., Abstr. Progr.*, 8, 992-993.

MAHE, J. & M. SOURDAT (1972). Sur l'extinction des vertébrés subfossiles et l'aridification du climat dans le sud-ouest de Madagascar. *Mém. Soc. Géol. France*, 17, 295-309.

MAJOR, C.I.F. (1897). On the Malagasy rodent genus *Brachyuromys*; and on the mutual relations of some groups of the Muridae (Hesperomyinae, Microtinae, Murinae, and "Spalacidae") with each other and with the Malagasy Nesomyinae. *Proc. Zool. Soc. Lond*, 1897, 695-720.

MARIVAUX, L., J.-L. WELCOMME, P.-O. ANTOINE, G. METAIS, I. M. BALOCH, M. BENNAMI, Y. CHAIMANEE, S. DUCROCQ & J.-J. JAEGER (2001). A fossil lemur from the Oligocene of Pakistan. *Science*, 294, 587-591.

MARTIN, R. D. (2003). Combing the primate record. *Nature*, 422, 388-391.

MCCALL, R. A. (1997). Implications of recent geological investigations of the Mozambique Channel for the mammalian colonization of Madagascar. *Proc. Roy. Soc. Lond.* B, 264, 663-665.

MCKENNA, M. (1967). Classification, range and deployment of the prosimian primates. *Colloq. Int. Cent. Nat. Rech. Sci. (Paris)*, 163, 603-610.

MCKENNA, M. C. & S. K. BELL (1997). *Classification of Mammals Above Species Level*, 1-820. New York (Columbia University Press).

MITTERMEIER, R. A., I. TATTERSALL, W. R. KONSTANT, D. M. MEYERS & R. B. MAST (1994). *Lemurs of Madagascar,* 1-356. Washington DC (Conservation International).

OLSON, L. E. (1999). *Systematics, evolution and biogeography of Madagascar's tenrecs (Mammalia: Tenrecidae)*. PhD Diss., University of Chicago.

OLSON, L. E. & S. M. GOODMAN (2003). Phylogeny and biogeography of tenrecs. *In:* GOODMAN, S. M. & J. P. BENSTEAD *(Eds). The Natural History of Madagascar*, 1235-1242. Chicago (University of Chicago Press).

PETTER, F. (1990). Relations de parenté des rongeurs de Madagascar. *Att. Convegni Lincei*, 85, 829-837.

PODUSCHKA, W. & C. PODUSCHKA (1985). Zur Frage des Gattungsnamens von "*Geogale aletris*" Butler und Hopwood, 1957 (Mammalia: Insektivora) aus dem Miozän Ostafrikas. *Zeitschr. Für Säugetierkunde*, 50, 129-140.

PORTER, C. A., I. SAMPAIO, M. P. C. SCHNEIDER, J. CZELUSNIAK & M. GOODMAN (1997). Evidence on primate phylogeny from ε-globin gene sequences and flanking regions. *Jour. Molec. Evol.*, 40, 30-55.

RAZAFIMAHATRATRA, R. E. (1988). Evolution chromosomique des carnivores malgaches. *In:* RAKOTOVAO, L, V. BARRE & J. SAYER *(Eds). L'Equilibre des Ecosystèmes Forestiers à Madagascar*, 110-115. Gland (IUCN).

ROOS, C., J. SCHMITZ & H. ZISCHLER (2004). Primate jumping genes elucidate strepsirrhine phylogeny. *Proc. Natl. Acad. Sci. USA*, 101, 10650-10654.

SCHWARTZ, J. H. & I. TATTERSALL (1985). Evolutionary relationships of living lemurs and lorises (Mammalia, Primates) and their potential affinity with European Eocene Adapidae. *Anthrop. Pap. Amer. Mus. Nat. Hist.*, 60, 1-100.

SEIFFERT, E., E. L. SIMONS & Y. ATTIA (2003). Fossil evidence for an ancient divergence of lorises and galagos. *Nature*, 422, 421-424.

SIMONS, E. L. (1997). Lemurs: Old and new. *In:* GOODMAN, S. M. & B. D. PATTERSON (*Eds*). *Natural Change and Human Impact in Madagascar*, 142-166. Washington, DC (Smithsonian Institution Press).

SIMONS, E. L., D. A. BURNEY, P. S. CHATRATH, L. R. GODFREY, W. L. JUNGERS & B. RAKOTOSAMIMANANA (1995). AMS C14 dates for extinct lemurs from caves in the Ankarana Massif, northern Madagascar. *Quat. Res.*, 43, 249-254.

SIMPSON, G. G. (1967). The Tertiary lorisiform primates of Africa. *Bull. Mus. Comp. Zool.*, 136, 39-62.

SLATTERY, J. P. & S. J. O'BRIEN (1995). Molecular phylogeny of the red panda (*Ailurus fulgens*). *Jour. Hered.*, 86, 413-422.

SMITH, A. G., D. G. SMITH & B. M. FUNNELL (1994). *Atlas of Mesozoic and Cenozoic Coastlines*. Cambridge, UK (Cambridge University Press).

STANDING, H. (1908). On recently discovered subfossil primates from Madagascar. *Trans. Zool. Soc. Lond.*, 18, 69-162.

STOREY, B. C. (1995). The role of mantle plumes in continental breakup: Case histories from Gondwanaland. *Nature*, 377, 301-308.

STOREY, B. C., J. J. MAHONEY & A. D. SAUNDERS (1997). Cretaceous basalts in Madagascar and the transition between plume and continental lithosphere mantle sources. *Geophys. Monogr. Amer. Geophys. Union*, 100, 95-122.

SZALAY, F. S. & C. C. KATZ (1973). Phylogeny of lemurs, galagos and lorises. *Folia Primatol.*, 19, 88-103.

TATTERSALL, I. (1982). *The Primates of Madagascar*. 1-382. New York (Columbia University Press).

VAN COUVERING, J. A. & J. A. HARRIS (1991). Late Eocene age of Fayum mammal fauna. *Jour. Hum. Evol.*, 21, 241-260.

VERON, G. (1995). La position systématique de *Cryptoprocta ferox* (Carnivora). Analyse cladistique des caractères morphologiques de carnivores Aeluroidea actuels et fossiles. *Mammalia*, 59, 551-582.

VERON, G. & F. M. CATZEFLIS (1993). Phylogenetic relationships of the endemic Malagasy carnivore *Cryptoprocta ferox* (Aeluroidea): DNA /DNA hybridization experiments. *Jour. Mammal. Evol.*, 1, 169-185.

WELLS, A. A. (2003). Some hypotheses on the Mesozoic and Cenozoic paleoenvironmental history of Madagascar. *In:* GOODMAN, S. M. & J. P. BENSTEAD (*Eds*). *The Natural History of Madagascar* 16-34. Chicago (University of Chicago Press).

WOZENCRAFT, W. C. (1993). Order Carnivora. *In:* WILSON, D. E. & D. M. REEDER (*Eds*). *Mammal Species of the World: A Taxonomic and Geographic Reference*, 279-348. Washington DC (Smithsonian Institution Press).

YODER, A. (2003). Phylogeny of the lemurs. *In:* GOODMAN, S. M. & J. P. BENSTEAD (*Eds*). *The Natural History of Madagascar*, 1242-1247. Chicago (University of Chicago Press).

YODER, A. & J. J. FLYNN (2003). Origin of Malagasy Carnivora.

In: GOODMAN, S. M. & J. P. BENSTEAD (*Eds*). *The Natural History of Madagascar*, 1253-1256. Chicago (University of Chicago Press).

YODER, A. & Z. YANG (2004). Divergence dates for Malagasy lemurs estimated from multiple gene loci: Geological and evolutionary context. *Molec. Ecol.*, 13, 757-773.

YODER, A., M. CARTMILL, M. RUVOLO, K. SMITH & R. VILGALYS (1996). Ancient single origin for Malagasy primates. *Proc. Natl. Acad. Sci. USA*, 93, 5122-5126.

YODER, A., M. M. BURNS, S. ZEHR, T. DELEFOSSE, G. VERON, S. M. GOODMAN & J. J. FLYNN (2003). Single origin of Malagasy Carnivora from an African ancestor. *Nature*, 421, 734-737.