

## Chapter 2

# Species-Level Diversity Among Malagasy Lemurs

Ian Tattersall

**Abstract** The number of Malagasy lemur species recognized has skyrocketed over the past quarter-century, from 22 in 1982 to almost 100 today. This is largely a result of the wholesale application of phylogenetic species concepts and the elimination of subspecies from the lemur fauna. I argue that “silver-bullet” approaches to species recognition ignore real biological complexity, and that species are best recognized through weighing *all* available evidence including that furnished by morphology, molecules, behavior, communication, demography, and distributions. Only about 50 lemur species are fully justified by current evidence, although this is certainly a conservative estimate.

**Resume** Le nombre d'espèces de Lémuriens reconnus à Madagascar a explosé au cours du dernier quart de siècle, passant de 22 en 1982 à presque 100 aujourd'hui. Ceci découle de l'application sans limite du concept “d'espèce phylogénétique”, et de l'élimination de toutes les sous-espèces de lémuriens. Je conteste cette approche réductrice de l'espèce, qui ignore la complexité du vivant, et j'affirme que les espèces sont mieux reconnues si *tous* les caractères identifiés sont pris en compte, combinant les approches morphologiques, moléculaires, comportementales (incluant les systèmes de communication), démographiques et géographiques. Une cinquantaine d'espèces de lémuriens seulement apparaît clairement justifiée, bien que cette estimation soit presque certainement conservatrice.

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Introduction

Nobody doubts that Madagascar’s lemur populations are coming under increasing pressure, and that a large part of the island’s fauna has already disappeared (Godfrey et al. 2006). It is thus cause for celebration when any new and distinctive lemur population is located, but I still question whether more is always merrier for lemur species.

In 1982 I published (Tattersall 1982) a consensus classification of the lemurs for that time (Table 2.1). This consensus had endured in its essentials since Ernst

**Table 2.1** Mittermeier et al. (2006, 2010) classifications of the Malagasy lemurs, annotated to show contrasts with Tattersall’s (1982) classification

Tattersall (1982)	Mittermeier et al. (2006)	Mittermeier et al. (2010)
Family Cheirogaleidae		
Genus <i>Microcebus</i>		
		<i>M. arnholdi</i>
	<i>M. berthae</i>	<i>M. berthae</i>
		<i>M. bongolavensis</i>
		<i>M. danfossi</i>
	<i>M. griseorufus</i>	<i>M. griseorufus</i>
		<i>M. jollyae</i>
	<i>M. lehilahytsara</i>	<i>M. lehilahytsara</i>
		<i>M. macarthurii</i>
		<i>M. mamiatra</i>
		<i>M. margotmarshae</i>
		<i>M. mittermeieri</i>
<i>M. murinus</i>	<i>M. murinus</i>	<i>M. murinus</i>
	<i>M. myoxinus</i>	<i>M. myoxinus</i>
	<i>M. ravelobensis</i>	<i>M. ravelobensis</i>
<i>M. rufus</i>	<i>M. rufus</i>	<i>M. rufus</i>
	<i>M. sambiranensis</i>	<i>M. sambiranensis</i>
		<i>M. simmonsii</i>
	<i>M. tavaratra</i>	<i>M. tavaratra</i>
Genus <i>Allocebus</i>		
<i>A. trichotis</i>	<i>A. trichotis</i>	<i>A. trichotis</i>
Genus <i>Mirza</i>		
<i>M. coquereli</i>	<i>M. coquereli</i>	<i>M. coquereli</i>
	<i>M. zaza</i>	<i>M. zaza</i>
Genus <i>Cheirogaleus</i>		
	<i>C. adipicaudatus</i>	
	<i>C. crossleyi</i>	<i>C. crossleyi</i>
<i>C. major</i>	<i>C. major</i>	<i>C. major</i>
<i>C. medius</i>	<i>C. medius</i>	<i>C. medius</i>
	<i>C. minusculus</i>	<i>C. minusculus</i>
	<i>C. ravus</i>	
	<i>C. sibreei</i>	<i>C. sibreei</i>

(continued)

**Table 2.1** (continued)

Tattersall (1982)	Mittermeier et al. (2006)	Mittermeier et al. (2010)
Genus <i>Phaner</i>		
<i>P. furcifer</i>	<i>P. furcifer</i> <i>P. electromontis</i> <i>P. pallescens</i> <i>P. parienti</i>	<i>P. furcifer</i> <i>P. electromontis</i> <i>P. pallescens</i> <i>P. parienti</i>
Family Lepilemuridae		
Genus <i>Lepilemur</i>		
		<i>L. aeeclis</i> <i>L. ahmansonii</i> <i>L. ankaranensis</i> <i>L. ahmansonorum</i> <i>L. betsileo</i> <i>L. dorsalis</i> <i>L. edwardsi</i> <i>L. fleuretae</i> <i>L. grewcockorum</i> <i>L. hollandrum</i> <i>L. hubbardorum</i> <i>L. jamerosum</i> <i>L. leucopus</i> <i>L. microdon</i> <i>L. mittermeieri</i> <i>L. milanoii</i> <i>L. mustelinus</i> <i>L. otto</i> <i>L. petteri</i> <i>L. randrianasoloi</i> <i>L. ruficaudatus</i> <i>L. sahamalazensis</i> <i>L. scottorum</i> <i>L. septentrionalis</i> <i>L. seali</i> <i>L. tymerlachsonorum</i> <i>L. wrighti</i>
	<i>L. ankaranensis</i>	
	<i>L. dorsalis</i> <sup>a</sup> <i>L. edwardsi</i> <sup>a</sup>	
	<i>L. leucopus</i> <sup>a</sup> <i>L. microdon</i>	
<i>L. mustelinus</i>	<i>L. mustelinus</i> <sup>a</sup>	
	<i>L. ruficaudatus</i> <sup>a</sup>	
	<i>L. septentrionalis</i> <sup>a</sup>	
Family Lemuridae		
Genus <i>Hapalemur</i>		
	<i>H. alaotrensis</i> <sup>a</sup> <i>H. aureus</i> <i>H. gilberti</i> <i>H. griseus</i> <sup>a</sup> <i>H. meridionalis</i> <i>H. occidentalis</i> <sup>a</sup>	<i>H. alaotrensis</i> <i>H. aureus</i>  <i>H. griseus</i> <i>H. meridionalis</i> <i>H. occidentalis</i>
Genus <i>Prolemur</i> <sup>b</sup>	<i>P. simus</i>	<i>P. simus</i>
Genus <i>Lemur</i>		
<i>L. catta</i>	<i>L. catta</i>	<i>L. catta</i>

(continued)

**Table 2.1** (continued)

Tattersall (1982)	Mittermeier et al. (2006)	Mittermeier et al. (2010)
Genus <i>Eulemur</i> <sup>b</sup>		
	<i>E. albifrons</i> <sup>a</sup>	
	<i>E. albocollaris</i> <sup>a</sup>	<i>E. albocollaris</i>
		<i>E. cinereiceps</i>
	<i>E. collaris</i> <sup>a</sup>	<i>E. collaris</i>
<i>E. coronatus</i>	<i>E. coronatus</i>	<i>E. coronatus</i>
		<i>E. flavifrons</i> <sup>a</sup>
<i>E. f. fulvus</i>	<i>E. fulvus</i> <sup>a</sup>	<i>E. fulvus</i>
<i>E. macaco</i>	<i>E. macaco</i>	<i>E. macaco</i>
<i>E. mongoz</i>	<i>E. mongoz</i>	<i>E. mongoz</i>
<i>E. rubriventer</i>	<i>E. rubriventer</i>	<i>E. rubriventer</i>
		<i>E. rufifrons</i>
	<i>E. rufus</i> <sup>a</sup>	<i>E. rufus</i>
	<i>E. sanfordi</i> <sup>a</sup>	<i>E. sanfordi</i>
Genus <i>Varecia</i>		
<i>V. v. variegata</i>	<i>V. variegata</i>	<i>V. variegata</i>
<i>V. v. Rubra</i>	<i>V. rubra</i>	<i>V. rubra</i>
Family Indriidae		
Genus <i>Avahi</i>		
		<i>A. betsileo</i>
	<i>A. cleesei</i>	<i>A. cleesei</i>
<i>A. laniger</i>	<i>A. laniger</i> <sup>a</sup>	<i>A. laniger</i>
		<i>A. meridionalis</i>
		<i>A. mooreorum</i>
	<i>A. occidentalis</i> <sup>a</sup>	<i>A. occidentalis</i>
		<i>A. peyrierasi</i>
		<i>A. ramanantsoavanai</i>
	<i>A. unicolor</i>	<i>A. unicolor</i>
Genus <i>Propithecus</i>		
<i>P.d. candidus</i>	<i>P. candidus</i> <sup>a</sup>	<i>P. candidus</i>
	<i>P. coquereli</i> <sup>a</sup>	<i>P. coquereli</i>
	<i>P. coronatus</i> <sup>a</sup>	<i>P. coronatus</i>
	<i>P. deckenii</i> <sup>a</sup>	<i>P. deckenii</i>
<i>P. d. diadema</i>	<i>P. diadema</i> <sup>a</sup>	<i>P. diadema</i>
	<i>P. edwardsi</i> <sup>a</sup>	<i>P. edwardsi</i>
<i>P. d. perrieri</i>	<i>P. perrieri</i> <sup>a</sup>	<i>P. perrieri</i>
	<i>P. tattersalli</i>	<i>P. tattersalli</i>
<i>P. v. verreauxi</i>	<i>P. verreauxi</i> <sup>a</sup>	<i>P. verreauxi</i>
Genus <i>Indri</i>		
<i>I. indri</i>	<i>I. indri</i>	<i>I. indri</i>
Family Daubentoniidae		
Genus <i>Daubentonia</i>		
<i>D. madagascariensis</i>	<i>D. madagascariensis</i>	<i>D. madagascariensis</i>

Table enlarged and modified from Tattersall (2007)

<sup>a</sup>Recognized as subspecies in Tattersall (1982)<sup>b</sup>Genus not recognized in Tattersall (1982)

Schwarz's (1931) revision recognized 22 living lemur species in Madagascar. Several were strongly polytypic (with a total of 38 species/subspecies) and most were at least mildly so. The only major debate in lemur species systematics was whether the discreetly colored nocturnal genus *Lepilemur* contained one polytypic species or several monotypic ones. I opted for a single *Lepilemur* species with six subspecies. So much for the lumpers' fate. There are now 24 *Lepilemur* species, with no upper limit in sight. *Lepilemurs* are not alone; since 1982, the overall number of lemur species has skyrocketed. It had risen to 83 when Mittermeier et al. (2006) published the 2nd edition of their field guide and has now surpassed 100 (Mittermeier et al. 2010; see Table 2.1 for the state of play as this goes to press). Yet, remarkably, not many formerly unknown lemur populations have been discovered since 1982.

What *has* happened is that many previously known lemur communities are now considerably better known; and there is, without question, a lot more specific diversity than we suspected. Yet it is also true that much of the spectacular increase in species number has come at the price of the almost total elimination of subspecies, i.e., of morphologically and/or chromatically recognizable and geographically discrete intraspecific variants. By some reckonings there are only three polytypic lemur species in Madagascar today—and these are polytypic only by dint of containing subspecies for which I was unable to find adequate justification in 1982.

## The Role of Local Populations

To anyone interested in evolutionary processes, this wholesale elimination of subspecies is disturbing, since subspecies are the indispensable cauldrons of innovation in evolution. Mechanisms of differentiation in primate populations are still poorly understood, but it is clearly routine for a widely distributed species to develop local variants in different parts of its range (Tattersall 1994). Indeed, across the spectrum of mammals, it is exceptional for local differentiation *not* to occur. It is also evident that natural selection drift must take place *within* local populations.

This is not to say that evolutionarily important triage takes place *only* at the intraspecific level, but it is differentiation *within* pre-existing species that potentiates the emergence of new, distinct lineages. Speciation is *not* simply a passive consequence of morphological divergence—although taxonomists would find it mightily convenient if it were, since it would make species recognition an easily quantifiable process. Some species undergo a huge amount of morphological differentiation without speciating, while in other cases one has to look closely to distinguish populations that have no evident reproductive interest in each other. The bottom line is that both speciation *and* morphological differentiation are essential for producing the patterns we see among living and fossil species, and both take place within local subunits of more widespread populations.

It might be argued that, in its splendid isolation, Madagascar's lemur fauna long ago achieved evolutionary equilibrium, and that its lack of subspecies reflects this. However, molecular estimates of divergence times among lemur populations argue

strongly against such a view. In fact, they indicate that the lemur fauna is actively diversifying—in which case the purported absence of subspecies on this huge land-mass is curious indeed. Further, I question whether more is merrier in the lemur species department not only because the multiplication of lemur species has far outstripped the discovery of new lemur populations but also because the spectacular increase in lemur species has been effected largely—though not entirely—by the wholesale application by many lemurologists of a particularly fundamentalist interpretation of Cracraft's (1989) phylogenetic species concept.

## Recognizing Species

By default, Cracraft's concept effectively eliminates subspecies as either biological or taxonomic units. Phylogenetic species are defined as the *minimal diagnosable units*—basically, any group you can recognize, even when presented with spotty evidence. But while in theory it simplifies matters for taxonomists, does this classificatory device really *mean* anything in terms of the way the luxuriant variety of nature is packaged? When we indulge in simple trait spotting, are we recognizing anything that is evolutionarily or biologically meaningful? The answer to these questions is no; and it is important because species are more than just the playthings of taxonomists. They are the primary actors in the evolutionary play. The adoption of the minimal diagnosability criterion has been justified on the basis of one arbitrary species definition; and any declarative definition of this kind must presuppose that species are straightforwardly definable entities. In one sense of course, they are. Species are the basic *kinds* of organisms, which corresponds to the intuitive way we interpret the world around us. Discontinuities are evident everywhere in nature, the larger ones corresponding neatly to the words—the discrete symbols—by which we categorize and explain our world. No one has any trouble telling a lion from a lobster from a mushroom. But as the categories get finer, the difficulties multiply, as witness the fact that there are at least 30 published definitions of species currently on offer.

In this regard we have not come very far since 1865, when Pierre Trémaux observed that “of definitions of species, there are as many as there are naturalists.” Those definitions just keep piling up; and the crux of the problem is that species are not essentialist “kinds” defined by immutable sets of attributes. They are neither monothetic nor polythetic trait-based sets. Individuals of the same species resemble each other because they belong to the same population, not the other way around. Most importantly, it is they themselves, not taxonomists, who decide who's who.

At higher levels in the taxonomic hierarchy, morphology rules. Above the species level, potential reproductive compatibility ceases to be an issue—which is one reason why it is easier to demarcate genera than species, and so on up the line. But the unavoidable reality remains that, for sexually reproducing organisms, the boundaries between natural “kinds” are ultimately reproductive; and, sadly from the taxonomist's point of view, among close relatives those reproductive lines may not be clearly drawn. The manifold problems we have in species recognition stem from

the fact that speciation is an observed *result* rather than a unitary *mechanism*. Many different factors can affect reproductive choices or outcomes at the behavioral, anatomical, developmental, transcriptional or genetic level, and the resulting discontinuities may be expressed very differently. All are not equally irreversible. Additionally reproductive barriers may be absolute or permeable, complicating things further: a few instances of mating among sympatric or parapatric forms may be meaningless in the long term.

These limitations apply equally to cohesional and exclusionary approaches to identifying independent reproductive or historical units. To tidy-minded taxonomists, the inherent messiness in nature's packaging is a nasty inconvenience, so, rather than acknowledge this awkward truth—which would force them to deal with it, or at least admit that it is intractable—taxonomists have sought other, more clear-cut, ways of recognizing species. Which explains why species concepts based on gene exchange are currently in disfavor—and why the criterion of simple diagnosability exerts such siren attraction.

On a practical level, species definitions have also proliferated because systematists work with different kinds of data. Given that this is a reality that will not disappear, perhaps we should remove ourselves from abstract arguments of species definition and focus on the *roles* of species in nature. This inevitably brings us to Ghiselin's (1974) perceptive characterization—not definition—of species as *individuals*. In Ghiselin's perspective, species are populations that have embarked on independent evolutionary histories. Such populations compete on the ecological stage, and either flourish, persist, or go extinct. Whatever their fates, they can no longer cease by absorption into a larger entity.

This means that at fine degrees of evolutionary relationship, *no* single intellectual silver bullet can demonstrate infallibly what is and is not a species. One or two mtDNA base substitutions will no more indicate two species, than an occasional instance of hybridization between close relatives will indicate only one. So we have but one alternative: to look simultaneously at *all* the available evidence. This places alpha taxonomists in much the same position as judges trying pornography cases. Judges may never have developed a satisfactory definition of pornography, but they claim to know it when they see it, and their rulings are justified by weighing all the evidence presented. In the case of taxonomy, this means considering structural or transcriptional genetic information; karyology; size and external morphology; reproductive and activity rhythms; internal structure; vocalizations; olfactory signals; geographical and ecological distributions; behaviors in parapatry or sympatry; phylogenetic relationships; indeed, any information that throws light on the animals' own take on their population limits.

## Implications for the Lemur Fauna

I recently reviewed the alpha systematics of Madagascar's lemurs (Tattersall 2007) and will not repeat the details here. I will, however, consider briefly a couple of cases, one diurnal and the other nocturnal.

Generally when diurnal forms spread and diversify, they form local populations that are distinguishable visually (Paterson 1980, 1985; Masters 1988; Masters and Spencer 1989). Several brown lemur populations that vary in coloration were described as separate species before being lumped by Schwarz (1931) into the species *Lemur fulvus*: a species now placed, with all “true” lemurs other than ringtails, in the genus *Eulemur*. Morphological and genetic information reconstruct *Eulemur* as a clade, with *E. fulvus* variants forming a subclade within it. Recent classifications (e.g., Mittermeier et al. 2006, 2010) have accorded the *fulvus* subspecies full species rank alongside the more established forms: *rubriventer*, *macaco*, *coronatus*, and *mongoz*. This has occurred despite indications that the *fulvus* radiation is “superimposed” phylogeographically on the older *Eulemur* one, and despite clear evidence of interfertility with the odd exception of the parapatric, and karyotypically distinct, *albicollaris* and *collaris*.

While visually differentiated and diagnosable, the *fulvus/albifrons/rufus/sanfordi* group appears to be a single entity. While each component is potentially a new species, there is as yet no evidence that the components have diverged irreversibly along their own historical trajectories. The appropriate tests of how the animals perceive their population limits have not been done. Happily, nothing prevents us from using these or any other infraspecific taxa as units of historical and biogeographic analysis; and indeed, if we insist on regarding all subspecies as full species, we limit our opportunities to study speciation processes.

Another example to mention briefly is the nocturnal genus *Microcebus*, in which for many years just two species were recognized: a gray, long-eared western form and a reddish, shorter-eared eastern one. Today the count is around 15 species, and rising (Table 2.1). While it has been clear for some time that systematic complexity among the cryptically colored mouse lemurs was greater than the two-species division suggests, it is less clear how many species there actually are. Many new species have been recognized principally on mtDNA criteria and, as elsewhere in the expanding lemur fauna, new species descriptions follow a stereotypical pattern, whereby a nondifferential description is made on the basis of external features of individuals obtained at a particular location, followed by a differential diagnosis based principally or purely on mtDNA characterizations and genetic distances derived therefrom.

Using sophisticated techniques, researchers have identified a set of molecular characters that seem—on limited sampling—to differentiate populations of mouse lemurs around Madagascar. But is that the same as identifying species? Quite honestly, no. It’s a good start; but without supporting evidence it is impossible to tell whether we have a large set of species, or a smaller set of species that varies geographically in a continuous manner, or a species divided into discrete local populations. Although many localities have been sampled, we do not know how these molecular variants sort over the wider distributions of the taxa involved. More significantly, local samples tend to be small, and may consist of closely related individuals. Without resort to biological information, we cannot conclude that these variants are indicative of speciation rather than of intraspecific diversification by locale.

There are clearly more *Microcebus* species in the Malagasy forests than we once believed. The venerable *M. murinus* occurs in sympatry with several recently proposed or resurrected species such as *M. ravelobensis*, *M. berthae*, and *M. myoxinus*,



from which it does seem to be ecologically differentiated (Schmid and Kappeler 1994; Zimmermann et al. 1998). Information of this kind provides far firmer justification for species distinction. A similar argument applies to *M. rufus* and *M. lehilahytsara*, and likely in other cases too. So I am not arguing here against mouse lemur species diversity, but rather that claims for species identity require more justification than simply the simple possession of an mtDNA marker or two. Species are much more than containers for genetic or chromatic novelties.

## A Plea

I hope I have not sounded unduly negative. It has been gratifying over past decades to see so many new discoveries in lemur diversity through the efforts of so many colleagues. On current evidence it appears (Tattersall 2007) that at least 50 lemur species—an almost 50% increase on the number recorded in 1982—may legitimately be recognized. More species are undoubtedly out there; but it is of little benefit to rush to recognize more than the full span of evidence will support. Much more needs to be learned and placed on record; and I hope that this volume replete with evidence of the vigor of ongoing lemur studies, will help inspire the collection of the data we need, and encourage more collaboration: gone is the time when molecular, morphological, demographic, ecological, communication, and behavioral studies could be carried out in isolation. For each local population, we need data on all these aspects if we are properly to understand the structure of diversity among Madagascar's lemurs.

Finally, at a time when lemur populations are under such pressure, every new piece of demographic information should be recognized as valuable by everybody. This includes journal editors, whether or not a new species is demonstrably involved—a factor that now seems to ease the route to publication. Rather than simply cataloging new genetic or morphological variants by allocating them reflexively to new species, we should be thinking more about the wider *roles* of the subjects of our study in the complex ecological and historical webs of which they form part. This would much better serve a mature and comprehensive appreciation of lemur diversity.

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Leaping Ahead

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