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

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## Introduction

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.

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 1.1. 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 interspecific relationships within the various genera, while leaving the "skeleton" of the

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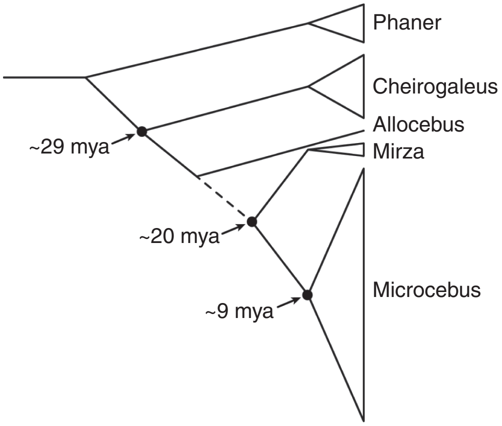

**Figure 1.1** A generalized phylogeny for the Cheirogaleidae. Relationships among genera represent a consensus across multiple phylogenetic studies. Branches within multispecies genera are collapsed for simplicity, with clade size proportional to taxonomic diversity. Branch lengths are not proportional 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.

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 (Yang and Yoder, 2003; Thiele *et al.*, 2013). 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), although with slightly younger age estimates with ~7 Mya for mouse lemurs and ~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.

Although it is true that several molecular phylogenetic studies have shown a weak relationship between *Phaner* and *Lepilemur* (e.g., Roos *et al.*, 2004; Springer *et al.*, 2012; Masters *et al.*, 2013), 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.*, 2009, 2010; Thiele *et al.*, 2013) and the mouse lemurs (Yoder *et al.*, 2000; Heckman *et al.*, 2006, 2007; Weisrock *et al.*, 2010) have shown complicated taxonomic expansions and rearrangements (Tables 1.1 and 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 (Moore, 1995; Knowles and Carstens, 2007; 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 composed of all other mouse lemur species including strong support for a distal subclade composed of *M. berthae*, *M. rufus*, and *M. myoxinus* (Figure 1.2; Heckman *et al.*, 2006, 2007; Weisrock *et al.*, 2010, 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 (Chapter 2) gives a comprehensive summary of the finest details of cheirogaleid taxonomy, leaving little need for us to cover the same ground. Rather, we examine here 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 multilocus 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 multilocus 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.

**Table 1.1** Evidence for and history of taxonomic revisions to the genus *Microcebus* (mouse lemurs).

| Latin binomial | Common name | Original evidence | Synonyms/Revisions | Publication |
|---|---|---|---|---|
| *M. murinus* | Gray mouse lemur | Morphology | | Miller (1777) |
| *M. rufus* | Brown mouse lemur | Morphology | *M. smithii* (Gray, 1842) | Geoffroy (1834) |
| *M. myoxinus* | Pygmy mouse lemur | Morphology | (Peters, 1852) | Schmid and Kappeler (1994) |
| *M. ravelobensis* | Golden-brown mouse lemur | Morphology | | Zimmermann *et al.* (1998) |
| *M. tavaratra* | Northern rufous mouse lemur | Morphology | | Rasoloarison *et al.* (2000) |
| *M. sambiranensis* | Sambirano mouse lemur | Morphology | | Rasoloarison *et al.* (2000) |
| *M. griseorufus* | Reddish-gray mouse lemur | Morphology | Kollman (1910) | Rasoloarison *et al.* (2000) |
| *M. berthae* | Madame Berthe's mouse lemur | Morphology | *M. myoxinus* (Schmid and Kappeler, 1994) | Rasoloarison *et al.* (2000) |
| *M. griseorufus* | | Morphology | | Rasoloarison *et al.* (2000) |
| *M. lehilahytsara* | Goodman's mouse lemur | Morphology; mtDNA | | Kappeler *et al.* (2005) |
| *M. mittermeieri* | Mittermeier's mouse lemur | Morphology; mtDNA | | Louis *et al.* (2006) |
| *M. jollyae* | Jolly's mouse lemur | Morphology; mtDNA | | Louis *et al.* (2006) |
| *M. simmonsi* | Simmons' mouse lemur | Morphology; mtDNA | | Louis *et al.* (2006) |
| *M. mamiratra* | Claire's mouse lemur | Morphology; mtDNA | *M. lokobensis* (Olivieri *et al.*, 2007) | Andriantompohavana *et al.* (2006) |
| *M. margotmarshae* | Margot Marsh's mouse lemur | Morphology; mtDNA | | Andriantompohavana *et al.* (2006) |
| *M. bongolavensis* | Bongolava mouse lemur | Morphology; mtDNA | | Olivieri *et al.* (2007) |
| *M. danfossi* | Danfoss' mouse lemur | Morphology; mtDNA | | Olivieri *et al.* (2007) |
| *M. lokobensis* | Lokobe mouse lemur | Morphology; mtDNA | *M. mamiratra* (Andriantompohavana *et al.*, 2006) | Olivieri *et al.* (2007) |
| *M. arnholdi* | Arnhold's mouse lemur | Morphology; mtDNA | | Louis *et al.* (2008) |
| *Microcebus* spp. | | Morphology; mtDNA | | Radespiel *et al.* (2008) |
| *M. macarthurii* | MacArthur's mouse lemur | Morphology; mtDNA | | Radespiel *et al.* (2008) |
| *M. gerpi* | Gerp's mouse lemur | Morphology; mtDNA | | Radespiel *et al.* (2012) |
| *M. marohita* | Marohitra mouse lemur | Morphology; mtDNA; nDNA | | Rasoloarison *et al.* (2013) |
| *M. tanosi* | 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 1.2** Evidence for and history of taxonomic revisions to the genus *Cheirogaleus* (dwarf lemurs).

| Latin binomial | Common name | Original evidence | Publication |
|---|---|---|---|
| *C. medius* | Fat-tailed dwarf lemur | Morphology | Saint-Hilaire (1812) |
| *C. adipicaudatus* | Southern fat-tailed dwarf lemur | Morphology | Grandidier (1868) |
| *C. major* | Greater dwarf lemur | Morphology | Saint-Hilaire (1812) |
| *C. crossleyi* | Furry-eared dwarf lemur | Morphology | Grandidier (1870) |
| *C. sibreei* | Sibree's dwarf lemur | Morphology | Forsyth Major (1896) |
| *C. ravus* | Greater iron gray dwarf lemur | Morphology | Groves (2000) |
| *C. minusculus* | Lesser iron gray dwarf lemur | Morphology | Groves (2000) |
| *C. lavasoensis* | Lavasoa dwarf lemur | Morphology; mtDNA; nDNA | Thiele *et al.* (2013) |

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

## 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 rainforest 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*, although 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 2 species to one containing at least 20

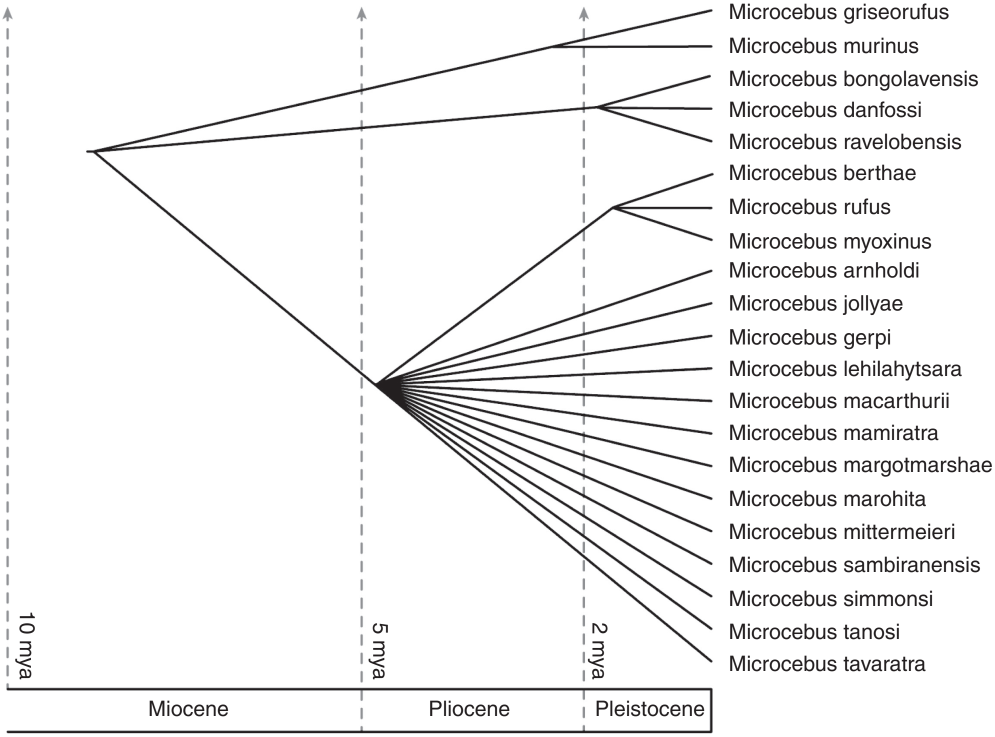

**Figure 1.2** A phylogeny depicting our current best understanding of phylogenetic relationships within *Microcebus*. As the figure indicates, considerable uncertainty remains regarding the interrelationships among mouse lemur species. Branches are scaled to be proportional to time.

species (Kappeler *et al.*, 2005; Andriantompohavana *et al.*, 2006; Louis *et al.*, 2006, 2008; Olivieri *et al.*, 2007; Radespiel *et al.*, 2008, 2012; Rasoloarison *et al.*, 2013), and with many of these based primarily if not entirely on small DNA data sets.

Not surprisingly, there has been resistence 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. 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. Although 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-descendant 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, although 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' view, the lack of visual information concomitant with a noctunal lifestyle will be compensated by other means of interindividual 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' 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 complicatedly, 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 coexist sympatrically (Radespiel *et al.*, 2006; Dammhahn and Kappeler, 2008b; Rakotondranary and

Ganzhorn 2011; Rakotondranary *et al.*, 2011a, 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 (although 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; Scheumann *et al.*, 2007; Braune *et al.*, 2008; Leliveld *et al.*, 2011; Hohenbrink *et al.*, 2012; 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, Chapter 26).

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 26). 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 and Kappeler, 1998; Schmid, 1999; Terrien *et al.*, 2010a, 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 although it remains to be confirmed, there is the potential for overlap with *M. tavaratra*, *M. sambiranensis*, 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 (Genin, 2008; Bohr *et al.*, 2011; 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 (Genin, 2008). Another long-term study showed that *M. 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), so 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, although 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 and 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 ($\delta^{15}$N), but not in basal resources ($\delta^{13}$C; Dammhahn and Kappeler, 2010, 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 intraspecific 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.*, 2015). 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). 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, although 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. However, 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 petite 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., Yoder *et al.*, 2000, 2005; Heckman *et al.*, 2006; Weisrock *et al.*, 2010; Markolf *et al.*, 2011; 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 study of Thiele *et al.* (2013). 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., Yoder *et al.*, 2000; Weisrock *et al.*, 2010; Thiele *et al.*, 2013). 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.

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