

## **Cheirogaleid diversity and evolution: big questions about small primates**

Anne D. Yoder<sup>1,5</sup>, David W. Weisrock<sup>2</sup>, Rodin M. Rasoloarison<sup>3,4</sup>, and Peter M. Kappeler<sup>4</sup>

<sup>1</sup>Department of Biology, Duke University, Durham, NC, 27708, USA

<sup>2</sup>Department of Biology, University of Kentucky, Lexington, KY 40506, USA

<sup>3</sup>Département de Biologie Animale, Université d'Antananarivo, BP 906, Antananarivo (101), Madagascar

<sup>4</sup>Behavioral Ecology and Sociobiology Unit, German Primate Center (DPZ), 37077 Göttingen, Germany

<sup>5</sup>Corresponding author:

Anne D. Yoder

Department of Biology

Duke University, Box 90338

130 Science Drive

Durham, NC 27708

ph: 919-660-7275

fax: 919-660-7293

[anne.yoder@duke.edu](mailto:anne.yoder@duke.edu)

**In press:** Evolutionary Biology and Ecology of the Cheirogaleidae. S. L. Lehman, L. Radespiel and E. Zimmermann (eds). Cambridge, Cambridge University Press.

## **Abstract**

The family Cheirogaleidae is arguably the most interesting group of primates alive today. Within this single clade, hypothesized to have originated approximately 25 - 30 Mya, we find the world's smallest living primate (genus *Microcebus*), one species that went "missing" for more than three decades (genus *Allocebus*), the only known obligate hibernator within the primates (genus *Cheirogaleus*), the only primate species that preys upon other members of its phylogenetic family (genus *Mirza*), and also, a taxonomic system that has exploded within the past two decades. This taxonomic explosion has been decidedly lopsided, however. Whereas the genus *Allocebus* has remained monotypic, containing the single species *A. trichotis* since its original description in 1875 (Günther 1875), the genus *Microcebus* (mouse lemurs) has gone from a two species system as recently as 1993 to one that that now contains more than 20 recognized species. This apparent skew in species-level diversity cries out for further exploration. Is it an artifact of organismal and geographic sampling bias, with certain species and ecosystems preferentially sampled, or is it based in biology, with some branches of the cheirogaleid tree (namely, the mouse lemurs) intrinsically more prone to evolutionary divergence? An exploration of these themes and questions is our goal in this chapter.

## Introduction

The first genus level phylogeny of the cheirogaleid lemurs was published by Rumpler et al. (1994) and has remained virtually unchanged in the subsequent decades. Using karyotype data and restriction fragment analysis, the authors found strong support for the phylogeny illustrated in Figure 1. Notably, Rumpler and Albignac (1972) had long before discovered that the karyotype of *Phaner* ( $2n = 46$ ) is quite distinct from that of the other four genera ( $2n = 66$ ), leading those authors to propose a two-subfamily taxonomy of the Cheirogaleidae, the monotypic Phanerinae (including only the genus *Phaner*) and the Cheirogaleinae (comprising the four remaining genera). More recent molecular phylogenetic analyses have sampled more densely at the species level and have yielded fresh insights into inter-specific relationships within the various genera, while leaving the "skeleton" of the phylogeny unchanged. The stability of the cheirogaleid clade has made divergence time estimations feasible. Divergence time analysis has consistently shown the basal radiation of mouse lemurs to be on the order of 10 - 9 Mya (Thiele et al. 2013; Yang and Yoder 2003). Interestingly, the Thiele et al. (2013) study found the dwarf lemur radiation to be of approximately the same age, with a basal divergence date of 9.6 Mya (depending upon the loci examined). These authors concluded that the genus *Cheirogaleus* contains deeply divergent lineages "which are considerably older than several species of mouse lemur" (p. 602). Similar conclusions were reached by Springer et al. (2012), though with slightly younger age estimates with  $\sim 7$  Mya for mouse lemurs and  $\sim 9$  Mya for dwarf lemurs. Unfortunately, none of the divergence time studies to date has included the basal lineage, genus *Phaner*, and thus all age estimates of the ancestral cheirogaleid radiation will be underestimates. That said, all studies agree in finding diversification within the Cheirogaleidae to have originated by the late Oligocene, at least.

Though it is true that several molecular phylogenetic studies have shown a weak relationship between *Phaner* and *Lepilemur* (e.g., Masters et al. 2013; Roos et al. 2004; Springer et al. 2012), this result is likely to be an artifact of the rapid rate of mitochondrial evolution perhaps exacerbating the effects of long-branch attraction (Felsenstein 1978; Hillis 1996; Huelsenbeck 1997; Wiens and Hollingsworth 2000). Rather, a synthetic view

of recent molecular phylogenetic studies indicates that it is the entire cheirogaleid clade that is the sister to the genus *Lepilemur* (e.g., see Masters et al. 2013; Yoder 2013 for recent reviews). Looking more closely at the cheirogaleid clade, the dwarf lemurs (Groeneveld et al. 2010; Groeneveld et al. 2009; Thiele et al. 2013) and the mouse lemurs (Heckman et al. 2007; Heckman et al. 2006; Weisrock et al. 2010; Yoder et al. 2000) have shown complicated taxonomic expansions and rearrangements (Tables 1 & 2). In the majority of studies that have examined both mitochondrial (mtDNA) and nuclear (nDNA) DNA, it is typical to find poorly supported internal nodes and a high level of gene tree discordance across the loci under investigation (Heckman et al. 2007; Weisrock et al. 2010). Such results are typical of species radiations that are both recent and explosive (Knowles and Carstens 2007; Moore 1995; Shaffer and Thomson 2007). Within the mouse lemur clade, several studies have shown strong support for three deep lineages, one that contains *M. murinus* plus *M. griseorufus*, another deeply-diverged lineage represented by *M. ravelobensis*, *M. danfossi*, and *M. bongolavensis*, and a third lineage that is comprised of all other mouse lemur species including strong support for distal subclade comprised of *M. berthae*, *M. rufus*, and *M. myoxinus* (Figure 2) (Heckman et al. 2007; Heckman et al. 2006; Weisrock et al. 2010; Weisrock et al. 2012). This latter subclade is especially intriguing given that *M. rufus* (an eastern, rainforest adapted animal) is markedly divergent both ecologically and geographically from *M. berthae* and *M. myoxinus*, both of which occur in the dry deciduous forests of western Madagascar.

The chapter by Groves (this volume) gives a comprehensive summary of the finest details of cheirogaleid taxonomy, leaving little need for us to cover the same ground. Rather, we here examine the evidence that has driven the dazzling proliferation of species designations in one genus (*Microcebus*) while leaving others essentially unchanged since their original descriptions (i.e., *Allocebus*, *Mirza* and *Phaner*). Not terribly surprisingly, the proliferation of mouse lemur species coincides closely with the advent of readily available DNA sequences via the polymerase chain reaction (PCR) and with the development of user-friendly software for phylogenetic analysis of these sequences (e.g., Swofford 1990). An empirical investigation of the mouse lemur radiation has verified the theoretical predictions of recent and rapid species diversification (Weisrock et al. 2012). These

authors, in an effort to apply a multi-locus approach to reconstructing a species-level phylogeny for the mouse lemurs, found that the lingering effects of incomplete lineage sorting within the mouse lemur radiation severely compromise our ability to conduct standard phylogenetic analysis. That study, despite its inability to resolve the mouse lemur species tree, nonetheless came to a fundamental conclusion: depending upon which alleles were selected for concatenation in the multi-locus analysis, phylogenetic resolutions could differ, often dramatically, and with convincing statistical support. Thus, mouse lemurs show the classic hallmarks of a rapid species radiation wherein phylogenetic relationships will be difficult to reconstruct.

### **Lumping and Splitting**

Prior to the ready acquisition of DNA sequences for phylogenetic analysis, primatologists had favored a two-species taxonomy of mouse lemurs that included *M. murinus*, a long-eared gray animal from the southern and western regions of Madagascar, and *M. rufus*, a short-eared reddish animal from the east. Martin (1972), in particular, made note of the differing habitats and ecological constraints defining the two species, with *M. murinus* inhabiting dry deciduous and xerophytic forest and specializing on insectivory, and *M. rufus* inhabiting humid rain forest and showing dietary tendencies toward omnivory. This taxonomic stability first quavered with the description of a third, measurably smaller, species from the dry deciduous forests of western Madagascar (Schmid and Kappeler 1994). Initially, this third species was referred to as *M. myoxinus*, though this designation was to be shortly overturned by Rasoloarison et al. (2000). In the interim, a fourth and much larger species was identified in northwestern Madagascar and designated as *M. ravelobensis* (Zimmermann et al. 1998). Thus, even though new mouse lemur species were being recognized and described at an increasing rate throughout the 1990s, the pace was rather moderate when species designations relied upon combined assessments of ecology and morphology.

The pace accelerated abruptly with the introduction of genetic data into the species discovery process. With the combined efforts of a morphological team lead by

Rasoloarison et al. (2000) and a genetics team led by Yoder et al. (2000), the rate of taxonomic revision accelerated rapidly with the description of five new species. Along with the revised taxonomy of *M. myoxinus*, now recognized as *M. berthae*, so began the era of seemingly outlandish taxonomic proliferation. In two decades, *Microcebus* expanded from a genus containing two species to one containing at least 20 species (Andriantompohavana et al. 2006; Kappeler et al. 2005; Louis et al. 2006; Louis et al. 2008; Olivieri et al. 2007; Radespiel et al. 2008; Radespiel et al. 2012; Rasoloarison et al. 2013), and with many of these based primarily if not entirely on small DNA datasets.

Not surprisingly, there has been resistance from the primatological community, with assertions made of "a remarkable lack of introspection" (Tattersall 2007) as well as concerns that "species are based solely on evidence of genetic distance and diagnostic characters of mitochondrial DNA sequences sampled from a few individuals per location" (Markolf et al. 2011). We take these concerns seriously, and indeed, this is the impetus for our contribution to this very special volume on "Evolutionary Biology and Ecology of the Cheirogaleidae". Here, we wish to address the issue of species recognition both specifically --- asking how many species of mouse lemurs are there? And are they "real"? --- and more generally, examining the criteria and analytical framework for recognizing species. Though it is something of a tautology to say that species are the product of speciation, it is useful to remind ourselves that "speciation is a multi-level process unfolding through time and space" (Abbott et al. 2013; p.231). In this vein, de Queiroz (2007) has elegantly made the point that by attempting to pin a name to an organismal unit that is the product of an ongoing process we are setting ourselves up for disagreement and controversy. Here, we couch our discussion in the light of Simpson's Evolutionary Species Concept as expressed in Weisrock et al. (2010). That is, a "lineage (an ancestral-descendent sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies" (Simpson 1961). As for how to identify these lineages as species, de Queiroz (2007; p. 879) again describes matters succinctly by pointing out that "all of the properties formerly treated as secondary species criteria are relevant to species delimitation to the extent that they provide evidence of lineage

separation ... and thus more lines of evidence are associated with a higher degree of corroboration."

In other words, an integrative approach that combines genetic distance, morphometric distinction, behavioral variation and biogeographic separation establishes the lines of evidence supporting species recognition hypotheses (Markolf et al. 2013). Moreover, the careful assessment of this evidence can justify the recognition of species identities, even when there is clear-cut indication of limited gene flow among and between hypothesized species (Yoder, 2014), a phenomenon that is clearly of significance for the mouse lemur radiation (Hapke et al. 2011; Rakotondranary et al. 2011a).

### **What is it about mouse lemurs?**

Why is it that mouse lemurs show such clear patterns of genetic divergence and evolutionary isolation even though they are morphologically and ecologically so similar? One putative explanation relates to their nocturnal habits. Primatologists have sporadically discussed the possible relationship between nocturnality and cryptic speciation for several decades, though it is an essay on bats that offers the most detailed analysis. In a perceptive essay on the issue, Jones (1997) describes the biological complexities of cryptic species, particularly as they relate to nocturnality. In Jones's view, the lack of visual information concomitant with a nocturnal lifestyle will be compensated by other means of inter-individual signaling and communication such as acoustic and olfactory cues. Moreover, Jones predicted that biologists are significantly underestimating evolutionary diversity when we rely solely on visual information (i.e., morphological characters) as our guide for species identification, asserting that untold amounts of genetic biodiversity will be underappreciated using such methods. Jones anticipated that "advances in molecular biology may allow insights into speciation in cryptic species" (p. 345), a scenario that has been unfolding over the past two decades as we have investigated the mouse lemur radiation. Despite the appeal of Jones's cryptic speciation hypothesis, we must note that all cheirogaleid primates are nocturnal, so the apparent imbalance in species diversity within the clade cannot be reduced to this single explanation. Moreover,

and even more complicated, biologists have found it difficult to explain how primate species that occupy the same ecological niche --- as mouse lemurs appear to do --- and are difficult if not impossible to distinguish morphologically, can co-exist sympatrically (Dammhahn and Kappeler 2008b; Radespiel et al. 2006; Rakotondranary and Ganzhorn 2011; Rakotondranary et al. 2011a; Rakotondranary et al. 2011b; Thoren et al. 2011b). As we have gained increased knowledge of the precise details of mouse lemur behavioral ecology, however, these mysteries are resolving.

### **Mouse Lemurs as a Model System**

Rather than view these conundrums as obstacles to biodiversity discovery, we believe that mouse lemurs can more usefully be presented as a model system for investigating the often subtle and overlooked biological forces that can drive species radiations and maintain species boundaries (though these forces may act differentially, with some as "drivers" and others as "maintainers"). Beyond the intriguing idea of looking towards alternative signaling mechanisms of olfactory and acoustic communication for driving and maintaining species boundaries (e.g., Braune et al. 2005; Braune et al. 2008; Hohenbrink et al. 2012; Leliveld et al. 2011; Scheumann et al. 2007; Yoder et al. 2014), it is becoming increasingly clear that painstaking investigations of behavior and ecology are necessary for disentangling the relevant parameters (e.g., see Radespiel, this volume).

Among mouse lemurs, *Microcebus murinus* is unique in having a relatively vast geographic distribution. Whereas all other *Microcebus* species have geographically limited ranges --- with some restricted to isolated forest fragments --- *M. murinus* is distributed along most of the western half and along the south of the island. It is presently not known what are the genotypic and phenotypic traits possessed by *M. murinus* that apparently confer an adaptive flexibility that has promoted its spread across vast areas of Madagascar (but see chapter by Radespiel, this volume). Like other species within the genus, *M. murinus* is known to exhibit episodic bouts of torpor, presumably in the face of resource limitations. Unlike other species, however, there appears to be a sex bias to this behavior that is distinctive. For example, *M. murinus* populations have been shown to exhibit different torporing



patterns both by age and by sex (Schmid 1999; Schmid and Kappeler 1998; Terrien et al. 2010a; Terrien et al. 2010b), with one study finding that whereas 73% of females undergo prolonged torpor bouts, only 19% of males show the same behavior (Schmid 1999). Over the extensive range of *M. murinus*, the species has been confirmed or hypothesized to overlap with multiple congeners including *M. griseorufus* (its sister species), *M. berthae*, *M. myoxinus*, *M. bongolavensis*, and *M. ravelobensis*. And though it remains to be confirmed, there is the potential for overlap with *M. tavaratra*, *M. sambarinensis*, and *M. danfossi* given the latitudinal distribution of these species. Irrespective of their sympatric status, all species in the genus compared to *M. murinus* show much smaller species ranges, with some showing alarming patterns of geographic restriction and microendemism.

Here, we review the literature on the behavioral ecology of *Microcebus*, focusing on three regions of sympatric overlap between *M. murinus* and *M. griseorufus*, *M. berthae*, and *M. ravelobensis*, respectively. Notably, all of these investigations of ecological and behavioral distinction in sympatry involve *M. murinus*, by far the most geographically widespread of the recognized species of mouse lemur. Potentially, this introduces an unwanted bias to the generalities and conclusions that can be drawn from a synthetic view of these studies, but at present, they are the best available. Moreover, despite their relatively limited taxonomic scope, these studies provide insight into the subtlety and power of environmental forces that can create almost invisible niche heterogeneity wherein each species can occupy a unique ecological domain.

## **Mouse lemur niche heterogeneity: from southern to northern Madagascar**

### Lessons from *Microcebus griseorufus*

One example of this pattern of sympatry couples *M. murinus* with *M. griseorufus*, with multiple lines of evidence for distribution overlap and potential hybridization between the two species in southern Madagascar. Within their respective ranges, *M. murinus* and *M. griseorufus* exhibit marked differences in abundance. *M. murinus* is typically common throughout its range and has been studied extensively since its description (Kappeler and Rasoloarison 2003). Conversely, *M. griseorufus* has been recorded from relatively few

locations within a narrow range in the southwest of the island in the recent past and remains poorly studied (Bohr et al. 2011; Genin 2008; Kobbe et al. 2011). A recent study (Blair et al. 2014) used a multilocus coalescent framework to test the hypothesis that the relatively limited range of *M. griseorufus* relative to *M. murinus* is the consequence of peripatric speciation wherein *M. griseorufus* was initially formed via the isolation of a relatively small ancestral population that was on the geographic limits of a more widely distributed ancestral *M. murinus* population. The study rejected this hypothesis soundly, finding instead that historical demographic data much better fit a model of allopatric divergence from a range-restricted common ancestor in southwestern Madagascar, with subsequent range expansions for *M. murinus*. Whether due to ecological constraint (Bohr et al. 2011) or interspecific competition, *M. griseorufus* is presently restricted to the arid spiny forest in the south, whereas *M. murinus* has successfully expanded northward throughout much of western Madagascar and to limited areas in the southeast.

*Microcebus griseorufus* is special within the mouse lemur radiation for apparently thriving in one of the most challenging environments inhabited by any primate: the dry spiny forests of the southwest. Rainfall and accordingly resources are unpredictable both in amount and distribution, and this species has developed a number of physiological and behavioral strategies for coping with this uncertainty. A four-year study of one population showed that individuals used daily torpor and expressed opportunistic seasonal fattening when food availability was high, reverting to dependence on plant exudates when experiencing periods of regional drought (Génin 2008). Another long-term study showed that *griseorufus* shows high levels of seasonal as well as individual flexibility in thermoregulation (Kobbe et al. 2011). Whereas all individuals remained normothermic during the rainy season when resources are abundant, heterothermy ranging from irregular short torpor bouts, to regular daily torpor, to prolonged torpor of a few days, and even hibernation over several weeks were observed during the dry season. When compared with *M. murinus*, *M. griseorufus* shows an interesting combination of habitat fidelity, strongly preferring spiny forest to gallery or transitional forest types, as well as greater flexibility in thermoregulation.

Early genetic work found that *M. griseorufus* and *M. murinus* show species-specific mtDNA haplotypes, which at the time was regarded as evidence for reproductive isolation in sympatry (Yoder et al. 2002). More recent and sophisticated genetic analyses that examined both mitochondrial and nuclear autosomal loci have revealed a much more complicated picture of genetic exchange between the two species (Gligor et al. 2009; Hapke et al. 2011). In the 2009 study, the authors found that whereas mitochondrial haplotypes displayed a sharply delimited boundary at the eastern edge of spiny forest, nuclear loci yielded evidence for a mixed ancestry of mouse lemurs in the ecotone between the spiny forest habitat of *M. griseorufus* and the littoral forest habitat of *M. murinus*. In this case, the authors concluded that asymmetric nuclear introgression was due to male-biased dispersal, divergent environmental selection, and an expansion of dry spiny forest in the course of aridification (Gligor et al. 2009). In the 2011 study, in another field setting, the authors found that whereas *M. griseorufus* is restricted to the spiny forest habitat, *M. murinus* occurs in the gallery forest but locally invades the dryer habitat of *M. griseorufus*. In this setting, the authors found evidence for bidirectional introgressive hybridization, in contrast to the asymmetric patterns previously observed. In comparing the two settings and the coincident patterns of introgressive gene flow, the authors found that hybridization could enhance the adaptability of mouse lemurs without necessarily leading to a loss of distinctiveness (Hapke et al. 2011), a finding very much in keeping with emerging views of the genomics of speciation (Seehausen et al. 2014; Yoder 2014). Finally, and in keeping with the "sine qua non" of speciation theory, a recent study by Sommer et al. (2014) has found that hybrids formed by *M. murinus* and *M. griseorufus* show reduced fitness as measured by higher parasite loads.

To summarize, it appears that interactions between *M. murinus* and *M. griseorufus* can differ depending upon ecological and environmental context. This has been confirmed empirically: when the two species exist in allopatry, both behave as ecological generalists, yet, when they occur in sympatry, both species show distinct microhabitat preferences, allowing them to partition the environment (Rakotondranary and Ganzhorn 2011). Moreover, stable isotope analysis revealed that their dietary niches diverge most markedly in the dry "lean" season (Rakotondranary et al. 2011b). The results pertaining to *M.*

*griseorufus* and *M. murinus* have been extended to a three-species comparison in southeastern Madagascar where they co-occur with *M. rufus*. This study further confirmed the preference for gallery forest in *M. murinus* and spiny forest for *M. griseorufus*, adding the observation that *M. rufus* shows a strong fidelity to evergreen humid forest (Rakotondranary et al. 2011a).

Finally, with regard to heterothermy, *M. griseorufus* was found to exhibit even greater flexibility than *M. murinus*, with individuals exhibiting variability in energy-saving strategies ranging from irregular short torpor bouts, regular daily torpor, prolonged torpor of a few days, and hibernation over several weeks as a function of individual variation in fat reserves (Kobbe et al. 2011). Moreover, *M. griseorufus* also exhibits similar dietary flexibility between habitats and seasons (Crowley et al. 2014) that the relative ecological success of *M. murinus* is even more enigmatic. Taken together, these patterns of range expansion, ecological flexibility, and potential competitive advantage make this pair of species a particularly interesting system for future studies within the mouse lemur radiation.

#### Lessons from *Microcebus berthae*

As *M. griseorufus* overlaps with *M. murinus* in the south, so does *M. berthae* in the west, though with a considerably smaller area of geographic overlap (Schäffler and Kappeler 2014). Detailed field studies are emerging to illustrate that just as with *M. griseorufus*, *M. berthae* and *M. murinus* partition their environment in subtle though biologically meaningful ways. Both species are omnivorous and experience similar seasonal fluctuations in food supply (Schwab & Ganzhorn 2004); nonetheless, they exhibit fine-grained differences in annidation. Feeding niche overlap is high in terms of food categories, but stable isotope analyses revealed niche differentiation in fruit and animal matter ( $\delta^{15}\text{N}$ ), but not in basal resources ( $\delta^{13}\text{C}$ ) (Dammhahn and Kappeler 2010; Dammhahn and Kappeler 2014). *M. berthae* is more insectivorous and has a narrower feeding niche than *M. murinus*, which includes more fruits and gum in its diet (Dammhahn and Kappeler 2008a), resulting in different intra-specific competitive regimes and spatial requirements (Dammhahn and Kappeler 2010). In addition, *M. berthae* does not hibernate and is less able

to use spontaneous torpor than *M. murinus* (Ortmann et al. 1997; Schmid et al. 2000). These studies lend further support to the notion of a strong propensity for *M. berthae* and *M. murinus* to partition the environment spatially by microhabitat, with the two species showing a non-overlapping "checkerboard" pattern of spatial segregation in sympatry (Schwab and Ganzhorn 2004), and with *M. berthae* occupying home ranges nearly twice as large as those of *M. murinus* (Dammhahn and Kappeler 2005). More recent analyses indicate that the distribution and abundance of the two mouse lemur species may also depend on that of other cheirogaleid members of their local community, with *Cheirogaleus medius* locally displacing *M. murinus* and *Mirza coquereli* acting as an opportunistic predator of *M. murinus* (Schäffler et al. ms.). Thus, coexistence of mouse lemurs here and elsewhere may also be stabilized by additional factors and species.

#### Lessons from *Microcebus ravelobensis*

Perhaps the most intensively studied of the areas of species overlap is that in the far northwest of Madagascar where *M. murinus* and *M. ravelobensis* occur sympatrically. A range of behavioral differences diagnoses the two species. Spatially, densities of *M. murinus* have been shown to increase with altitude while those of *M. ravelobensis* decrease (Rakotondravony and Radespiel 2009). And, as with the other two species comparisons, detailed ecological studies have shown distinct differences in microhabitat choice and species-specific patterns of spatial distribution (Rendigs et al. 2003), including choice of nest site type and composition of nesting groups. Whereas *M. murinus* tends towards female-only sleeping groups, *M. ravelobensis* is more likely to show mixed sex sleeping groups (Radespiel et al. 2003). Dietary distinctions are also detectable, though they are subtle (Radespiel et al. 2006; Sehen et al. 2010; Thoren et al. 2011b). In direct interactions, *M. murinus* is dominant when paired with *M. ravelobensis*, despite a lack of a significant size difference (Thoren et al. 2011a).

Surprisingly, *M. ravelobensis* also appears to violate at least two of the "rules" that govern mouse lemur behavior. Whereas studies of other species (primarily, of *M. murinus*) consistently show patterns of a strong bias towards male dispersal and female philopatry (Schliehe-Diecks et al. 2012), male dispersal in *M. ravelobensis* is significantly delayed

(Radespiel et al. 2009). The greatest surprise, however, relates to female dominance. Whereas behavioral studies of all other mouse lemur species show strong patterns of female dominance, *M. ravelobensis* does not (Eichmueller et al. 2013). Whether and how these behavioral differences contribute to species coexistence remains to be explored in more detail.

### **Now what?**

The section above will, we hope, convince the reader that the remarkable taxonomic proliferation of mouse lemur species has biological merit. It appears that these animals are using an array of behavioral, dietary, physiological, and signaling mechanisms to divide up their world and maintain their separate evolutionary trajectories, thus destined for unique evolutionary endpoints. But many challenges remain towards fully comprehending this fascinating species radiation. Their diminutive size, nocturnal habits, and remote geographic distribution require determined and sometimes extraordinary effort on the part of field biologists who wish to study these petit primates. We predict that the coming years will continue to provide rich insight into the unique ecological and behavioral traits of these animals that in turn will further inform our understanding of the mechanisms that have driven and continue to maintain species boundaries.

But what can be done immediately, and over the coming few years, to deepen our understanding of species diversity, not just of mouse lemurs, but of the entire cheirogaleid clade? As was predicted by Jones (1997), genetic data have opened up a previously obscured world of biodiversity in the cryptic mouse and dwarf lemur radiations. Presently, these studies provide a very lopsided view of rampant speciation on one branch in the clade (i.e., the mouse lemurs) and virtual evolutionary stasis in others (e.g., *Allocebus*). This begs for further exploration. Is it a function of intrinsic biology? Do mouse lemurs have some innate genomic or phenotypic properties that predispose them to divergent speciation? Or is it rather a function of sampling bias and experimental approach?

Recent work focused on the dwarf lemurs (genus *Cheirogaleus*) appears to suggest the latter, at least to some appreciable extent. Thiele et al. (2013) forcefully make the case that taxonomic partitioning can strongly influence interpretations of species range limits and genetic diversity among any number of other important measures of biodiversity. By directly comparing homologous data within the same analytical framework for mouse and dwarf lemurs (e.g., see their Figure 4), these authors are able to make a strong case for claiming either that mouse lemur diversity is overestimated, or dwarf lemur diversity is underestimated. We suspect that the most likely explanation is "a bit of both". Accordingly, the conclusion must be drawn that much work lies ahead before we can claim that the full diversity of the cheirogaleid clade is known.

So how do we proceed? From the earliest phases of "mouse lemur mania" there have been repeated calls for an integrative approach to species discovery, one that takes into account morphology, behavior, ecology, sensory signaling, geography, and autosomal as well as sex-linked genetic loci (e.g., Heckman et al. 2006; Markolf et al. 2011; Weisrock et al. 2010; Yoder et al. 2005; Yoder et al. 2000; Zimmermann and Radespiel 2014). The collection of behavioral and ecological data is arduous and time-consuming, however, with results slow to emerge. We therefore make the urgent call that the community of scientists interested in species discovery within this fascinating clade of primates adopt a uniform genetic "toolkit" such that each individual, population, and putative species can be examined within a general and universal framework, much as has been recently illustrated in the Thiele et al. (2013) study. Moreover, when depositing genetic data, investigators should be assiduous in also depositing their aligned matrices. It is well understood that the process of sequence alignment is rife with assumptions. When investigators are required to download individual gene sequences, concatenate and align them, assumptions made (either computationally or by eye) can impact downstream results, especially with regard to the estimation of branch lengths in phylogenetic analysis --- the very evidence upon which so many species hypotheses have been founded (e.g., Thiele et al. 2013; Weisrock et al. 2010; Yoder et al. 2000). If such standards can be developed and implemented, we can enter a new era of analysis wherein investigators work as a community, united in the goals

of biodiversity discovery and conservation of the Cheirogaleidae as a whole. This approach will be both collegial and scientifically rigorous.

### **Acknowledgements**

We would like to thank the editors for their invitation to contribute to this special volume on the cheirogaleid primates and for their patience during the preparation of our manuscript. Our contribution was significantly improved thanks to their editorial oversight and by the constructive critique of two anonymous reviewers. We also thank and recognize the Malagasy institutions and collaborators who have made our work possible over the years, namely the Département Biologie Animale, CAFF-CORE and the Ministry of Forest and the Environment. This is Duke Lemur Center publication #1284.



## References Cited

- Abbott R, Albach D, Arntzen JW, and al. e, 2013. Hybridization and speciation. *Journal of Evolutionary Biology* 26, 229-246.
- Andriantompohavana R, Zaonarivelo JR, Engberg SE, Randriamampionona R, McGuire SM, Shore GD, Rakotonomenjanahary R, Brenneman RA, and Louis EE, 2006. Mouse lemurs of north-western Madagascar with a description of a new species at Lokobe Special Reserve. *Occasional Papers Museum of Texas Tech University* 259.
- Blair C, Heckman KL, Russell AL, and Yoder AD, 2014. Multilocus coalescent analyses reveal the demographic history and speciation patterns of mouse lemur sister species. *BMC Evolutionary Biology* 14.
- Bohr YEMB, Giertz P, Ratovonamana YR, and Ganzhorn JU, 2011. Gray-brown Mouse Lemurs (*Microcebus griseorufus*) as an Example of Distributional Constraints through Increasing Desertification. *International Journal of Primatology* 32, 901-913.
- Braune P, Schmidt S, and Zimmermann E, 2005. Spacing and group coordination in a nocturnal primate, the golden brown mouse lemur (*Microcebus ravelobensis*): the role of olfactory and acoustic signals. *Behavioral Ecology and Sociobiology* 58, 587-596.
- Braune P, Schmidt S, and Zimmermann E, 2008. Acoustic divergence in the communication of cryptic species of nocturnal primates (*Microcebus* spp.). *BMC Biology* 6, 1-10.
- Crowley BE, Rasoazanabary E, and Godfrey LR, 2014. Stable isotopes complement focal individual observations and confirm dietary variability in reddish-gray mouse lemurs (*Microcebus griseorufus*) from southwestern Madagascar. *American Journal of Physical Anthropology* 155, 77-90.
- Dammhahn M and Kappeler P, 2008a. Comparative Feeding Ecology of Sympatric *Microcebus berthae* and *M. murinus*. *International Journal of Primatology* 29, 1567-1589.
- Dammhahn M and Kappeler PM, 2005. Social system of *Microcebus berthae*, the world's smallest primate. *International Journal of Primatology* 26, 407-435.
- Dammhahn M and Kappeler PM, 2008b. Small-scale coexistence of two mouse lemur species (*Microcebus berthae* and *M. murinus*) within a homogeneous competitive environment. *OECOLOGIA* 157, 473-483.
- Dammhahn M and Kappeler PM, 2010. Scramble or contest competition over food in solitarily foraging mouse lemurs (*Microcebus* spp.): New insights from stable isotopes. *American Journal of Physical Anthropology* 141, 181-189.
- Dammhahn M and Kappeler PM, 2014. Stable isotope analyses reveal dense trophic species packing and clear niche differentiation in a malagasy primate community. *American Journal of Physical Anthropology* 153, 249-259.
- de Queiroz K, 2007. Species concepts and species delimitation. *Systematic Biology* 56, 879 - 886.
- Eichmueller P, Thoren S, and Radespiel U, 2013. The lack of female dominance in golden-brown mouse lemurs suggests alternative routes in lemur social evolution. *American Journal of Physical Anthropology* 150, 158-164.
- Felsenstein J, 1978. Cases in which parsimony or compatibility methods will be positively misleading. *Systematic Zoology* 27, 401-410.
- Genin F, 2008. Life in unpredictable environments: First investigation of the natural history of *Microcebus griseorufus*. *International Journal of Primatology* 29, 303-321.

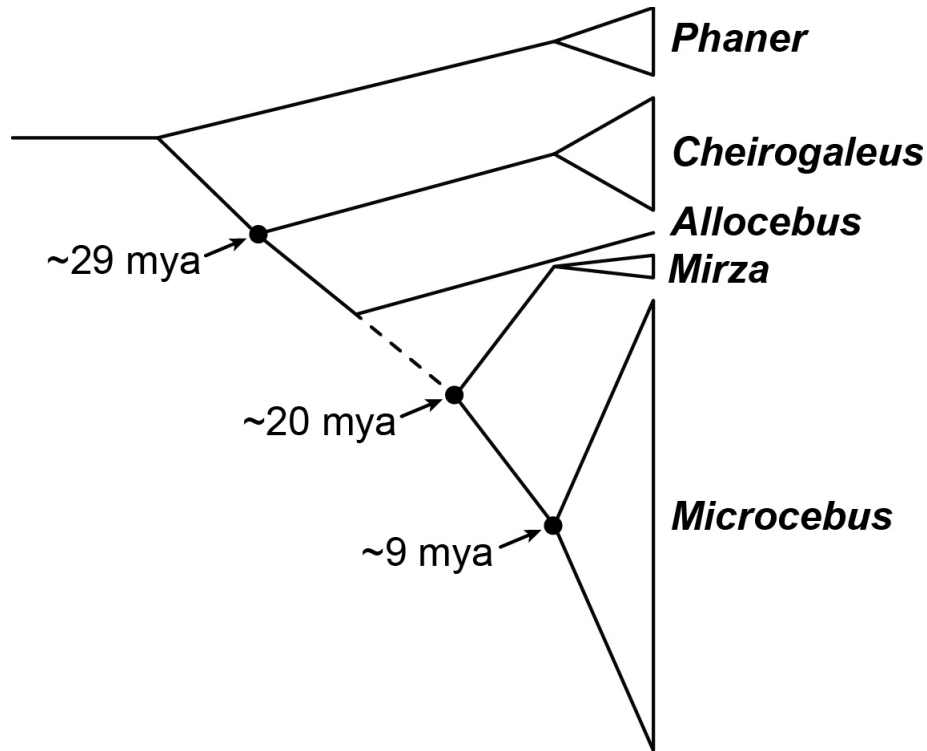
- Gligor M, Ganzhorn JU, Rakotondravony D, Ramilijaona OR, Razafimahatratra E, Zischler H, and Hapke A, 2009. Hybridization between mouse lemurs in an ecological transition zone in southern Madagascar. *Molecular Ecology* 18, 520-533.
- Groeneveld LF, Blanco MB, Raharison JL, Rahalinarivo V, Rasoloarison RM, Kappeler PM, Godfrey LR, and Irwin MT, 2010. MtDNA and nDNA corroborate existence of sympatric dwarf lemur species at Tsinjoarivo, eastern Madagascar. *Molecular Phylogenetics and Evolution* 55, 833-845.
- Groeneveld LF, Weisrock DW, Rasoloarison RM, Yoder AD, and Kappeler PM, 2009. Species delimitation in lemurs: multiple genetic loci reveal low levels of species diversity in the genus *Cheirogaleus*. *BMC Evolutionary Biology* 9.
- Hapke A, Gligor M, Rakotondranary SJ, Rosenkranz D, and Zupke O, 2011. Hybridization of mouse lemurs: different patterns under different ecological conditions. *BMC Evolutionary Biology* 11.
- Heckman KL, Mariani CL, Rasoloarison R, and Yoder AD, 2007. Multiple nuclear loci reveal patterns of incomplete lineage sorting and complex species history within western mouse lemurs (*Microcebus*). *Molecular Phylogenetics and Evolution* 43, 353-367.
- Heckman KL, Rasoazanabary E, Machlin E, Godfrey LR, and Yoder AD, 2006. Incongruence between genetic and morphological diversity in *Microcebus griseorufus* of Beza Mahafaly. *BMC Evolutionary Biology* 6.
- Hillis DM, 1996. Inferring complex phylogenies. *Nature* 383, 130-131.
- Hohenbrink P, Radespiel U, and Mundy NI, 2012. Pervasive and ongoing positive selection in the vomeronasal-1 receptor (V1R) repertoire of mouse lemurs. *Molecular Biology and Evolution* 29, 3807-3816.
- Huelsenbeck JP, 1997. Is the Felsenstein zone a fly trap? *Systematic Biology* 46, 69-74.
- Hutchinson GE, 1957. Population studies - animal ecology and demography - concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22, 415-427.
- Jones G, 1997. Acoustic signals and speciation: The roles of natural and sexual selection in the evolution of cryptic species. *Advances in the Study of Behavior* 26, 317-354.
- Kappeler PM, Rasoloarison R, Razafimanantsoa L, Walter L, and Roos C, 2005. Morphology, behaviour and molecular evolution of giant mouse lemurs (*Mirza* spp.) Gray, 1870, with description of a new species. *Primate Report* 71, 3-26.
- Kappeler PM and Rasoloarison RM. 2003. *Microcebus*, mouse lemurs, Tsidy. Pages 1310-1315 in Goodman, S. M. and Benstead, J. P., editors. *The Natural History of Madagascar*. University of Chicago Press, Chicago.
- Knowles LL and Carstens BC, 2007. Delimiting species without monophyletic gene trees. *Systematic Biology* 56, 887-895.
- Kobbe S, Ganzhorn JU, and Dausmann KH, 2011. Extreme individual flexibility of heterothermy in free-ranging Malagasy mouse lemurs (*Microcebus griseorufus*). *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology* 181, 165-173.
- Leliveld LMC, Scheumann M, and Zimmermann E, 2011. Acoustic correlates of individuality in the vocal repertoire of a nocturnal primate (*Microcebus murinus*). *Journal of the Acoustical Society of America* 129, 2278-2288.
- Louis EE, Coles MS, Andriantompohavana R, Sommer JA, Engberg SE, Zaonarivelo JR, Mayor MI, and Brenneman RA, 2006. Revision of the mouse lemurs (*Microcebus*) of eastern Madagascar. *International Journal of Primatology* 27, 347-389.

- Louis EE, Engberg SE, McGuire SM, McCormick MJ, Randriamampionona R, Ranaivoarisoa JF, Bailey CA, Mittermeier RA, and Lei R, 2008. Revision of the mouse lemurs, *Microcebus* (Primates, Lemuriformes), of northern and northwestern Madagascar with descriptions of two new species at Montagne d'Ambre National Park and Antafondro Classified Forest. *Primate Conservation* 23, 19-38.
- Markolf M, Brameier M, and Kappeler PM, 2011. On species delimitation: Yet another lemur species or just genetic variation? *BMC Evolutionary Biology* 11.
- Markolf M, Rakotonirina H, Fichtel C, von Grumbkow P, Brameier M, and Kappeler PM, 2013. True lemurs ... true species - species delimitation using multiple data sources in the brown lemur complex. *BMC Evolutionary Biology* 13.
- Martin RD, 1972. A preliminary field-study of the lesser mouse lemur (*Microcebus murinus* J.F. Miller, 1777). *Zeitschrift für Tierpsychologie* Suppl. 9, 43-89.
- Masters JC, Silvestro D, Génin F, and DelPero M, 2013. Seeing the wood through the trees: the current state of higher systematics in the Strepsirrhini. *Folia Primatologica* 84, 201-219.
- Moore WS, 1995. Inferring phylogenies from mtDNA variation: mitochondrial-gene trees versus nuclear-gene trees. *Evolution* 49, 718-726.
- Olivieri G, Zimmermann E, Randrianambinina B, Rasoloharijaona S, Rakotondravony D, Guschanski K, and Radespiel U, 2007. The ever-increasing diversity in mouse lemurs: Three new species in north and northwestern Madagascar. *Molecular Phylogenetics and Evolution* 43, 309-327.
- Ortmann S, Heldmaier G, Schmid J, and Ganzhorn JU, 1997. Spontaneous daily torpor in Malagasy mouse lemurs. *Naturwissenschaften* 84, 28-32.
- Radespiel U, Ehresmann P, and Zimmermann E, 2003. Species-specific usage of sleeping sites in two sympatric mouse lemur species (*Microcebus murinus* and *M.ravelobensis*) in Northwestern Madagascar. *American Journal of Primatology* 59, 139-151.
- Radespiel U, Juric M, and Zimmermann E, 2009. Sociogenetic structures, dispersal and the risk of inbreeding in a small nocturnal lemur, the golden-brown mouse lemur (*Microcebus ravelobensis*). *Behaviour* 146, 607-628.
- Radespiel U and Olivieri G and Rasolofoson DW and Rakotondratsimba G and Rakotonirainy O and Rasoloharijaona S and Randrianambinina B and Ratsimbazafy JH and Ratelolahy F and Randriamboavonjy T et al., 2008. Exceptional diversity of mouse lemurs (*Microcebus* spp.) in the Makira region with the description of one new species. *American Journal of Primatology* 70, 1033-1046.
- Radespiel U, Ratsimbazafy JH, Rasoloharijaona S, Raveloson H, Andriaholinirina N, Rakotondravony R, Randrianarison RM, and Randrianambinina B, 2012. First indications of a highland specialist among mouse lemurs (*Microcebus* spp.) and evidence for a new mouse lemur species from eastern Madagascar. *Primates* 53, 157-170.
- Radespiel U, Reimann W, Rahelinirina M, and Zimmermann E, 2006. Feeding ecology of sympatric mouse lemur species in northwestern Madagascar. *International Journal of Primatology* 27, 311-321.
- Rakotondranary SJ and Ganzhorn JU, 2011. Habitat Separation of Sympatric *Microcebus* spp. in the Dry Spiny Forest of South-Eastern Madagascar. *Folia Primatologica* 82, 212-223.
- Rakotondranary SJ, Hapke A, and Ganzhorn JU, 2011a. Distribution and Morphological Variation of *Microcebus* spp. Along an Environmental Gradient in Southeastern Madagascar. *International Journal of Primatology* 32, 1037-1057.

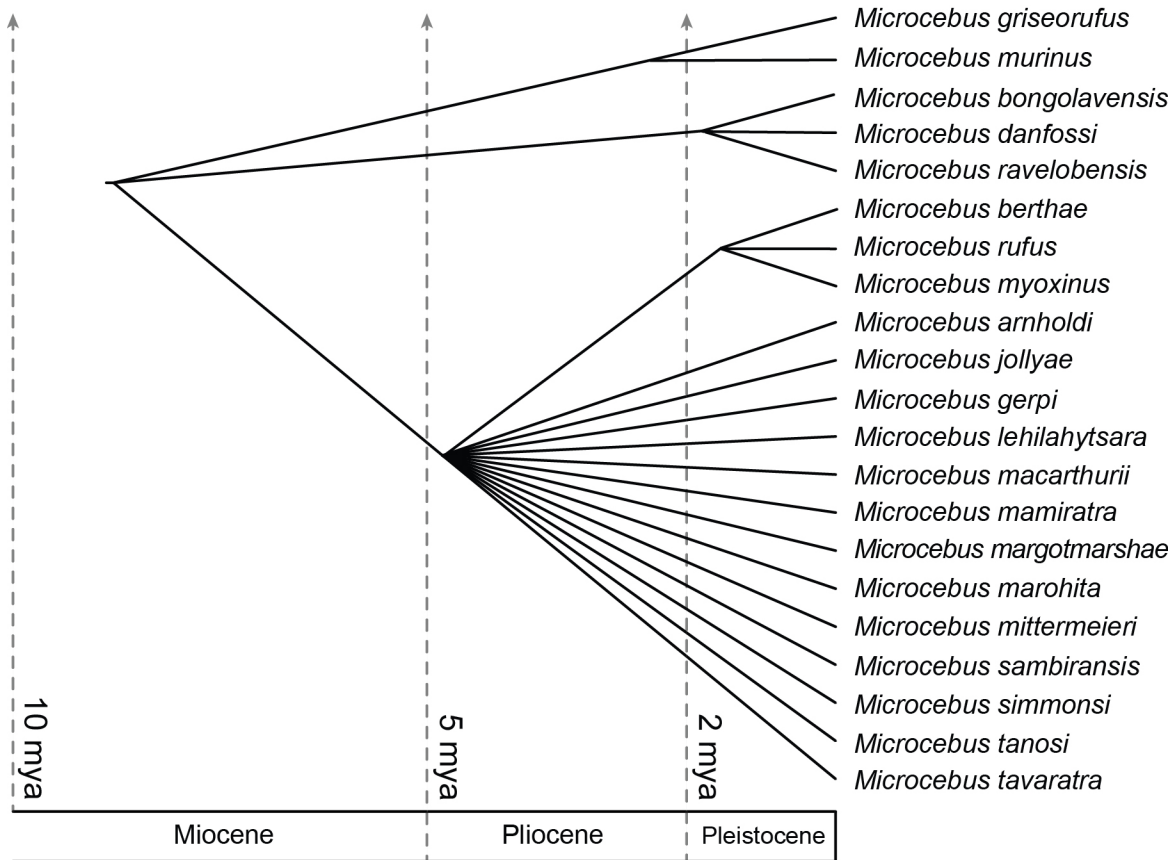
- Rakotondranary SJ, Struck U, Knoblauch C, and Ganzhorn JU, 2011b. Regional, seasonal and interspecific variation in (15)N and (13)C in sympatric mouse lemurs. *Naturwissenschaften* 98, 909-917.
- Rakotondravony R and Radespiel U, 2009. Varying patterns of coexistence of two mouse lemur species (*Microcebus ravelobensis* and *M. murinus*) in a heterogeneous landscape. *American Journal of Primatology* 71, 928-938.
- Rasoloarison RM, Goodman SM, and Ganzhorn JU, 2000. Taxonomic revision of mouse lemurs (*Microcebus*) in the western portions of Madagascar. *International Journal of Primatology* 21, 963-1019.
- Rasoloarison RM, Weisrock DW, Yoder AD, Rakotondravony D, and Kappeler PM, 2013. Two new species of mouse lemurs (Cheirogaleidae: *Microcebus*) from Eastern Madagascar. *International Journal of Primatology* 34, 455-469.
- Rendigs A, Radespiel U, Wrogemann D, and Zimmermann E, 2003. Relationship between microhabitat structure and distribution of mouse lemurs (*Microcebus* spp.) in Northwestern Madagascar. *International Journal of Primatology* 24, 47-64.
- Roos C, Schmitz J, and Zischler H, 2004. Primate jumping genes elucidate strepsirrhine phylogeny. *Proceedings of the National Academy of Sciences of the United States of America* 101, 10650-10654.
- Rumpler Y and Albignac R, 1972. Cytogenetic study of the endemic Malagasy lemurs subfamily Cheirogaleinae Gregory 1915. *American Journal of Physical Anthropology* 38: 261-264.
- Rumpler Y, Crovella S, and Montagnon D, 1994. Systematic relationships among Cheirogaleidae (Primates, Strepsirhini) determined from analysis of highly repeated DNA. *Folia Primatologica* 63, 149-155.
- Schäffler L and Kappeler P, 2014. Distribution and abundance of the world's smallest primate, *Microcebus berthae*, in Central Western Madagascar. *International Journal of Primatology* 35, 557-572.
- Schäffler L, Saborowski J, and Kappeler PM, ms. Agent-mediated spatial storage effect in heterogeneous habitat stabilizes competitive mouse lemur coexistence in Menabe Central, Western Madagascar.
- Scheumann M, Zimmermann E, and Deichsel G, 2007. Context-specific calls signal infants' needs in a strepsirrhine primate, the gray mouse lemur (*Microcebus murinus*). *Developmental Psychobiology* 49, 708-718.
- Schliehe-Diecks S, Eberle M, and Kappeler PM, 2012. Walk the line - dispersal movements of gray mouse lemurs (*Microcebus murinus*). *Behavioral Ecology and Sociobiology* 66, 1175-1185.
- Schmid J, 1999. Sex-specific differences in activity patterns and fattening in the gray mouse lemur (*Microcebus murinus*) in Madagascar. *Journal of Mammalogy* 80, 749-757.
- Schmid J and Kappeler PM, 1994. Sympatric mouse lemurs (*Microcebus* spp.) in western Madagascar. *Folia Primatologica* 63, 162-170.
- Schmid J and Kappeler PM, 1998. Fluctuating sexual dimorphism and differential hibernation by sex in a primate, the gray mouse lemur (*Microcebus murinus*). *Behavioral Ecology and Sociobiology* 43, 125-132.
- Schmid J, Ruf T, and Heldmaier G, 2000. Metabolism and temperature regulation during daily torpor in the smallest primate, the pygmy mouse lemur (*Microcebus myoxinus*) in Madagascar. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology* 170, 59-68.

- Schwab D and Ganzhorn JU, 2004. Distribution, population structure and habitat use of *Microcebus berthae* compared to those of other sympatric cheirogaleids. *International Journal of Primatology* 25, 307-330.
- Seehausen O and Butlin RK and Keller I and Wagner CE and Boughman JW and Hohenlohe PA and Peichel CL and Saetre GP and Bank C and Brannstrom A et al., 2014. Genomics and the origin of species. *Nature Reviews Genetics* 15, 176-192.
- Sehen L, Goetze D, Rajeriarison C, Roger E, Thoren S, and Radespiel U, 2010. Structural and floristic traits of habitats with differing relative abundance of the lemurs *Microcebus murinus* and *M. ravelobensis* in Northwestern Madagascar. *Ecotropica* 16, 15-30.
- Shaffer HB and Thomson RC, 2007. Delimiting species in recent radiations. *Systematic Biology* 56, 896-906.
- Simpson GG. 1961. *Principles of Animal Taxonomy*. Columbia University Press, New York.
- Sommer, S. et al. (2014). Maintaining microendemic primate species along an environmental gradient - parasites as drivers for species differentiation. *Ecology and Evolution* 4(24): 4751-4765.
- Springer MS and Meredith RW and Gatesy J and Emerling CA and Park J and Rabosky DL and Stadler T and Steiner C and Ryder OA and Janecka JE et al., 2012. Macroevolutionary dynamics and historical biogeography of primate diversification inferred from a species supermatrix. *PLoS One* 7, e49521.
- Swofford DL. 1990. *PAUP: Phylogenetic Analysis Using Parsimony*. Illinois Natural History Survey, Champaign, Illinois.
- Tattersall I, 2007. Madagascar's lemurs: Cryptic diversity or taxonomic inflation? *Evolutionary Anthropology* 16, 12-23.
- Terrien J, Ambid L, Nibbelink M, Saint-Charles A, and Aujard F, 2010a. Non-shivering thermogenesis activation and maintenance in the aging gray mouse lemur (*Microcebus murinus*). *Experimental Gerontology* 45, 442-448.
- Terrien J, Perret M, and Aujard F, 2010b. Gender markedly modulates behavioral thermoregulation in a non-human primate species, the mouse lemur (*Microcebus murinus*). *Physiology and Behavior* 101, 469-473.
- Thiele D, Razafimahatratra E, and Hapke A, 2013.. Discrepant partitioning of genetic diversity in mouse lemurs and dwarf lemurs – Biological reality or taxonomic bias? *Molecular Phylogenetics and Evolution* 69, 593-609.
- Thoren S, Linnenbrink M, and Radespiel U, 2011a. Different competitive potential in two coexisting mouse lemur species in Northwestern Madagascar *American Journal of Physical Anthropology* 145, 156-162.
- Thoren S, Quietzsch F, Schwochow D, Sehen L, Meusel C, Meares K, and Radespiel U, 2011b. Seasonal changes in feeding ecology and activity patterns of two sympatric mouse lemur species, the Gray Mouse Lemur (*Microcebus murinus*) and the Golden-brown Mouse Lemur (*M. ravelobensis*), in Northwestern Madagascar. *International Journal of Primatology* 32, 566-586.
- Weisrock DW, Rasoloarison RM, Fiorentino I, Ralison JM, Goodman SM, Kappeler PM, and Yoder AD, 2010. Delimiting species without nuclear monophyly in Madagascar's mouse lemurs. *PLoS One* 5, e9883.
- Weisrock DW, Smith SD, Chan LM, Biebow K, Kappeler PM, and Yoder AD, 2012. Concatenation and concordance in the reconstruction of mouse lemur phylogeny: an empirical demonstration of the effect of allele sampling in phylogenetics. *Molecular Biology and Evolution* 29, 1615-1630.

- Wiens JJ and Hollingsworth BD, 2000. War of the iguanas: conflicting molecular and morphological phylogenies and long-branch attraction in iguanid lizards. *Systematic Biology* 49, 143-159.
- Yang ZH and Yoder AD, 2003. Comparison of likelihood and Bayesian methods for estimating divergence times using multiple gene loci and calibration points, with application to a radiation of cute-looking mouse lemur species. *Systematic Biology* 52, 705-716.
- Yoder AD, 2013. The lemur revolution starts now: The genomic coming of age for a nonmodel organism. *Molecular Phylogenetics and Evolution* 66, 442-452.
- Yoder AD, 2014. Gene flow happens. *Evolutionary Anthropology* 23, 15-17.
- Yoder AD, Burns MM, and Genin F, 2002. Molecular evidence of reproductive isolation in sympatric sibling species of mouse lemurs. *International Journal of Primatology* 23, 1335-1343.
- Yoder AD and Chan LM and dos Reis M and Larsen PA and Campbell CR and Rasoloarison R and Barrett M and Roos C and Kappeler P and Bielawski J et al., 2014. Molecular evolutionary characterization of a V1R subfamily unique to strepsirrhine primates. *Genome Biology and Evolution* 6, 213-227.
- Yoder AD and Olson LE and Hanley C and Heckman KL and Rasoloarison R and Russell AL and Ranivo J and Soarimalala V and Karanth KP and Raselimanana AP et al., 2005. A multidimensional approach for detecting species patterns in Malagasy vertebrates. *Proceedings of the National Academy of Sciences of the United States of America* 102, 6587-6594.
- Yoder AD, Rasoloarison RM, Goodman SM, Irwin JA, Atsalis S, Ravosa MJ, and Ganzhorn JU, 2000. Remarkable species diversity in Malagasy mouse lemurs (primates, *Microcebus*). *Proceedings of the National Academy of Sciences of the United States of America* 97, 11325-11330.
- Zimmermann E, Cepok S, Rakotoarison N, Zietemann V, and Radespiel U, 1998. Sympatric mouse lemurs in north-west Madagascar: a new rufous mouse lemur species (*Microcebus ravelobensis*). *Folia Primatologica* 69, 106-114.
- Zimmermann E and Radespiel U, 2014. Species concepts, diversity, and evolution in primates: lessons to be learned from mouse lemurs. *Evolutionary Anthropology* 23, 11-14.



**Figure 1.** A generalized phylogeny for the Cheirogaleidae. Relationships among genera represent a consensus across multiple phylogenetic studies. Branches within multi-species genera are collapsed for simplicity, with clade size proportional to taxonomic diversity. Branch lengths are not proportional to time due to a lack of divergence time estimates for nodes involving *Allocebus* and *Phaner*. Mean estimated divergence times are presented for some nodes (Yang and Yoder, 2003; Yoder and Yang, 2004; Thiele et al., 2013). The dashed line highlights the fact that, in the multilocus study of Weisrock et al. (2012), the number of gene trees that support the *Mirza-Microcebus* clade is roughly similar to the number of gene trees supporting an alternative placement of *Allocebus* and *Microcebus* in a clade. In contrast, all remaining branches received support from the majority of sampled loci.



**Figure 2.** A phylogeny depicting our current best understanding of phylogenetic relationships within *Microcebus*. As the figure indicated, considerable uncertainty remains regarding the interrelationships among mouse lemur species. Branches are scaled to be proportional to time.



Table 1 Evidence for and history of taxonomic revisions to the genus *Microcebus* (mouse lemurs)

Latin binomial	Common name	Original evidence	Synonyms/Revisions	Publication
<i>M. murinus</i>	Gray mouse lemur	morphology		Miller (1777)
<i>M. rufus</i>	Brown mouse lemur	morphology	<i>M. smithii</i> (Gray, 1842)	Geoffroy (1834)
<i>M. myoxinus</i>	Pygmy mouse lemur	morphology	(Peters, 1852)	Schmid & Kappeler (1994)
<i>M. ravelobensis</i>	Golden-brown mouse lemur	morphology		Zimmerman et al. (1998)
<i>M. tavaratra</i>	Northern rufous mouse lemur	morphology		Rasoloarison et al. (2000)
<i>M. sambariensis</i>	Sambirano mouse lemur	morphology		Rasoloarison et al. (2000)
<i>M. griseorufus</i>	Reddish-grey mouse lemur	morphology	Kollman (1910)	Rasoloarison et al. (2000)
<i>M. berthae</i>	Madame Berthe's mouse lemur	morphology	<i>M. myoxinus</i> (Schmid & Kappeler, 1994))	Rasoloarison et al. (2000)
<i>M. griseorus</i>		morphology		Rasoloarison et al. (2000)
<i>M. lehilahytsara</i>	Goodman's mouse lemur	morphology; mtDNA		Roos & Kappeler (2005)
<i>M. mittermeieri</i>	Mittermeier's mouse lemur	morphology; mtDNA		Louis et al. (2006)
<i>M. jollyae</i>	Jolly's mouse lemur	morphology; mtDNA		Louis et al. (2006)
<i>M. simmonsii</i>	Simmons' mouse lemur	morphology; mtDNA		Louis et al. (2006)
<i>M. mampiratra</i>	Claire's mouse lemur	morphology; mtDNA	<i>M. lokobensis</i> (Olivieri et al., 2007)	Andriantompohavana et al. (2006)
<i>M. margotmarshae</i>	Margot Marsh's mouse lemur	morphology; mtDNA		Andriantompohavana et al. (2006)
<i>M. bongolavensis</i>	Bongolava mouse lemur	morphology; mtDNA		Olivieri et al. (2007)
<i>M. danfossi</i>	Danfoss' mouse lemur	morphology; mtDNA		Olivieri et al. (2007)
<i>M. lokobensis</i>	Lokobe mouse lemur	morphology; mtDNA	<i>M. mampiratra</i> (Andriantompohavana et al., 2006)	Olivieri et al. (2007)
<i>M. arnholdi</i>	Arnhold's mouse lemur	morphology; mtDNA		Louis et al. (2008)

<i>M. spp.</i>		morphology; mtDNA		Radespiel et al. (2008)
<i>M. macarthurii</i>	MacArthur's mouse lemur	morphology; mtDNA		Radespiel et al. (2008)
<i>M. gerpi</i>	GERP's mouse lemur	morphology; mtDNA		Radespiel et al. (2012)
<i>M. marohitra</i>	Marohitra mouse lemur	morphology; mtDNA; nDNA		Rasoloarison et al. (2013)
<i>M. tanosi</i>	Anosy mouse lemur	morphology; mtDNA; nDNA		Rasoloarison et al. (2013)

**Note:** All species descriptions take geographic distributions into account as evidence for species designation.

Table 2 Evidence for and history of taxonomic revisions to the genus *Cheirogaleus* (dwarf lemurs)

<b>Latin binomial</b>	<b>Common name</b>	<b>Original evidence</b>	<b>Publication</b>
<i>C. medius</i>	fat-tailed dwarf lemur	morphology	Saint-Hilaire (1812)
<i>C. adipicaudatus</i>	southern at-tailed dwarf lemur	morphology	Grandidier (1868)
<i>C. major</i>	greater dwarf lemur	morphology	Saint-Hilaire (1812)
<i>C. crossleyi</i>	furry-eared dwarf lemur	morphology	Grandidier (1870)
<i>C. sibreei</i>	Sibree's dwarf lemur	morphology	Forsyth Major (1896)
<i>C. ravus</i>	greater iron gray dwarf lemur	morphology	Groves (2000)
<i>C. minusculus</i>	lesser iron gray dwarf lemur	morphology	Groves (2000)
<i>C. lavasoensis</i>	Lavaso dwarf lemur	morphology; mtDNA; nDNA	Thiele et al. (2013)

**Note:** All species descriptions take geographic distributions into account as evidence for species designation.