

LAZY LEAPERS : ENERGETICS, PHYLOGENETIC INERTIA AND THE LOCOMOTOR DIFFERENTIATION OF THE MALAGASY PRIMATES

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ABSTRACT. - The separation of Madagascar from the African mainland is generally thought to have substantially predated the earliest known euprimates in Africa and the northern continents. There now seems little alternative to the implantation of primates on Madagascar by the « sweepstakes » route: rafting. The width of the Mozambique Channel even in the late Cretaceous period seems to have been such that survival of sufficient founders to establish a viable population requires explanation. In the absence of fossil evidence of Malagasy lemurs from the Eocene and earlier, we must base our reconstruction of the early adaptive radiation on the island from neontology. The radiation of living strepsirrhine primates on Madagascar is distinctly different from those on mainland Africa, and in East and S.E. Asia. While the Malagasy radiation is more diverse, it curiously appears to lack the small, saltatory animalivores occupying the lowest strata of primary forest, which are found today in large parts of Africa and S.E. Asia, and which have close resemblance to one of the dominant morphotypes among the Eocene northern-continent primate radiations. The most specialized leapers found on Madagascar are much larger, and at least partially folivorous. Moreover, they include species which have amongst the lowest metabolic rates among placental mammals. This paradox suggests that low metabolic rates, and the seasonal torpor which is present in many of the mouse and dwarf lemurs, may have been key to the implantation of the lemurs on Madagascar. Whether or not this is so, the combination of low metabolic rates, and a frugivorous/folivorous diet with the hindlimb dominated locomotion which characterizes the whole order, has closely constrained the nature of the radiation, not only of the living lemurs, but their relatives among the subfossil lemurs.

KEY WORDS. - Strepsirhini, Haplorhini, Prosimians, *Lepilemur*, *Avahi*

RESUME. - Il est généralement accepté que la séparation entre Madagascar et l'Afrique aurait substantiellement supprimé les euprimates les plus primitifs d'Afrique et des continents septentrionaux. Il reste ainsi, peu d'alternatives à l'implantation des primates à Madagascar, sinon par la voie des radeaux. La largeur du canal du Mozambique était très importante, même au Crétacé supérieur, ainsi les possibilités de survie des éléments fondateurs mérite d'être expliquée. En raison de l'absence des fossiles de Lémuriens malgaches du Eocène, ou plus anciens, nous devons baser la reconstruction de l'évolution adaptative primitive dans l'île, à partir de la néontologie. L'évolution des Primates Strepsirrhine actuels de Madagascar est nettement différente de celle observée pour les primates du continent africain et de l'Est et S.E. de l'Asie. Bien que l'évolution des éléments malgaches soit plus diverse elle semble curieusement lacunaire en ce qui concerne les petits animalivores sauteurs qui occupent l'étage le plus bas des forêts primaires, et qui sont à présent trouvés dans des larges régions de l'Afrique et du S.E. de l'Asie. Ces éléments ont une grande ressemblance avec un des morphotypes dominants dans l'évolution des primates de l'Eocène du continent septentrional. Les « leapers » les plus spécialisés trouvés à Madagascar sont plus grands et au moins partiellement folivores. De plus, le groupe

comporte des espèces qui ont des taux métaboliques parmi les plus bas retrouvés chez les mammifères à placenta. Ce paradoxe peut suggérer que le faible taux métabolique et la torpeur saisonnière présentée par plusieurs éléments du groupe, pourrait être la clé de l'implantation des Lémuriens à Madagascar. Que cette suggestion soit vraie ou non, la combinaison du faible taux métabolique et d'une diète frugivore/folivore avec le type de locomotion qui caractérise l'ordre, aurait certainement contraint le type d'évolution, non seulement des Lémuriens actuels mais aussi de leurs ancêtres subfossiles.

MOTS-CLES.- Strepsirhini, Haplorhini, Prosimians, *Lepilemur*, *Avahi*

Whether or not Madagascar broke away from the African mainland, as traditionally held, or drifted across from India after that continent had parted with Gondwanaland, as has been suggested recently (STOREY *et al.* 1995), it is clear that by about 85-120 MYA (*i.e.* by the Cretaceous) the Mozambique Channel and the Indian Ocean were both already sufficiently large to act as a significant barrier to settlement of Madagascar by Palaeocene or Eocene euprimates. This leaves only two options for the origins of the prosimian radiation of Madagascar. Firstly, that the ancestor or ancestors of this radiation were already in place on Madagascar by the time of the separation of Madagascar. Or, secondly, that the radiation was derived from an ancestor or ancestors that drifted across to Madagascar on rafts of vegetation, the so-called « sweepstakes route ».

In either case, in considering the origins and evolution of the Malagasy prosimians, we must first ask whether they are a real biological entity, that is, whether they are monophyletic. Majority opinion today holds that the tarsiers are more closely related to monkeys and apes than they are to other prosimians, and should therefore be grouped with the anthropoids in Haplorhini, leaving Malagasy lemurs (the infraorder Lemuriformes) and the bushbabies and lorises (the infraorder Lorisiformes) in the clade Strepsirhini (reviewed in MARTIN, 1990). However, evidence from the basicranium has suggested to some that mouse and dwarf lemurs (Cheirogaleidae) and the bushbabies and lorises (Lorisiidae) have a special relationship (CARTMILL, 1975). But the living and subfossil Malagasy lemurs are linked by common possession of an intrabullar ectotympanic; while all lorises have a tympanic at the entrance to the bulla (MARTIN 1990). Taken together with molecular data implying a common ancestor to all Malagasy primates (YODER, this publication), genetic work suggesting that all living lemur karyotypes can be derived from a single common karyotype distinct from the pattern seen in the lorises (DUTRILLEAUX *et al.*, 1986) and further biochemical evidence of close relationship of the cheirogaleines with the Malagasy lemurs (DENE *et al.*, 1976), it seems that Cheirogaleidae do belong with the Lemuriformes and not with Lorisiformes. Resemblances of the carotid circulation in mouse and dwarf lemurs to that seen in Lorisiformes may be either retentions from a common strepsirhine ancestor or a parallel result of small body size (MARTIN, 1990). These arguments are only strengthened by recent discoveries in North Africa of fossils including *Plesiopithecus* and *Afrotarsius* from the Fayum, which suggest that the Lorisiform-Lemuriform division, as well as the haplorhine-strepsirhine division, is as old as the Eocene (SIMONS & RASMUSSEN, 1994; SIMONS, in press; RASMUSSEN & BIELA, in press), and by other discoveries (*e.g.* GODINOT & MAHBOUBI, 1992) suggesting that the simian-tarsier division may be as old as the late Eocene.

If the strepsirhines are indeed monophyletic, and we reject (as we probably should until evidence becomes available) separation of Lorisiformes and Lemuriformes by the late Cretaceous) we can consider the implantation and radiation of primates on

Madagascar to be a consequence of rafting of a single small founder population. The probability of such an event is greater if the founder population was composed of a small-bodied species like the living mouse lemurs, and indeed CHARLES-DOMINIQUE and MARTIN (1970) have argued persuasively that the mouse lemurs, and the adaptively rather similar Demidoff's bushbabies, represent a good model for the ancestral stock of primates of modern aspect, and hence, of the strepsirhines. However, a viable population would be unlikely to have been established if just two or three individuals had survived the crossing. How could sufficient founders have survived? In this paper, we argue that the adaptive radiation as a whole is characterised by relatively low basal metabolic rates, and a tendency for torpor in periods of unfavourable environmental conditions. This adaptation not only enhanced the survival chances of the founders, but has constrained and guided the ecological and locomotor diversification of the Malagasy lemurs.

The radiation of living strepsirhine primates on Madagascar (Lemuriformes) is more diverse than that on mainland Africa and East and South East Asia. For example, although both Lemuriformes and Lorisiformes are numerically dominated by species which may be described as « vertical clingers and leapers » (VCLS, NAPIER & WALKER, 1967), or at least « hindlimb dominated » (ROLLINSON & MARTIN, 1981) those on Madagascar include folivores as well as insectivorous, gummivorous and frugivorous species. The lower dietary diversity outside Madagascar is likely to be a consequence of post-Palaeocene extinctions and ecological replacement of all but nocturnal Lorisiformes by simians. On the other hand, the Malagasy primate fauna lacks vicars of the small specialist leaping species found today occupying the lower strata of primary and secondary forests in large parts of Africa (*Galago moholi*, *G. senegalensis* and *G. alleni*, Lorisidae, Lorisiformes, Strepsirhini) and the even more specialized animalivorous species of South East Asia (*Tarsius spp.*, Tarsiidae, Tarsiiformes, Haplorhini). Animalivory is the province of *Microcebus* (and other cheirogaleids) and *Daubentonia*, while the most specialized leapers found on Madagascar are much larger (800 g - 6 kg, versus 80 - 300 g for *Tarsius* and *Galago spp.*) and are at least partially folivorous. The specialist leapers among the Malagasy primates also differ in having a distinct morphological adaptation for leaping (increase in lower limb length by elongation of the femur rather than by an elongated tarsus, as in the Asian and African VCLS). The latter adaptation has been shown to be more efficient (ALEXANDER, 1995). Moreover, the specialized prosimian leapers of Asia and Africa are morphologically similar to species which constituted a large part of the Eocene northern-continent primate radiation, but the specialist Malagasy lemurs have no Eocene parallel. We might therefore conclude that the persistence of a less efficient system in all Malagasy VCLS indicates the influence of phylogenetic inertia, as well as less competition, on the adaptive radiation of primates that succeeded implantation of the founder population on Madagascar.

We have recently reported studies of the locomotion and locomotor energetics of two of the smallest specialized lemurid leapers, *Lepilemur edwardsi*, and *Avahi occidentalis*, living in sympatry at Ampijoroa (WARREN & CROMPTON, in press, submitted manuscript). We showed that *L. edwardsi* had much smaller home ranges and nightly travel distance than *A. occidentalis*, climbed more and used larger, more vertical supports. On the other hand, *Avahi* leaped more often and further, utilized smaller supports, at lower angles to the horizontal, and occupied a higher stratum in the same trees. We showed that the behaviour of the two species could be related to the dietary difference between the two species, *Avahi* feeding selectively on younger leaves, fruit and flowers, *Lepilemur* feeding indiscriminantly on older leaves. We then compared the energetic cost of locomotion in these two Malagasy species to that in two species of

Galago, including *G. moholi* (WARREN & CROMPTON, in press, submitted manuscript) and to *Tarsius bancanus*. The former is one of the most specialized African VCLs, and the latter the Asian equivalent. We showed that *Avahi* had the highest absolute energy cost of locomotion, and the highest cost relative to its resting metabolic costs, and *L. edwardsi* had the lowest absolute costs of locomotion and a low relative cost similar to *Tarsius*. But while *Tarsius*, as a small bodied obligate animalivore, gains relatively large energy rewards for a successful hunt, *L. edwardsi* feeds on an energy poor diet, which needs fermentation in the gut to be fully utilizable, and may also need to detoxify its old-leaf food. *Tarsius* can afford to spend a high proportion of its energy on locomotion, as the locomotion brings high rewards: for *Lepilemur*, it does not, and *Lepilemur* cannot afford to invest extensively in leaping.

Both fermentation and detoxification impose their own energy costs, and are associated with relatively low basal metabolic rates (MCNAB, 1978). Usually, a low-quality, bulky diet is typical of the largest primates, but both *Avahi* and *Lepilemur* are near the lower empirical threshold of body size for folivory in primates (KAY, 1984). Moreover, their leaping locomotion imposes relatively high energy demands as it is a non-cyclic mode of locomotion, unlike walking or running and energy can only be carried over from one leap to the next if it is stored as elastic strain energy: internally, in tendons, or externally, in branches. To date there is no evidence that this occurs in large saltatory primates (DEMES *et al.*, 1995) and it seems unlikely in most small mammals (BIEWENER *et al.*, 1981)

A clue to the manner in which *L. edwardsi* may balance its energy budget is found in its choice of sleeping site during the day. While *Avahi* sleeps in huddles on relatively exposed tree forks, high up in the trees, and only moves to more sheltered sites during the hottest part of the day, we found that *L. edwardsi* always sleeps in holes in trees, and while most sleeping holes are found at about 4-5 metres above the forest floor, it may often be found in holes at less than a metre above ground level. Since the entrance to these holes is of usually quite large, such low sleeping sites obviously expose *Lepilemur* to predation by the most important terrestrial predator on Malagasy lemurs, the fossa, *Cryptoprocta ferox*. The smallest Malagasy primates, the mouse lemurs, have long been known to live in tree holes, and SCHMID (in press) has reported that at Kirindy, both species, *M. murinus* and *M. myoxis*, are often found in holes near ground level. She has shown that all three also go into periods of torpor during which their body temperature may drop to as little as 7°C, and their basal metabolic rates drop considerably, and associated the low sleeping holes with the need to reduce body temperature by going into the coldest part of the forest. These periods of torpor increase in drier seasons, when food is less available. Kirindy, like Ampijoroa, is Western dry deciduous forest. Here, the trees are slow growing, short in stature and often with relatively low diameter at breast height. The highly seasonal west coast of Madagascar has protracted periods without rain and many trees lose their leaves completely for half of the year. Insect and reptile numbers also rapidly decline in this period, as insects hibernate or overwinter as eggs and cocoons. In the Western dry forest, some insectivore-frugivores among the Malagasy lemurs (including *Cheirogaleus medius*) hibernate for the driest three months of the year and may also go into daily torpor (MCCORMICK, 1981). At Kirindy, SCHMID and GANZHORN (in press) have shown that *Lepilemur ruficaudatus* have the lowest recorded resting metabolic rate of any mammal yet measured. Thus, both Cheirogaleidae and Lepilemuridae appear to use torpor and low basal metabolic rates as a response to dietary energy shortages. However, low metabolic rates are not confined to these two families: *Eulemur fulvus*, although primarily frugivorous, has a metabolic rate well below

the expectation from KLEIBER's relationship (1961; MCNAB & WRIGHT, 1987). Amongst other Malagasy folivores, the fact that *Haplemur spp.* eat cyanide-bearing bamboos would suggest (MCNAB, 1978) that they too are also likely to be found to have low metabolic rates for their size, while the precocious teething of the indriids (GODFREY *et al.*, in press.) suggests that they encounter seasonal shortages of food, and need to reduce lactation time.

Since torpor, low metabolic rates, and other indications of a need to survive seasonal shortages of energy are found in several families of Malagasy lemurs, it is parsimonious to conclude that these features, among Cheirogaleidae, are not the consequence of a characteristic which has been acquired by this group independently and in parallel with similar developments in at least the Lepilemuridae, but of one which was present in the ancestor of all Malagasy prosimians. We may also suggest that living Cheirogaleidae are likely to have changed least during their evolution from the common ancestral stock (CHARLES-DOMINIQUE & MARTIN, 1970). In possessing the characteristic of an ability to reduce basal metabolic energy requirements during seasonal scarcities in food supply, they were preadapted for surviving rafting across the Mozambique Channel. Low metabolic rates are not, however, confined to the Lemuriformes: *Loris* and *Nycticebus* have rates only 42% and 53% respectively of values to be expected from Kleiber's relationship (1961, MCNAB & WRIGHT, 1987) although rates in *Galago* are close to expectations from body mass.

Cheirogaleidae are also among the least specialized lemurs with respect to their locomotor system: as one of us has shown (CROMPTON, 1980, 1995, in press; OXNARD *et al.*, 1990; CROMPTON *et al.*, 1993) their elongated trunk makes it difficult, in leaping, for them to take off at the distance- or energy-efficient angle of 45°, or to rotate their bodies in flight so that the long hind limbs can be used to absorb landing forces. Thus, we should expect that differences in the kinematics of leaping should exist between the more specialized leapers among Lemuriformes, as a corollary of their distinct phylogenetic history. We have recently shown (WARREN & CROMPTON, in press, submitted manuscript) that *Avahi* shares with other Indriidae (DEMES & GÜNTHER, 1989) the ability to use the forelimb to rotate the body in flight, which *Lepilemur* lacks, and have further suggested that in this aspect, as in the more frequent use of forelimb-powered « ladder-climbing », it is reflecting a tendency towards suspensory postures and forelimb-powered locomotion found in the two other living indriids, *Indri* and *Propithecus*, (especially *P. tattersalli*; pers. obs.) which may at least in part be a response to the requirements of selective feeding on flowers and young leaves at large body size. The subfossil indriids *Babakotia* and *Palaeopropithecus* represent two progressive stages in the complete abandonment of leaping in favour of suspension by one lineage of very large indriids, while *Indri* represents the other extreme of ricochetel thigh-powered leaping, at smaller body size (JUNGERS *et al.* 1991). We would suggest that there must be some threshold along the body size range in Indriidae beyond which leaping locomotion in pursuit of a selective diet of leaves is no longer energetically feasible, and/or mechanically tolerable, as it clearly is in the living indriids. Equally, in its hindlimb-powered climbing and greater use of vertical supports, *Lepilemur edwardsi* shows the same « vertical clinger and climber » behaviour suggested for its subfossil relative, the giant lemur *Megaladapis*, by JUNGERS (1977). Again, we would predict a threshold of increased body size where *Lepilemur* could not compensate adequately for the increased costs of locomotion by dormancy or reduced metabolic rates, and where leaping would be totally abandoned for clinging and hindlimb-powered climbing on vertical supports (in particular).

CONCLUSIONS

Thus, we would argue that the absence of an avatar in Madagascar for the small-bodied specialist leaper-animalivores of the African and Asian undergrowth, like *Tarsius* and *G. moholi*, and their apparent ecological replacement by the unspecialized frugivore-animalivore *Microcebus*, is a consequence of filtering-out of high-metabolic rate, high-energy-consumption primates during implanting of the ancestral Malagasy lemur stock on Madagascar, and the suitability of *Microcebus*-like abilities for torpor for survival in the dry forest typical of the rain-shadowed Western coast of Madagascar (where the ancestor would presumably have landed).

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