

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024

Number 3376, 26 pp., 4 figures, 2 tables

July 25, 2002

Do Ruffed Lemurs Form a Hybrid Zone? Distribution and Discovery of *Varecia*, with Systematic and Conservation Implications

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ABSTRACT

Since their discovery by Western explorers traveling to Madagascar in the 17th century, the ruffed lemurs have undergone numerous taxonomic revisions. During the 19th and 20th centuries, it was intermittently suggested that black-and-white and red ruffed lemurs hybridize in nature. Despite the fact that a natural hybrid zone has never been documented, this suggestion has played a large role in designating the two forms as subspecies of the single species *Varecia variegata*. Through a review and synthesis of historical documents, taxonomic literature, museum collections, menagerie and zoo records, recent survey work, genetic data, and vocalization data, we examine the evidence for a natural hybrid zone and suggest taxonomic revisions. Our work indicates a more extensive hybrid zone than previously suggested—but one in which hybridization is the exception rather than the rule. Furthermore, our findings warrant upgrading the black-and-white ruffed lemur and the red ruffed lemur from subspecies to full species, *Varecia variegata* (Kerr, 1792) and *Varecia rubra* (E. Geoffroy, 1812). Our results support the current captive breeding practices of U.S. and European zoos participating in the ruffed lemur “Species Survival Plan” and the “European Endangered Species Programme”. Lastly, and possibly most importantly, we can now set specific geographic priorities for conserving the habitat of these highly endangered lemurs in northern Madagascar.

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INTRODUCTION

The French explorers François Cauche (1651) and Etienne de Flacourt (1658) provided Westerners with the first descriptions of the Malagasy primate now commonly known as the “variegated” or “black-and-white ruffed” lemur. More than a century later, these animals were formally named *Lemur macaco variegatus* by Kerr (1792). A related red-and-black form, *Lemur ruber*, was named shortly afterward by E. Geoffroy (1812) and now goes by the common name of “red ruffed lemur”. Tremendous variability in coat color and pattern (see fig. 1), the ability of the black-and-white form to hybridize with the red form in captivity, and the relatively recent discovery of the unusual life history traits of both ruffed lemurs have subsequently spurred repeated taxonomic revisions. Currently the two color forms are generally classified as subspecies of the same species and are united within the genus *Varecia* Gray, 1863 in the strepsirhine primate family Lemuridae. The black-and-white form is usually known as *Varecia variegata variegata* and the red form as *Varecia variegata rubra*.

In his pathbreaking review of lemur systematics, Schwarz (1931) alluded to the existence of a natural hybrid zone between the two color forms north of the Bay of Antongil (northeastern Madagascar; see figs. 2 and 3), but he provided no direct evidence for such a zone. Documentation of such a natural hybrid zone would be of great biological interest in designating geographic priorities for habitat conservation, for captive management, and for lemur systematics generally. However, no recent surveys have located such a zone. The balance of evidence on published record so far rests on the somewhat slim foundation of a single hybrid specimen housed at the American Museum of Natural History which was collected 40 km NW of Maroantsetra by the Archbold expedition in 1930 (Rand, 1936; Tattersall, 1982; Buettner-Janusch and Tattersall, 1985), although various similarly puzzling specimens also exist elsewhere. In writing a review of the natural history of *Varecia*, Vasey (in press) was disinclined to broach the biological mys-

tery concerning a natural hybrid zone, and instead we try to solve this problem here. To assess whether a natural hybrid zone ever existed, we undertook a review and synthesis of historical documents, taxonomic literature, museum collections, menagerie and zoo records, and recent survey work. We also summarize recent genetic work on ruffed lemurs and previously published work on their vocalizations. These reviews suggest that hybridization in the wild probably occurred over a much larger area than previously thought, but that it is the exception rather than the rule. Only remnants of the hybrid zone habitat as it existed prior to human interference may remain, given the subsequent extensive habitat loss north of the Bay of Antongil. Alternatively, it is possible that a poorly documented variety or subspecies of ruffed lemur has virtually been lost, and that the so-called hybrids are remnants of this population; however, there is little substantiating evidence for this. In conservation terms, forest corridors are needed to connect *Varecia* populations across the watersheds north of the Bay of Antongil. Finally, the results of our review support upgrading both the black-and-white ruffed lemur and the red ruffed lemur to full species, *Varecia variegata* (Kerr, 1792) and *Varecia rubra* (E. Geoffroy 1812), as has also been suggested by Groves (2001). However, we are unable to follow Groves in promoting the pelage variants of the black-and-white species to subspecies status.

ABBREVIATIONS

| | |
|------|---------------------------------------------------------------|
| AMNH | American Museum of Natural History, New York |
| BMNH | British Museum of Natural History, London |
| DUPC | Duke University Primate Center, Durham, North Carolina |
| MCZ | Museum of Comparative Zoology, Cambridge, Massachusetts |
| MNHN | Muséum National d'Histoire Naturelle, Paris |
| RMNH | Rijksmuseum van Natuurlijke Historie, Leiden |
| USNM | United States National Museum (Smithsonian), Washington, D.C. |

NORMATIVE DESCRIPTIONS OF BLACK-AND-WHITE AND RED RUFFED LEMURS

Varecia is the largest-bodied genus of the primate family Lemuridae, possessing an especially long, luxuriant coat relative to other lemurs. Within this genus the sexes are more or less identical in body size and pelage coloration. Adult wild *Varecia* range in body mass from 2.6 to 4.1 kg (Vasey, in press). Both black-and-white and red forms possess black fur on the ventrum, tail, inner aspect of limbs, manus, pes, crown, forehead, and face. Surrounding the face and ears is a ruff of long fur: white in black-and-white ruffed lemurs and red or honey-blond in red ruffed lemurs. But consistency in coat color and pattern ends there, particularly in the black-and-white variant: *Varecia* was aptly named the “variegated” lemur. In a review published two decades ago, one of us (Tattersall, 1982) recognized four principal variants among the black-and-white ruffed lemurs (shown in schematic form in fig. 1). Three of these had already been established in the mid-nineteenth-century account of I. Geoffroy (1851), who elaborated three varieties of his *Lemur varius* (“variétés” a, b, and c). These varieties correspond, respectively, to the forms represented by Kerr’s *Lemur macaco variegatus* (Kerr, 1792), Osman Hill’s *Lemur variegatus editorum* (Hill, 1953), and Smith’s *Prosimia subcincta* (Smith, 1833). For other equivalences, see Tattersall (1982), who also divided variety b (*editorum*) into two subvariants (b1 and b2). Figure 1 displays the basic pelage coloration differences on which the four resulting varieties are based (see also below).

A thorough examination of almost all available museum black-and-white specimens indicates the presence of more pelage-color variation than is reflected in these four simple descriptions: an unpublished review by one of us (I.T.) several years ago revealed that as many as 10 repeated variants could be recognized in museum collections. However, especially in view of the regrettably little that we know of geographic distributions (see fig. 2), an infinite multiplication of formalized variants hardly seems desirable or even possible. Examination of the available

evidence of coat pattern among black-and-white ruffed lemurs contradicts the notion of a simple north–south cline, although the modest trend noted by Petter et al. (1977) and Tattersall (1982) toward a reduction in the overall amount of black in the pelage in favor of white toward the south does seem to hold in a general way. Nonetheless, there is some notable geographic randomization of pelage pattern distribution (see fig. 2 and below). Analysis of the matter is complicated by the fact that while ruffed lemur skins are quite well represented in museum collections, locality records are not. Moreover, reliable field reports are sparse. However, there are clearly broad areas within which more than one variant is to be found (see fig. 2 and below). We are thus unable to concur with Groves (2001) that at least three distinct subspecies of *Varecia variegata* are to be recognized.

To summarize the data presented in figure 1, in lighter forms (e.g., the *variegata* variety), the dorsal fur is white with black restricted to the shoulder, the upper arm to the elbow, and front of the thigh (color plate); whereas in darker forms known from the north (e.g., the *subcincta* variety), the dorsum is mainly black with two variably thick bands of white fur—one band encircles the torso and sometimes extends longitudinally toward the nape of the neck, and the other band extends across the rump, down the posterior aspect of the thigh, and onto the lateral surface of the lower leg. In another variety (*editorum*), the black shoulder patches extend posteriorly onto the flanks and meet midsagittally, forming a black mantle across the back and shoulders. These various coat patterns have been illustrated frequently (see Historical Documents, Taxonomy, and Illustrations). Indistinct white rings on the tail, said to resemble those of the ring-tailed lemur, have also been noted in museum specimens collected by J.-P. Audebert (Handfest, 1968, cited in Ceska et al., 1992) and in living wild animals (Evans et al., 1993–1994). Dark regions are not always pure black, but may grade into silver, light brown, or dark brown.

While the variegated coat of the black-and-white ruffed lemur has long been known, the pied pelage of the red ruffed le-

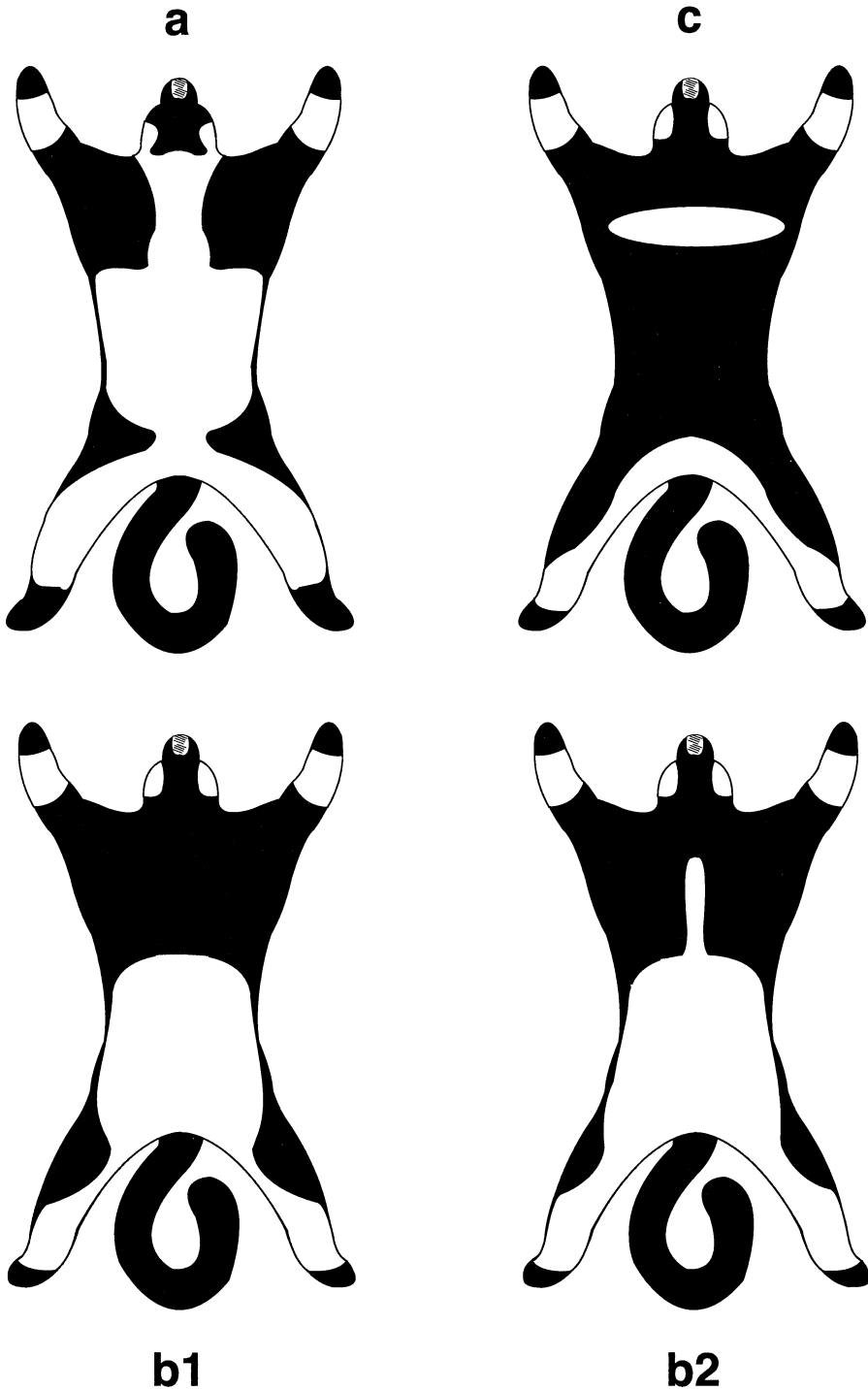


Fig. 1. Schematic dorsal view of the four pelage variants recognized here among black-and-white ruffed lemurs. Demarcation between black and white pelage areas is generally but not invariably sharp; black noses are usually frosted.

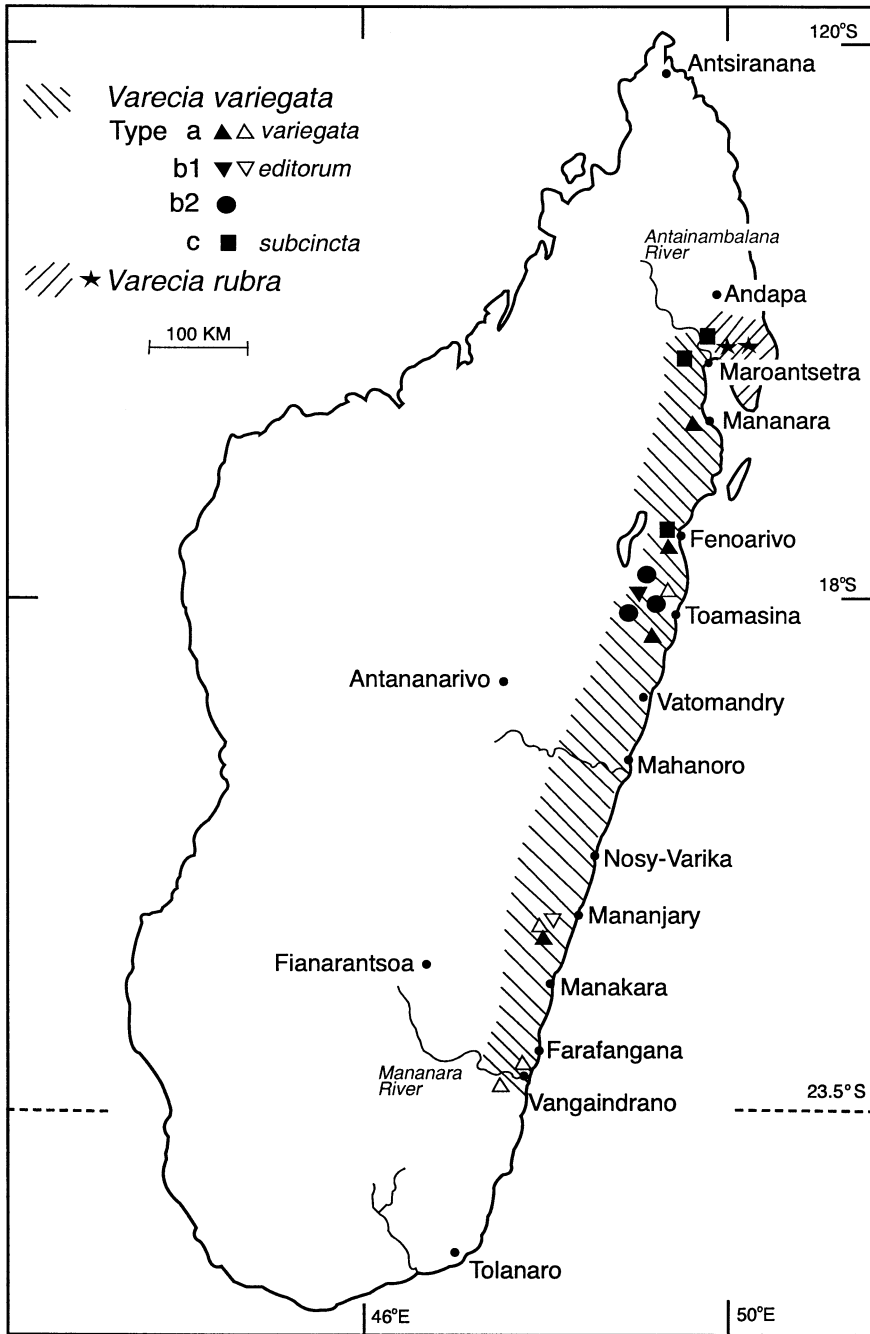


Fig. 2. Map showing the general areas of distribution of black-and-white and red ruffed lemurs. See figure 3 for detail of the contact area in the region of Maroantsetra, with field sightings located; refer to the key at upper left for symbols (filled symbols are museum records, open ones are field sightings). Hatched areas indicate approximate distribution limits and do not imply continuous distribution within the regions indicated. Field identifications indicated here in the black-and-white ruffed lemur range south of the Bay of Antongil are by Andrea Katz (Betampona), Elizabeth Balko (Ranomafana/Kianjavato region), and I.T. (extreme south).

mur has not been fully appreciated (Vasey, 1997, in press). In this form, dorsal fur varies from blood red, to red-orange, to honey-blond. Bands of white, honey-blond, or light red fur may encircle the base of the tail, tarsus, metatarsus, or digits. White fur may appear on the muzzle and lateral aspect of the ankle, extending up to the knee or thigh; and the nape of the neck almost always bears a large patch of white fur (see color plate). A pale line across the nuchal region, tipped with white laterally, has also been observed. Some of these characteristics were noted by E. Geoffroy (1824a), I. Geoffroy (1851), Elliot (1913), Hill (1953), Petter et al. (1977), Tattersall (1982), Hekkala and Rakontondratsima (1999), and were also illustrated early on (see Historical Documents, Taxonomy, and Illustrations). Tattersall (1982) found several museum specimens “much lighter in color than are typical *V. v. rubra*” and likened them to captive-bred hybrids. It is now clear, however, that lighter coloration by itself (i.e., honey blond vs. dark red) falls well within the normative description, and deep within the geographic range, of red ruffed lemurs: animals from within a single community in the Andranobe Forest, for example, show all of the variation in coat color and patterning described above, and in particular the honey-blond coloration (color plate).

Hybrids and putative hybrids (see color plate) are black-capped and ventrally black, but vary in the proportions of darker fur on the dorsum. The spectrum generally runs from a predominantly rufous hue to a whitish pelage lightly washed with raspberry tones, especially near the shoulders and rump. None, however, possesses the precise patterning of coloration typical of either of the parental populations, although in the occasional hybrid the principal effect is of black vs. white, with the addition of some reddish fur.

HISTORICAL DOCUMENTS, TAXONOMY, AND ILLUSTRATIONS

Buffon (1765) provided the first scientific description of the black-and-white ruffed lemur, referring to it simply by the vernacular names “vari” and “maki-pie”. His descrip-

tion and accompanying illustration (Buffon, 1765: pl. XXVII) represent what is currently referred to as the *variegata* variety (see above). Almost thirty years later, Kerr (1792) assigned this form the trinomen *Lemur macaco variegatus*,³ referencing the animal described by Buffon and providing the vernacular English names “pied vari” and “ruffed maucauco”. Shortly afterward, E. Geoffroy (1796) introduced le “vari á ceinture” (the “vari” with a belt), currently identified as the *subcincta* variety after Smith (1833). Jean Baptiste Audebert illustrated both of these black-and-white forms in his monograph, *Histoire Naturelle des Singes et Makis* (Audebert, 1797, pls. V and VI). Buffon, Kerr, J. B. Audebert, and later E. Geoffroy and (1824b) and Pollen (1868) all recounted the few details known of these animals in their wild state that had been given by Flacourt in his *Histoire de la grande Isle Madagascar* (1658: 153):

Il y a de diuerses sortes de singes, il y en a de grands, qui sont blancs, & ont des tâches noires sur les costez, & sur la teste, ils ont le museau long comme vn renard, ils les nomment à Mangabei *varicosy*⁴: ceux cy sont furieux comme des tigres, ils font tel bruit dans les bois, que s'il y en a deux, il semble qu'il y en a vn cent. I'en ay eu deux que ie fis porter dans nostre barque; mais ils se jetterent dans la mer, ils sont très difficilles à apprivoiser; si on ne les a de ieunesse.⁵

³ Kerr built on a binomen and description published earlier by Gmelin—*Lemur macaco*: corpore nigro and albo mixto (*Systema Naturae*, 13th ed.1788). However, Linnaeus had previously assigned the binomen *Lemur macaco* to the black lemur (*Systema Naturae*, 12th ed. 1766). The latter has long been considered a separate species, but in early days it was considered one and the same species as the black-and-white ruffed lemur until sufficient numbers of captive animals had passed through European menageries so that coat colors of males and females could be distinguished and habits revealed.

⁴ Today the Malagasy vernacular “varicosy” (= “varikosy”) refers to the white-fronted brown lemur, *Eulemur fulvus albifrons*, which is found sympatrically with the ruffed lemur in the northeast of Madagascar. The Malagasy vernaculars for black-and-white and red ruffed lemurs are “varikandana” (or “varikandra”) and “varinena” (or “varikamena”), respectively.

⁵ “There are several kinds of monkey, there are big ones, which are white, and have black patches on their ribs, and on their heads, they have a long muzzle like a fox, at Mangabey they call them *varicosy*: they are as fierce as tigers, they make so much noise in the trees, that if there are two of them it seems that there are a

Early in the 19th century, the red form was named *Lemur ruber* by E. Geoffroy (1812): in the vernacular, “maki rouge”. A more thorough description of the red form and illustrations of both the red and black-and-white forms were later published (E. Geoffroy 1824a, 1824b, *Livraisons XV and XLIII*). Although the botanist Commerson illustrated the red form in 1763, his drawings remained unpublished when they were sent back to Paris after his death shortly thereafter. Only after the naturalist Péron returned to France from Madagascar with skins (ca. 1802), and a merchant boat had brought a live animal back to France from Madagascar, was Commerson’s drawing of the red form unearthed from among his papers and a new species named (E. Geoffroy, 1824a, 1824b). The animal illustrated by Geoffroy and Cuvier (1824a) depicted the seaborne animal, which was then housed at the menagerie in the Jardin des Plantes at the Muséum d’Histoire Naturelle in Paris (now known as the MNHN). This female possessed a chestnut-red coat dorsally, with white bands of fur around each tarsus. Strangely, this animal never vocalized. Presumably this is why her close relationship to the black-and-white form was not yet obvious. Geoffroy and Cuvier (1824a, 1824b) assumed that, like other known lemurs, females and males of the “maki rouge” and the “maki vari” would have different coat colors and patterns.

Not surprisingly in light of ongoing broad efforts to name and precisely classify the lemurs during the 19th century, several milestones in ruffed lemur systematics would be passed before 1900. Importantly, however, that scientists in different parts of Europe were sometimes not aware of each other’s work for many years after each had published. The French savant I. Geoffroy (1851) disentangled the ruffed lemur from the black lemur (*Lemur macaco* Linnaeus, 1766, also

described as *Lemur niger* by E. Geoffroy, 1812) by advancing the species name *Lemur varius* to distinguish it; and he also retained the species *Lemur ruber*. He further briefly described varieties a, b, and c of the black-and-white form (which, as noted above, correspond to the varieties *variegata*, *editorum*, and *subcincta*, respectively). The Englishman Gray (1863) introduced the genus *Varecia* for the ruffed lemurs, thereby uniting the black-and-white form (*Varecia varia*) and the red form (*Varecia rubra*) at the generic level using as key characteristics the ruff surrounding the head and the tufted ears. This generic distinction was not immediately accepted. Gray continued to include the black lemurs with the ruffed lemurs (Gray 1863, 1870, 1871), yet later questioned his own taxonomic revisions (Gray, 1872), based on the observations of several other scientists (Bartlett, 1862; Schlegel, 1866; Sclater, 1871). Sclater (1871) correctly observed that among black lemurs the sexes were dichromatic, whereas in black-and-white ruffed lemurs the sexes had similar coat patterns. It was also recognized that *Lemur varius* and *Lemur niger* differed in their “voices” (vocalizations; Bartlett, 1862; Sclater, 1871). Despite these caveats, Gray’s examination of specimens in the BMNH, especially those collected by Alfred Crossley in the 1860s, led him to think that *Lemur niger*, *Lemur varius*, and *Lemur ruber* were “all one species, extremely variable in colour, some being black, others red, and others white, and all the intermediate shades and variations” (Gray, 1872). Schlegel, a museum naturalist in Leiden, and Pollen, a Dutch explorer, drew similar conclusions. Noting excessively variable coloration Schlegel (1866, 1876) considered *Lemur ruber* to be nothing more than a variety of *Lemur varius*, but was also the first to remark that *Lemur macaco* was sexually dichromatic, and that compared to *Lemur varius*, it was smaller in size, had a much weaker voice, and a far less thick, tufted, and woolly coat. Having traveled only through the northwest of Madagascar, Pollen relied on information provided by natives and by other explorers, and on observations he made on captive ruffed lemurs at the Musée de Saint-Denis (Réunion) where he saw a tricolored animal. Without providing any

hundred. I had two of them brought on our ship; but they threw themselves in the water, they are very difficult to tame unless you get them when they are young”. Note that in the original French text, the letter “j” was printed as “i”, the letter “v” as “u” when in the middle of a word, and the letter “u” as “v” when beginning a word. Two editions of Flacourt were consulted for this translation (see references), in addition to Tattersall (1982).

sources he drew a rather extreme conclusion, lumping all black, white, red, and black-and-white forms into *Lemur varius*. He claimed, moreover, that there were no differences in color by sex or age, and stated that *Lemur ruber* had the same habits as the *vari*, “with which [presumably in captivity] it lives and mates” (Pollen, 1868: 21). So, while some in this period came to understand that ruffed lemurs were not sexually dichromatic, were specifically distinct from black lemurs, and consisted of two distinct species (e.g., I. Geoffroy, 1851)—and perhaps even of a unique genus (Gray, 1863)—a polar view had also emerged: that animals of all colors and coat patterns belonged to one single species.

Schwarz (1931) attempted to sort I. Geoffroy’s (1851) three varieties geographically, but acknowledged that many original museum labels had disappeared and that he had encountered much difficulty in identifying geographical names on labels, in literature, and on older maps (Schwarz, 1931: 399–400). Schwarz unequivocally stated, however, that the red form was a color mutation of I. Geoffroy’s variety a, “with which it occurs and interbreeds”. The only evidence cited in support of this claim was that crosses born at the Berlin Zoo resembled some of A. Milne-Edwards and A. Grandidier’s (1890) illustrations (see color plate), which were, unfortunately, published without descriptions or subspecific designations.

Hill (1953) drew directly upon Schwarz (1931) with regard to taxonomy and distribution. He upgraded I. Geoffroy’s varieties a, b, and c to the subspecies *Lemur variegatus variegatus* (Kerr, 1792), *Lemur variegatus editorum* Hill, 1953, and *Lemur variegatus subcincta* (Smith, 1833), respectively. He produced a distribution map for the subspecies, taking considerable license in building on the information provided by Schwarz (1931). This map contains gross errors relative to distributional information known both at that time and currently (cf. Pollen, 1868; Jentink, 1892; Elliot, 1913; Kaudern, 1915⁶). Hill (1953: 400) further

embellished on Schwarz (1931) by stating that the red form and variety a (*L. v. variegatus*) occur together geographically and interbreed in nature. Unfortunately, Hill provided no documentation for this claim other than to cite Schwarz’s observations that hybrids were produced at the Berlin Zoo, and that the hybrids in turn resembled A. Milne-Edwards and A. Grandidier’s (1890) plates. Consequently, the idea (but no documentation) of a natural hybrid zone emerged in tandem with a notion (albeit misconstrued) of the geographical distribution of the red and black-and-white forms.

Thus, by the mid-20th century, notions reported by Pollen (1868) as unverified claims had become highly speculative “facts”. But one last other clue from the 19th century was yet to be seized upon. Schwarz (1931) noted that “black-and-white and red specimens have been collected in the same place by J.[-P.] Audebert in the coast region north of the Bay of Antongil”, citing Jentink of Leiden (*Catalogue Systématique des Mammifères*, 1892). Schwarz was alluding to the collections made by the German-born Josef-Peter Audebert, who worked in Madagascar between 1876 and 1879. His collection was

Jentink, using J.-P. Audebert’s collection records, demonstrated that *L. varius* occurred north of the Bay of Antongil and south as far as Mananare, Vidoutra, and Mahambo. Elliot indicated that the black-and-white form occurs in northeastern Madagascar from Adenpone to Cape Masoala at the entrance of Antongil Bay, and into the interior to Bengoa; and that the red form occurs in eastern Madagascar, from the Bay of Antongil in the north to Masindrano in the south. Many of the place names cited by Elliot cannot be located (presumably he drew these localities from museum labels). His distribution for the red form more accurately reflects the distribution for the black-and-white form, assuming Masindrano refers to the town bearing this name in southeastern Madagascar, not the village bearing this name just south of Mahalevona on the Bay of Antongil. Kaudern described a *subcincta*-like animal from one day west of Fenerive (“has only a white band around its body”, Kaudern, 1915, pl. 3, fig. 1), and an *editorum*-like animal from south of Tamatave (“almost all white in the rear”). Despite the availability of this distributional information, Hill (1953: 401, Fig. 130) illustrated the range of *L. variegatus* as extending only as far south as Tamatave, but well into the northern high plateau and all along the northern coast as far as Diego Suarez! He did not take the records from south of Tamatave, Antananarivo, and possibly Masindrano into account, whereas the distribution he gave for ruffed lemurs in northern Madagascar is hugely exaggerated.

⁶ Pollen, collating information from indirect sources, stated that *Lemur varius* (both forms) occurs in the region between Tintingue, Tamatave, and Antananarivo.

sold to various museums, but most of his ruffed lemurs went to the RMNH in Leiden and were well documented by Jentink (1892). It is important to remember that neither Schwarz nor Hill had examined the Leiden material firsthand, and more will be said of this in the section below on Museum Collections and Records.

Fieldwork and careful study of museum skins and their provenances by Petter et al. (1977) and Tattersall (1982) improved our understanding of the taxonomy and distribution of ruffed lemurs. However, these studies by no means resulted in a tidy, discrete distribution of the black-and-white forms. Considering cranial anatomy, social behavior, and the unusual reproductive traits of ruffed lemurs, Petter (1962) reintroduced the genus *Varecia* Gray, 1863 to distinguish ruffed lemurs from other members of the family Lemuridae. Petter et al. (1977) described and provided locality data, to the extent possible, for seven black-and-white forms. These authors retained the subspecies advanced by Hill in 1953 (*V. v. variegata*, *V. v. editorum*, and *V. v. subcincta*) and further described, but did not name, another four. The southernmost population then known, inhabiting the remaining coastal forest south of Farafangana, was said to be almost entirely white dorsally. Like various earlier workers, Petter et al. (1977) viewed the red form as simply another subspecies of ruffed lemur—*V. variegata rubra*. However, unlike earlier workers, these authors indicated that the Antainambalana River (fig. 3) clearly separates the red form from the black-and-white form, specifically *V. v. subcincta*⁷. This is the first reference to a geographic divide between the two color forms.⁸ Tattersall (1982) recognized just two subspecies, corresponding to the red form (*V. v. rubra*) on the one hand, and to all black-and-white forms combined (*V. v. variegata*) on the other. Building on Geoffroy (1851), he described four black-and-white types (a, b1, b2,

c) and indicated that better knowledge of the distribution of these varieties might ultimately warrant their recognition as distinct subspecies. Unfortunately, the key for this distribution map contained drafting errors; we reproduce it correctly in the footnote below⁹. Groves (2001) raised the variants of the black-and-white forms to subspecies of the species *Varecia variegata*.

The new distribution data presented by Petter et al. (1977) and Tattersall (1982) conflict in one particularly important way with those published earlier by Schwarz (1931) and Hill (1953). The latter authors placed the lightest form (type a, *variegata*) farthest north, interbreeding with the red form north of the Bay of Antongil, whereas the former determined that it was the darkest form (type c, *subcincta*) that occurred farthest north, largely separated from the red form by the Antainambalana River. Despite the discovery of a geographic divide, however, the idea of a natural hybrid zone reemerged. Based on reports of a rufous brown variant west of the Bay of Antongil, Tattersall (1977) suggested such animals might be hybrids or a local form of *V. v. variegata*. Later it was noted that several museum specimens are much lighter in color than are typical *V. v. rubra* and resemble 50/50 *V. v. rubra* × *V. v. variegata* hybrids bred in captivity at the DUPC (Tattersall, 1982; Buettner-Janusch and Tattersall, 1985). These authors thought at that time that only one such specimen was both wild-caught and documented to locality. This was collected by the Archbold expedition in 1930, 40 km NW of Maroantsetra up the Vohimaro River (Rand, 1936). On this basis, Tattersall (1982) suggested that *V. v. variegata* and *V. v. rubra* might be in secondary contact between the confluent Vohimaro and Antainambalana Rivers. This suggestion prompted several surveys, the findings of which are reviewed below (see Recent Surveys).

In concluding this section it is appropriate to summarize the basis upon which a natural hybrid zone was proposed. The black-and-

⁷ Black-and-white ruffed lemurs (*subcincta* type) were observed at 400 m in the hills to the west of the Antainambalana in 1969 by Petter et al. (1977: 225).

⁸ Hill (1953) produced a distribution map showing this divide as well, but he provided neither provenance data nor details of the specimens upon which the map was based.

⁹ The correct correspondence between *V. variegata* types and symbols in figure 3.15 of Tattersall (1982: 72) is as follows: type a (*variegata*) ▲; type b1 (*editorum*) ▽; type b2 (*editorum*) ○; type c (*subcincta*) □.

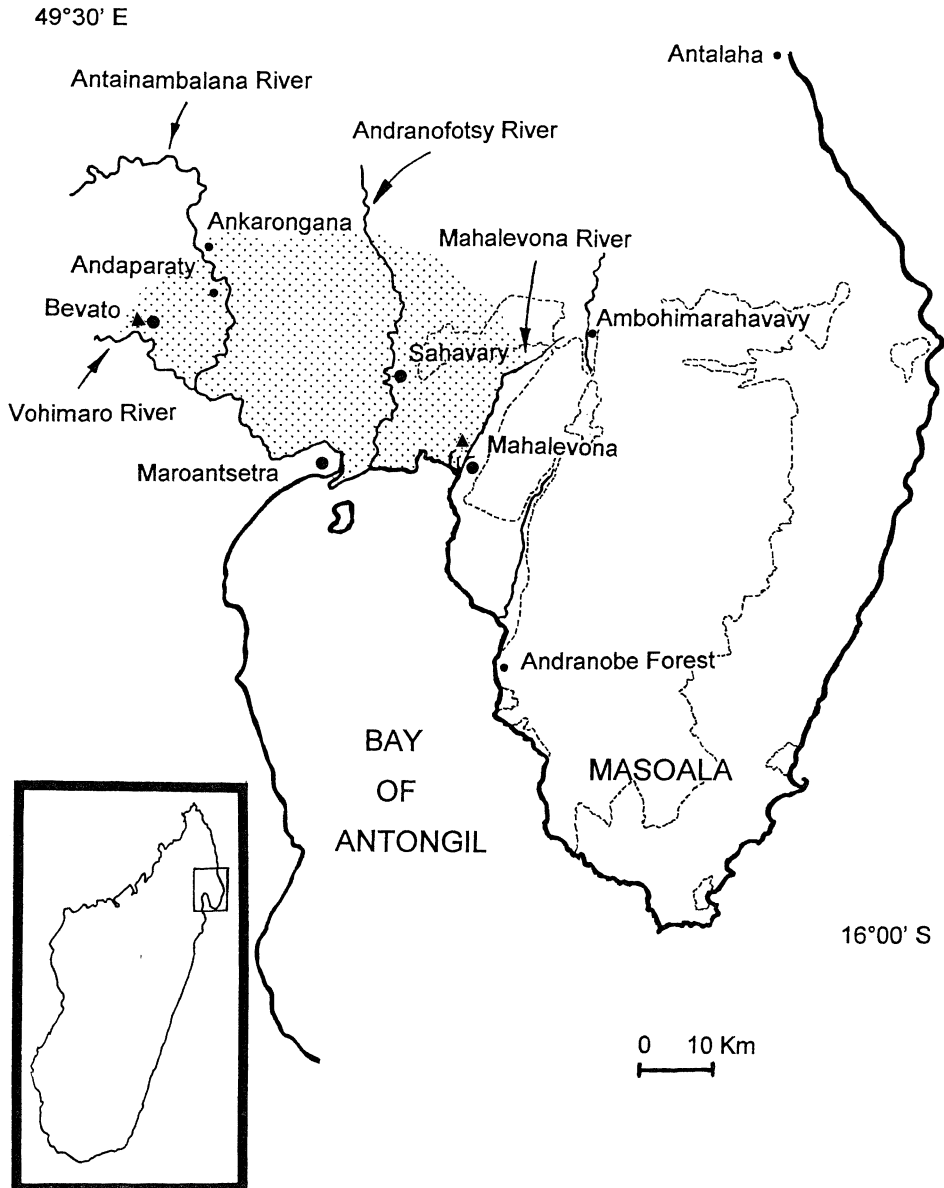


Fig. 3. Masoala Peninsula and region north of the Bay of Antongil and its major watersheds. Arrows (→) indicate the Vohimaro, Antainambalana, Andranofotsy, and Mahalevona rivers. Triangles (▲) show localities where hybrid ruffed lemurs were collected (see table 1). Large dots (●) show localities where more than one form of ruffed lemur was collected and/or sighted (see table 2). Stippling represents area of overlap between black-and-white and red ruffed lemurs where hybridization has occasionally occurred. Small dots (•) show other localities mentioned in the text. Andaparaty: black-and-white ruffed lemurs sighted; Ankarongana: red ruffed lemurs reported to the north (Ambodibilahy Mtn.) and to the east (Anjanaharibe Mtn.). At nearby Sahantaha village to the south, black-and-white ruffed lemurs kept as pets were apparently captured on the west side of the Antainambalana River. Andranobe Forest: red ruffed lemurs at this site show all the pelage variations described under the normative description. Samples used in genetic analyses were collected from this population (Vasey, 1997). Dashed lines indicate boundaries of the Masoala National Park. Note several narrow corridors bridging forested blocks. Coordinates for important localities during recent surveys: Andaparaty village 15°12'S, 49°37'E;

white and red forms were considered different species throughout most of the 19th century (E. Geoffroy, 1812; E. Geoffroy, 1824a, 1824b; Lesson, 1840, 1842; I. Geoffroy, 1851; Gray 1863, 1870), but by the end of the 19th century and throughout the 20th virtually all systematists classified them as subspecies or varieties of a single highly variable species (Schlegel, 1866, 1876; Gray, 1872; Forbes, 1894; Elliot, 1913¹⁰; Schwarz, 1931; G. Grandidier and Petit, 1932; Hill, 1953; Petter et al., 1977; Tattersall, 1982). While Schwarz (1931) and Hill (1953) both alluded to the existence of a hybrid zone, neither author documented any wild-caught hybrids in museum holdings. Rather, their work suggests that the gradual taxonomic downgrading of black-and-white and red ruffed lemurs, from species to subspecies, had been influenced largely by the existence of hybrids that had been produced in captivity. For, as evidence for a hybrid zone, they were able only to offer captive-bred crosses and the plates of A. Milne-Edwards and A. Grandidier (1890; see also color plate).

This observation prompts three questions. What did the oldest illustrations of ruffed lemurs look like? Were there any hybrids among them? And when were hybrids first produced in menageries and zoos? In answer to the first two questions, until we arrive at the plates published by A. Milne-Edwards and A. Grandidier (1890), all early illustrations of ruffed lemurs are true forms, either red or black-and-white (Commerson, 1763 unpubl.; Buffon, 1765; Schreber, 1775; J. B. Audebert, 1797; E. Geoffroy 1824a, 1824b; Gervais, 1854). A. Milne-Edwards and A. Grandidier (1890) illustrated three black-and-white forms corresponding to Geoffroy's

varieties a, b and c (pls. 123, 124, 125), two red forms falling within the normative description (pls. 127¹¹ and 128), and one possible hybrid (pl. 126; see color plate herein). Unfortunately these plates were published without descriptions, taxonomic assignments, or references as to where the illustrated animals originated. It is possible that these illustrations were based on wild (or wild-caught) animals, as A. Grandidier undertook detailed surveys in Madagascar and crossed the island in several directions between 1865 and 1870. However, it cannot be ruled out that the hybrid depicted was produced in captivity. And documentation of a hybrid zone requires more than zoo-bred hybrids and unannotated illustrations. It requires either the identification of such a zone in the wild, or precise locality documentation of wild-caught hybrids in existing museum holdings. We next turn our attention to museum collections before reviewing menagerie and zoo records, recent survey work, genetics, and vocalizations.

MUSEUM COLLECTIONS AND RECORDS

The above review suggests that collections made in northeastern Madagascar by J.-P. Audebert between 1876 and 1879, and by the Mission Zoologique Franco-Anglo-Américaine à Madagascar 1929–1931 (commonly referred to by Anglophones as the Archbold expedition), hold promise in documenting wild-caught hybrids and/or regions of overlap between the black-and-white and red forms of *Varecia*. We have studied these collections, in addition to many others, and we refer largely to published work of one of us

¹⁰ Elliot (1913) was the first author in 121 years properly to attribute the species name *Lemur variegatus* to Kerr (1792). Along with Forbes (1894) he was first to apply the now commonly used English vernaculars, "ruffed lemur" and "red ruffed lemur".

¹¹ Schwarz (1931: 418) considered plates 126 and 127 of Milne-Edwards and A. Grandidier (1890) to represent hybrids. However, upon examining these plates, one of us (N.V.) has determined that plate 127 lies within the normative description of the red ruffed lemur.

←

Ankorongana village 15°10'786"S, 49°35'458"E; Sahantaha village 15°11'300"S, 49°34'900"E; Sahavary village 15°19'S, 49°50'E; Belampona River 15°18'848"S, 49°54'508"E (see text for references). Ambohimarahavavy is an Archbold Expedition collecting locality ("2 days NE of Maroantsetra") where red ruffed lemurs were collected. Other important coordinates: Andranobe field site 15°40'906"S, 49°57'399"E; Ambohimarahavavy 15°16'020"S, 50°03'000"E; Bevato 15°10'740"S, 49°28'140"E.



(Tattersall, 1982; Buettner-Janusch and Tattersall, 1985) and to his museum notes in our search for undocumented hybrids. In addition, Jentink's *Catalogue Systématique des Mammifères* from Leiden (1892), Rand's detailed notes on collection localities of the Archbold Expedition (Rand, 1932, 1936), and the *Catalogue of Primates in the British Museum (Natural History) Part IV* (Jenkins, 1987) have been consulted, the last of these providing detailed information on Archbold material accessioned into the BMNH in addition to the field listings held by the Department of Mammalogy at the AMNH. We have also studied the holdings of the USNM, which include the excellent Abbott Collection, to improve upon the normative descriptions provided above and to search for ruffed lemur specimens collected in northern Madagascar. Topographic maps issued by the Institut Cartographique de Madagascar (FTM) at 1:100,000 scale, and several geo-referencing databases have been consulted to verify localities, place names, and topographic features. The latter resources include the United States Board on Geographic Names Gazetteer (USGS), the Madagascar Gazetteer (Missouri Botanical Garden), and, especially, the Platform d'Analyse Project for the Masoala Region, Madagascar (data courtesy of David Lees).

Three possible wild-caught hybrids with provenance data were located for this study, one each in museum holdings at the RMNH (*Lemur varius* w, aka "*Lemur ruber* Cr. g du Cat. Ost." in Jentink's 1892 catalog), the BMNH (ZD.1935.1.8.29), and the AMNH (100510). Of these, only the last had been published as a hybrid (Buettner-Janusch and Tattersall, 1985). Table 1 provides detailed information on these specimens and on two more for which there are no provenance data. Although Plate 126 (see color plate) of A. Milne-Edwards and A. Grandidier (1890) suggests that hybrids might have been deposited in the MNHN, we could not find any

there. The three wild-caught hybrids originate from 40 km NW of Maroantsetra along the Vohimaro River (Bevato village) and from the environs of Mahalevona village (table 1, fig. 3). These provenance records suggest that ruffed lemurs may have hybridized over a much larger area than previously suggested: one extending across three major drainage systems that empty south into the Bay of Antongil. From east to west, these are the valleys of the Mahalevona, the Andranofotsy, and the Antainambalana Rivers, the Vohimaro River being a major tributary of the last of these.

Currently, the RMNH hybrid is cataloged as *Lemur ruber* (Jentink, 1892). It comes from "Malewo" (old orthography for Mahalevona) and falls outside the range of variation seen in either red ruffed lemurs generally, or in comparison to other specimens collected in the same location. It is a light-colored specimen with many white hairs in the dorsal fur, giving it a "washed-out" look. The AMNH hybrid (100510) and the BMNH hybrid (ZD.1935.1.8.29) are cataloged under *V. v. rubra* (Buettner-Janusch and Tattersall, 1985; Jenkins, 1987) and both come from 40 km NW of Maroantsetra. BMNH 1935.1.8.29 is described as "light coloured" (Jenkins, 1987), with the top of the head and cheeks black; the ventrum, extremities, and tail black; and the rest of the dorsum whitish with reddish elements, especially posteriorly. According to our notes, BMNH 1935.1.8.29 resembles AMNH 100510. This AMNH specimen is whitish, with black headcap, ventrum and extremities. Its tail is very dark except at the proximal base, where it lightens up for about one-fourth of its length. There are red-brown patches bilaterally at the top of the forelimbs, and there are hints of reddish fur in the center of the dorsum and at the sides posteriorly. AMNH 100510 has previously been described as similar to *V. v. variegata* × *V. v. rubra* crosses from the DUPC (Buettner-Janusch and Tattersall,

←

COLOR PLATE. **A**, Black-and-white ruffed lemur, *variegata* variety (by D. Haring, DUPC). **B**, Red ruffed lemur, honey-blonde variety from Andranobe River, Madagascar (by N. Vasey). **C**, Putative hybrid in Plate 126 of Milne-Edwards and Grandidier (1890); courtesy of AMNH Library. **D**, Red ruffed lemur (by D. Haring, DUPC). See Normative Description section for further details.

TABLE 1
Wild-Caught Hybrids of *Varecia* in Museum Collections^a

| Museum ID | Date | Sex | Age | Locality | Altitude | Collector | References ^b |
|-----------------------------------------|--------------|-----|----------|-----------------------------|----------|------------------------|-------------------------|
| RMNH <i>Lemur varius</i> w ^c | 23 July 1878 | F | Subadult | Malewo (= Mahalevona) | 0–100 m | J.-P. Audebert | 1 |
| BMNH ZD.1935.1.8.29 | 18 May 1930 | M | Adult | Bevato village ^d | 0–500 m | Archbold Exp. #732 | 2, 3 |
| AMNH 100510 | 19 May 1930 | F | Adult | Bevato village ^d | 0–500 m | Archbold Exp. #733 | 2, 4 |
| AMNH 2674 | — | — | Adult | — | — | Ward's Nat. Hist. Est. | 4 |
| AMNH 2684 | — | — | — | — | — | Ward's Nat. Hist. Est. | 4 |

^a In all cases hybrids were designated based on Tattersall's museum notes and/or Tattersall (1982) and Tattersall and Buettner-Janusch (1985). See text for descriptions. Dashes (—) indicate no data are available.

^b References: 1, Jentink, 1892; 2, Rand, 1936; 3, Jenkins, 1987; 4, Buettner-Janusch and Tattersall, 1985.

^c The Audebert specimens in the RMNH also possess a museum ID in the osteological collection. Specimen *w* is also referred to as "Cr. g du Cat. Ost." (Jentink, 1892).

^d Place name not on FTM map; 40 km NW of Maroantsetra up Vohemar [Vohimaro] River (Rand, 1936); coordinates circa. 15°19'S 49°32'E (Jenkins, 1987), 15.179°S, 49.469°E (Lees, personal commun.).

^e These specimens are probably wild-caught. They arrived to the AMNH via a dealer, Ward's Natural History Establishment, Rochester, probably in the late 19th century.

1985). These wild hybrids resemble captive hybrids (color plate). Two specimens of unknown provenance from Ward's Natural History Establishment, AMNH 267 and 268, generally resemble the BMNH and AMNH hybrids just described. They have light fur, dark headcaps, white necks and most of the dorsum white, with faded reddish patches on the upper forelimbs and extending across the back. There are also darker patches on the insides of the upper legs and lighter reddish patches on the lower back, at the sides. Their tails are very dark.

Schwarz's indication that black-and-white and red forms were collected in the same place (Maroantsetra) by J.-P. Audebert fueled the provocative suggestion that a natural hybrid zone existed (e.g., Simons and Lindsay, 1987). Our review has revealed three, and possibly four, localities where more than one form was found, demonstrating that overlap occurred over a considerably larger area than previously recognized (table 2, fig. 3). In the 19th century, Alfred Crossley and J.-P. Audebert collected black-and-white and red forms in the environs of Maroantsetra and J.-P. Audebert collected red forms and one hybrid in the environs of Mahalevona village. In May 1930, the Archbold Expedition collected black-and-white forms and two hybrids 40 km NW of Maroantsetra near Be-

vato village. In the Andranofotsy valley, near the village of Savary, J.-P. Audebert collected black-and-white forms in 1878; in a recent survey, red ruffed lemurs were sighted near this village (see Recent Surveys). However, another village along the Antainambalana River (north of the confluence with the Vohimaro) bears a similar place name (Sahafary), so this co-occurrence must remain speculative. These regions of overlap, especially those where hybrids occur, buttress the claim for a natural hybrid zone. However, despite documenting a more expansive hybrid zone and several regions of overlap, museum holdings turned up only three documented hybrids. This being the case, hybridization appears to be the exception rather than the rule in the overlap zone of red and black-and-white ruffed lemurs.

MENAGERIE AND ZOO RECORDS

Those managing captive ruffed lemur breeding programs are well aware that black-and-white and red ruffed lemurs form hybrids readily in captivity, as do many other congeneric lemur taxa (Petter, 1969). Because the red ruffed lemur is rare in zoo holdings, it was commonly crossed with black-and-white ruffed lemurs, notably in European zoos, and these crosses have been

TABLE 2
Localities Where Two Forms of *Varecia* Were Collected or Sighted^a

| Museum ID | Date | Sex | Age | Locality ^b | Collector | Species Attribution | References |
|----------------------------|------------------|-----|----------|-----------------------|--------------------|------------------------------------------------|-------------------------------------|
| BMNH ZD.1873.3.20.5 | mid-19th century | I | Adult | Maransetra River | A. Crossley | <i>Varecia variegata variegata</i> | Jenkins, 1987 |
| BMNH ZD.1873.3.20.7a | mid-19th century | I | Adult | Maransetra River | A. Crossley | <i>Varecia variegata rubra</i> | Jenkins, 1987 |
| BMNH ZD.1873.3.20.7b | mid-19th century | I | Adult | Maransetra River | A. Crossley | <i>Varecia variegata rubra</i> | Jenkins, 1987 |
| BMNH ZD.1873.3.20.7c | mid-19th century | I | Adult | Maransetra River | A. Crossley | <i>Varecia variegata rubra</i> | Jenkins, 1987 |
| BMNH ZD.1873.3.20.7d | mid-19th century | I | Adult | Maransetra River | A. Crossley | <i>Varecia variegata rubra</i> | Jenkins, 1987 |
| RMNH Lemur varius <i>i</i> | January 1876 | F | Adult | Maranzettra | J.-P. Audebert | <i>Lemur varius [V. variegata variegata]</i> | Jentink, 1892 |
| RMNH Lemur varius <i>j</i> | January 1876 | F | Adult | Maranzettra | J.-P. Audebert | <i>Lemur varius [V. variegata variegata]</i> | Jentink, 1892 |
| RMNH Lemur varius <i>k</i> | January 1876 | F | Adult | Maranzettra | J.-P. Audebert | <i>Lemur varius [V. variegata variegata]</i> | Jentink, 1892 |
| RMNH Lemur varius <i>s</i> | January 1876 | I | Adult | Maranzettra | J.-P. Audebert | <i>Lemur ruber [V. variegata rubra]</i> | Jentink, 1892 |
| RMNH Lemur varius <i>t</i> | January 1876 | I | Adult | Maranzettra | J.-P. Audebert | <i>Lemur ruber [V. variegata rubra]</i> | Jentink, 1892 |
| RMNH Lemur varius <i>u</i> | January 1876 | I | Adult | Maranzettra | J.-P. Audebert | <i>Lemur ruber [V. variegata rubra]</i> | Jentink, 1892 |
| RMNH Lemur varius <i>v</i> | January 1876 | I | Adult | Maranzettra | J.-P. Audebert | <i>Lemur ruber [V. variegata rubra]</i> | Jentink, 1892 |
| RMNH Lemur varius <i>l</i> | 13 November 1877 | F | Adult | Savary | J.-P. Audebert | <i>Lemur varius [V. variegata variegata]</i> | Jentink, 1892 |
| RMNH Lemur varius <i>m</i> | 20 December 1877 | M | Adult | Savary | J.-P. Audebert | <i>Lemur varius [V. variegata variegata]</i> | Jentink, 1892 |
| RMNH Lemur varius <i>n</i> | 19 February 1878 | M | Adult | Savary | J.-P. Audebert | <i>Lemur varius [V. variegata variegata]</i> | Jentink, 1892 |
| RMNH Lemur varius <i>o</i> | 12 February 1878 | F | Adult | Savary | J.-P. Audebert | <i>Lemur varius [V. variegata variegata]</i> | Jentink, 1892 |
| RMNH Lemur varius <i>p</i> | 12 June 1878 | F | Adult | Savary | J.-P. Audebert | <i>Lemur varius [V. variegata variegata]</i> | Jentink, 1892 |
| Two animals sighted | Aug.-Oct.1986 | I | I | Sahavary | n.a. | <i>Varecia variegata rubra</i> | Lindsay & Simons, 1986 |
| RMNH Lemur varius <i>w</i> | 23 July 1878 | F | Subadult | Malewo | J.-P. Audebert | <i>Lemur ruber [hybrid3]</i> | Jentink, 1892 |
| RMNH Lemur varius <i>x</i> | 31 July 1878 | I | I | Malewo | J.-P. Audebert | <i>Lemur ruber [V. variegata rubra]</i> | Jentink, 1892 |
| RMNH Lemur varius <i>y</i> | 31 July 1878 | I | I | Malewo | J.-P. Audebert | <i>Lemur ruber [V. variegata rubra]</i> | Jentink, 1892 |
| RMNH Lemur varius <i>z</i> | 31 July 1878 | I | I | Malewo | J.-P. Audebert | <i>Lemur ruber [V. variegata rubra]</i> | Jentink, 1892 |
| AMNH 100511 | 12 May 1930 | F | Adult | Bevato | Archbold Exp.#695 | <i>Varecia variegata variegata</i> | Buettner-Janusch & Tattersall, 1985 |
| BMNH ZD.1935.1.8.32 | 15 May 1930 | F | Adult | Bevato | Archbold Exp. #700 | <i>Varecia variegata variegata</i> [subcincta] | Rand 1936; Jenkins 1987 |
| BMNH ZD.1935.1.8.29 | 18 May 1930 | M | Adult | Bevato | Archbold Exp. #732 | <i>Varecia variegata rubra</i> [hybrid3] | Rand 1936; Jenkins 1987 |
| AMNH 100510 | 19 May 1930 | F | Adult | Bevato | Archbold Exp. #733 | <i>Varecia variegata rubra</i> [hybrid3] | Buettner-Janusch & Tattersall, 1985 |

^a Information concerning sex and age of specimens may be available, but is not indicated in the referenced catalog (I = indeterminate).

^b Place names are written in the table as they were by the collectors. Modern orthography is used in the text.

^c Tattersall (museum notes).

referred to as “tri-colored ruffed lemurs” (Bernirschke and Miller, 1981). This breeding practice, however, has been discouraged for over two decades (e.g., Lindsay, 1977), and in particular by the Species Survival Plan (SSP, a branch of the American Zoo and Aquarium Association), by the European Endangered Species Programme (EEP), and by the Prosimian Taxon Advisory Group (a branch of the World Conservation Union, formerly the IUCN). This returns us to the question posed at the end of the first section (Historical Documents, Taxonomy, and Illustrations) regarding when hybrids were first produced in menageries and zoos. Since our review of museum collections and records places discussion of a natural hybrid zone on much firmer footing, why should one bother to determine the earliest occurrence of captive hybrids? This effort remains important because it affects ruffed lemur taxonomy and, in turn, conservation initiatives. The decision to lump the black-and-white and red forms into one species was initially made on the basis of their excessively variable coat coloration, without recognizing that some of the variation in the available sample might have been induced through captive hybridization (e.g., Pollen, 1868). Lumping was completed before J.-P. Audebert and the Archbold Expedition brought back natural hybrids in the late 19th and early 20th centuries, and long before the distinctive geographic distributions of the two color forms were known (Petter et al., 1977; Tattersall, 1977; see Survey Work). These facts suggest that the down-ranking of black-and-white and red ruffed lemurs to subspecies warrants reconsideration, especially if it can be demonstrated that their down-ranking was largely influenced by captive hybridization during the 19th century. This section is not intended to be an exhaustive review of captive breeding in ruffed lemurs, but rather to reveal the earliest records of captive breeding practices and to substantiate whether captive-bred hybrids had undue influence in collapsing the specific distinction between black-and-white and red ruffed lemurs.

Although lemurs were already kept in European menageries by the 18th century, turnover was high and captive lives short: mates

were rarely available¹² and illness went undiagnosed or untreated. Lemurs hardly fared better during the first part of the 19th century. One of the first references to a captive black-and-white ruffed lemur is found in Kerr (1792: 87): “The vari is fond of sunshine, yet always chooses to sleep in a dark place, and preserves its nest very clean. In confinement, it refuses to feed on eggs, flesh, or fish; and, when eating, growls, with a voice like that of a lion”. The Empress Joséphine Bonaparte kept a pair of black-and-white ruffed lemurs at Malmaison that were presented to the Muséum d’Histoire Naturelle in Paris in 1809, presumably upon their death. This pair mated and produced triplets, which did not survive (I. Geoffroy, 1851). The first red ruffed lemur brought live to Europe was mute and lived alone at the menagerie in the Jardin des Plantes in Paris ca. 1820, as did a second animal circa 1839. Few primates reproduced in the Paris menagerie between 1793 and 1851, and none that did were lemurs, despite the reception of 87 strepsirhines during that period (I. Geoffroy, 1851).

In the second half of the 19th century and during the early 20th century, life in menageries took something of a turn for the better. In an attack on Darwin’s *Origin of Species*, Gray inadvertently provided the most telling information regarding 19th century menageries and hybridization:

All the specimens that have come under my observation have been living in menageries; and all the skins in the Museum are obtained from specimens which have been so confined; and some of them have been even born in confinement, and are probably the hybrid offspring of two species, arising from the intermixture of different kinds in the same cages. Under such circumstances, it is very natural that there should be difficulties in separating them, and that there may be intermediate forms. Yet I may state that, when the specimens which have come under my examination have been carefully compared, I have had no difficulty in distinguishing them, and I have not found a single specimen which I have had the slightest reason to believe is a passage from one species to the other (Gray, 1863: 134, cf. Gray, 1872).

Pollen’s (1868) somewhat oblique reference

¹² Regarding his pet “mongous” (brown lemur), Buffon (1765: 177) wrote: “il cherchoit les chattes, & même se satisfaisoit avec elles, mais sans accouplement intime & sans production”.

to captive breeding and hybridization of ruffed lemurs at the Musée de St. Denis was followed by much more substantial records. Between 1845 and 1932, 66 lemur births were recorded in the London Zoo: eight were hybrids (two from before 1867), although none was a ruffed lemur (Zuckerman, 1932). Between 1899 and 1922, 120 lemurs were born at the Giza Zoological Gardens in Egypt, of which seven were black-and-white ruffed lemurs (Flower, 1933). By 1935, Dechambre of the Paris menagerie had achieved many successes in captive care and breeding of lemurs. He had produced three-generation lineages of five lemur species (including *Lemur variegatus*) and had defeated several types of illness in the lemur colony through improvements in diet and housing. Dechambre's success (Dechambre, 1935) was rewarded in that he was able to give the first detailed descriptions of *Varecia*'s unique reproductive pattern.

The documents at hand indicate that captive hybridization of lemurs occurred before 1870. Thus, it is highly likely that the taxonomic revisions of *Varecia* in the later 19th century were influenced by such practices, whether intentional or not. More recently, lemur subspecies, and even separate species and genera, have intentionally been hybridized as a means of clarifying their taxonomy (e.g., A. P. Gray, 1954; Petter, 1969). In this regard, Petter et al. (1977: 257) obtained a hybrid between a female *V. v. rubra* and a male *V. v. subcincta*. Although the ruffed lemur captive breeding program (established in the late 1960s) discourages interbreeding among the two color forms, hybrids are still occasionally produced (I. Porton, personal commun.), and crossings have been most common in European zoos (Bernirschke and Miller, 1981). Illustrations of pelage color and pattern based in any part on captive-bred animals with histories of hybridization (alive or in museum holdings) may complicate rather than clarify ruffed lemur taxonomy because some of the variation illustrated may not represent natural variation or natural hybrids (see, e.g., Ceska et al., 1992, pls. 1–4). It is also true that some unusual wild-collected forms have not yet been illustrated (e.g., USNM 84381, which combines *editorum* and *variegata* features, see also Tatter-

sall, 1982: 70). Clearly, it will be important to document the pelage and color patterns of wild-caught animals and especially of natural hybrids whenever such opportunities arise. One such opportunity existed at Zoo Ivoloïna in Tamatave, Madagascar, where an apparent wild hybrid resided from 16 July 1990 until her death on 2 July 1996. Zoo Ivoloïna staff were told that she was one of a pair of twins that had fallen from a tree along a river "near Maroantsetra". She was kept for some time as a pet in Maroantsetra and was only later transferred to Zoo Ivoloïna. She appeared similar to the 50–50 *V. v. rubra* × *V. v. variegata* hybrids that were at one time produced at the DUPC (A. Katz, personal commun.). Unfortunately, photographs were not taken of this hybrid, nor was the skin preserved.

SURVEY WORK

The largely separate geographic distributions of black-and-white and red ruffed lemurs throughout most of their range were not known until long after their reduction to subspecies of the same species had become entrenched. The red ruffed lemur occurs principally on the Masoala Peninsula, while the black-and-white ruffed lemur has a much larger range extending from south of the Mananara River (at least to the region north of Midongy du Sud) to the Antainambalana River in the north (near Maroantsetra) (fig. 2; Petter et al., 1977; Tattersall, 1977). Petter et al. (1977) and Tattersall (1982) stated that the Antainambalana River currently appears to divide the two subspecies; however, the northern and western reaches of the red ruffed lemur's range are incompletely known. Petter et al. (1977) illustrated the northernmost distribution of the red ruffed lemur as Andapa, whereas Tattersall's informants, in particular the late Georges Randrianasolo, a highly experienced observer, indicated that this form occurred only as far north as Cap Est—although it might have extended as far north as Antalaha until recently (Tattersall, 1977). Perhaps significantly, no ruffed lemur bony remains are known from any of the subfossil sites in northern Madagascar (L. Godfrey, personal commun.). Based on local reports of a rufous brown var-

iant NW of Maroantsetra (Tattersall 1977), and a study of museum holdings and collection records (Tattersall 1982; Buettner-Janusch and Tattersall, 1985), it was suggested that *V. v. variegata* and *V. v. rubra* are in secondary contact (i.e., hybridize) between the confluent Vohimara and Antainambalana Rivers. These suggestions prompted surveys in the environs of Maroantsetra, north of the Bay of Antongil, in tandem with conservation initiatives.

Two surveys completed since the mid-1980s seem to confirm the Antainambalana River as the current geographic divide between the black-and-white form and the red form, although neither survey was successful in actually locating hybrids. While *V. v. variegata* (*subcincta* type) was confirmed just west of the Antainambalana River near Andaparaty village (Lindsay and Simons, 1986; Simons and Lindsay, 1987), local villagers at Andaparaty, Ankorongana, and Sahantaha claim that “varinena” (vernacular for the red form) occur east of the Antainambalana River (fig. 3; Lindsay and Simons, 1986; Simons and Lindsay, 1987; Hekkala and Rakotonratsima, 1999). Unfortunately, lemur trapping and extensive swidden agriculture occur between the Antainambalana and Andranofotsy River valleys, but according to local reports, *V. v. rubra* may still be abundant in at least one locality there—on Anjanaharibe, a mountain rising to 1150 m (E. Hekkala, personal commun.). Although red ruffed lemurs were not actually sighted by survey teams between the Antainambalana and Andranofotsy River valleys, they were seen in two locations further east between the Andranofotsy and Mahalevona Rivers: near Sahavary village along the east bank of the Andranofotsy River (Lindsay and Simons, 1986; Simons and Lindsay, 1987), and along the Belampona, a small river between the Andranofotsy and Mahalevona watersheds south of the Masoala National Park border (Hekkala and Rakotonratsima, 1999). Lemur trapping and swidden agriculture are, unfortunately, common in this region as well (Hekkala and Rakotonratsima, 1999). Black-and-white ruffed lemurs may have been collected at Sahavary more than 100 years prior to 1986 (table 2).

These two surveys prompt further ques-

tions and suggest several conservation initiatives worthy of pursuit. First, the northern distribution of *Varecia* still remains unverified up to Andapa. Second, the survey teams paid special attention to the region approximately 40 km NW of Maroantsetra along the Antainambalana River (fig. 3), given the provenance of the one wild-caught hybrid known at the time. As this review indicates that the hybrid zone extended across two additional watersheds to the east, future surveys should investigate these regions in more depth, the Mahalevona watershed in particular. The survey by Lindsay and Simons did not include the Mahalevona watershed at all, and that by Hekkala and Rakotonratsima did not penetrate very far up it. There are verified reports of red ruffed lemurs in the upper reaches of the Mahalevona watershed from individuals involved in forest corridor work for the Masoala National Park (see Conservation Implications; Holloway, 1997; and see also Rand, 1932). Third, locating populations of ruffed lemurs between the Antainambalana and Andranofotsy rivers should be a priority. Local villagers refer to the lemurs in this region as “varinena” and indicate that they possess an abdominal belt of white fur, as in the black-and-white ruffed lemur (*subcincta* type) (Hekkala and Rakotonratsima, 1999). The suffix *mena* comes from *mena*, which in Malagasy refers not only to red, but also to light brown (as in brown sugar). Perhaps the “rufous brown variant” reported in this region by Malagasy informants, Georges Randrianasolo in particular (Tattersall, 1977), and hybrids are one and the same. Alternatively, if the “hybrid zone” is indeed much larger than previously suspected, it is worth pondering whether an entirely distinct variety or subspecies occurs or occurred within this region. If so, its numbers have been perilously reduced by human activity over the last century or more. This might explain why only “true” forms, black-and-white or red, have been witnessed in this region during recent surveys. Such populations might then be filtering in from areas farther east and farther west, where they have not been ravaged as extensively by habitat loss and hunting. It is well known that degraded habitat (and ecotones) are major factors that bring about hybridization as a result

of disrupted premating isolating mechanisms (i.e., ecological separation and normal behavioral incompatibility between congeners), especially under conditions where hybrids might be better adapted to disturbed habitat than are parental taxa (Moore, 1977).

GENETIC DATA

With modern methods that require no more than plucked hairs to assess relationships, museum hybrids and black-and-white and red forms of known provenance that co-occur comprise potential material for genetic study of the apparent ruffed lemur hybrid zone (tables 1 and 2). To date, however, genetic studies of ruffed lemurs have drawn primarily on captive animals whose lineages can in most cases be traced back to specific wild-caught individuals, but whose ancestral provenance is unclear or unknown. There are a few important exceptions. Tissue samples of wild red ruffed lemurs from Andranobe Forest in the Masoala National Park (Vasey, 1997) and of wild black-and-white ruffed lemurs from the Betampona Strict Nature Reserve (Britt et al., 1998), the Manombo Special Reserve (Ratsimbazafy, in prep.), and Ranomafana National Park (Balko, 1998) were recently collected. In combination with samples from captive ruffed lemurs, the samples from wild ruffed lemurs of known provenance have been used in recent genetic studies to assess variation within and among black-and-white and red ruffed lemurs. Two separate studies of variation between black-and-white and red ruffed lemurs, using different genes and different methods, are summarized here.

One study (Pastorini, 2000) includes wild red ruffed lemurs from Andranobe Forest ($n = 3$), captive red ruffed lemurs ($n = 3$), and captive black-and-white ruffed lemurs ($n = 3$). The captives originate from zoos in Europe and Madagascar, and all can be traced to wild-caught, true forms (I. Porton, personal commun.). The sample of red ruffed lemurs shows absolute pairwise genetic distances consistent with within-subspecies variation, whereas the sample of black-and-white ruffed lemurs shows genetic distances sufficient to designate two subspecies. Three separate tree-building methods (maximum

parsimony, neighbor-joining, maximum likelihood) show the red ruffed lemur samples clustering between two discrete sets of the black-and-white ruffed lemur samples. mtDNA genes used in this analysis consist of the 3' end of the COIII gene (53 bp), the complete NADH-dehydrogenase subunits ND3 (348 bp), ND4L (297 bp) and ND4 (1378 bp), along with the glycine (72 bp), arginine (68 bp), histidine (70 bp), serine (64 bp), and part of the leucine (47 bp) tRNA genes (Pastorini, 2000).

A second study includes wild red ruffed lemurs from Andranobe Forest ($n = 3$); wild black-and-white ruffed lemurs from Betampona ($n = 3$), Manombo ($n = 6$), and Ranomafana ($n = 14$); wild-caught animals recently held at Zoo Ivoloana, Tamatave ($n = 6$); captive ruffed lemurs from the Species Survival Plan (SSP) population ($n = 12$); a red ruffed lemur traceable to wild-caught parents ($n = 1$); and black-and-white ruffed lemurs traceable to wild-caught individuals ($n = 11$). The black-and-white ruffed lemur samples form two diagnosable units consisting of a southern group from Manombo and Ranomafana, and a northern group from Betampona (Wyner et al., 1999). Red ruffed lemurs comprise a distinct clade and form the sister group to all of the black-and-white ruffed lemurs sampled (Wyner, 2000; G. Amato, personal commun.). The highly variable control region (D-loop) mtDNA fragment (548 bp) was used to study variation among and between black-and-white ruffed lemur populations. The more conserved mtDNA ribosomal 12s rRNA and 16s rRNA regions were also sequenced, to examine the relationships between the black-and-white and red ruffed lemur samples. These phylogenetically informative ribosomal genes indicate that these two lineages had separated earlier than had the various black-and-white forms. We recognize that genetic distances as measured here are not absolutely correlated with speciation, and also that speciation is not an immediate or inevitable consequence of allopatry. Most if not all speciation events among primates probably occur only in allopatry, but morphological differentiation and speciation are not the same thing. Formally named subspecies may similarly be regarded as geographically subdivided popu-

lations (although, unlike species, they are variants that may intergrade phenotypically within a species' range, and in practical terms are essentially a taxonomist's convenience); and other processes besides allopatry can also result in speciation. These may even include hybridization (Arnold and Emms, 1998; Grant and Grant, 1998). Thus, the mtDNA ribosomal genetic data do not by themselves provide a definitive argument for a speciation event, although we regard the data given above as highly suggestive of this. Other approaches can thus usefully be brought to bear on recognizing species populations, and among them are the vocalization data we examine below.

VOCALIZATION DATA

Among vertebrates, species (and admittedly sometimes subspecies) commonly differ in their vocalizations. Vocalizations are especially good indicators of species status among nocturnal strepsirhines whose communication systems rely heavily on olfactory and auditory cues rather than on visual ones. Loud calls (advertisement calls in particular) give a strong indication that the communication systems of females and males have been finely tuned to one another, and, in effect, that a particular specific-mate recognition system has emerged (Patterson, 1985). Species definitions vary, but a stable specific-mate recognition system is generally agreed to be a critical feature in recognizing the reproductive inclusiveness of a species, whether in sympatry or allopatry, and is a strong indicator that divergence in the fertilization system inherited from the parental species has occurred. Specific-mate recognition systems have been especially well demonstrated in closely related galagos, whose advertisement calls show distinct, species-specific acoustic structures, which seem to be involved both in mate recognition and mate choice (Zimmerman et al., 1988; Zimmerman, 1995a, 1995b). Vocalization data are particularly useful for distinguishing strepsirhine species in the field, often providing the first clues that groups of animals may differ in other features of their fertilization system, anatomy, life history, genetics, ecological

niche, and social behavior (Masters, 1998; Bearder, 1999).

One loud call emitted by ruffed lemurs is referred to as the "pulsed squawk" (aka "uh-uh-uh . . ." call). It functions as a terrestrial predator alarm call but is also used in other high arousal contexts (Macedonia and Taylor, 1985; Morland, 1991; pers. obs.). This call differs between black-and-white and red ruffed lemurs in median high frequency, pulse rate, and pulse duration; and because of its relatively narrow frequency band pulse, it has been considered a good indicator of phyletic divergence (Macedonia and Taylor, 1985). Nonetheless, in the study in which this was revealed, Macedonia and Taylor (1985) did not consider upgrading black-and-white and red ruffed lemurs to full species based on their acoustic study of this call, since they simply retained the subspecific nomenclature that was available when they published. Divergence in the "pulsed squawk" call is clearly not just a matter of dialects, such as those recently discovered in neighboring populations of the grey mouse lemur, *Microcebus murinus* (Hafen et al., 1998); black-and-white and red ruffed lemurs are separated geographically, and do not normally form overlapping demes.

In conjunction with the evidence noted for phylogenetic splitting from mtDNA ribosomal genes, the two forms' largely distinct geographic distributions, their differences in pelage color and pattern, and other historical factors detailed in previous sections, such quantified differences in the ruffed lemurs' terrestrial antipredator calls constitute persuasive evidence that black-and-white and red ruffed lemurs warrant separate species status and should appropriately be referred to by the binomina *Varecia variegata* (Kerr, 1792) and *Varecia rubra* (E. Geoffroy, 1812), respectively. We feel reasonably confident that our case for upgrading black-and-white and red ruffed lemurs to separate species will be strengthened by field and captive studies of sexually dimorphic calls. Such studies would provide especially useful additional evidence to evaluate whether divergent specific-mate recognition systems have evolved in the two forms. The ruffed lemur vocal repertoire includes various sex-specific calls and a loud call to which females and

males contribute differently (e.g. the “roar-shriek”; Morland, 1991; personal obs.). Demonstration of specificity in such calls would form a solid basis for an acoustic study of specific-mate recognition systems among ruffed lemurs.

SYSTEMATIC SUMMARY

The fact that the two forms of *Varecia* may occasionally form hybrids, and readily do so in zoos, is not necessarily significant in determining their species status. Speciation, after all, is not a unitary mechanism, but is instead an outcome, with numerous potential underlying causes. Isolating mechanisms may operate at any of various levels, whether behavioral, chromosomal, anatomic, or developmental. The essential question is not whether hybrid zygotes may develop normally, or even reproduce successfully as adults, but is rather whether under normal circumstances there is any biologically meaningful gene exchange between the two populations. Among the two kinds of ruffed lemur this does not appear to be the case, for although there appears plausibly to be, or to have been, a geographically quite extensive zone of occasional hybridization between the black-and-white and red ruffed lemurs in the region shown in figure 3, hybridization within that zone has apparently been a rare occurrence at best. There is certainly nothing known that could be described as a zone of intergradation among the two populations. Habitat deterioration caused by human activity in the region might conceivably have resulted in the disappearance of a distinctive population bearing hybridlike characteristics. However, it is very much more likely that such habitat disruption has artificially facilitated hybridization within the zone. This, of course, would make the apparent rarity of hybridization even more puzzling if we were dealing with but one species. Our conclusion, then, is ineluctable. The two major forms of ruffed lemur warrant recognition as two distinct species (two effectively autonomous reproductive units): *Varecia variegata* and *V. rubra*.

As actual or potential evolutionary ephemera, subspecies may be recognized if they are useful to the taxonomist. And while, as not-

ed, there is more variation in pelage coloration amongst the red ruffed lemurs than has usually been appreciated, such variation appears to be relatively evenly distributed within the red ruffed lemur population and shows no geographical patterning. *Varecia rubra* can thus be regarded as variable but monomorphic. On the other hand, the black-and-white form does show at least four relatively distinctive variants, of which three have been given their own taxonomic designations: *variegata*, *editorum*, and *subcincta*. Distributional data on museum specimens representing these variants has been woefully lacking. But combining what little is certainly known from museum specimens with reliable recent field observations (kindly contributed by Andrea Katz [for Betampona] and Elizabeth Balko [for Ranomafana and Kianjavato], in addition to unpublished observations by I.T. both to the north and the south of the Mananara River in the far south) leads to a complex picture.

Although there appears to be a very vague tendency toward lightness in the pelage of *Varecia variegata* from north to south, the four distinctive variants recognized by Tattersall (1982) seem to be relatively randomly distributed across space (fig. 2). Individuals of the *variegata* type are found mainly south of Mananjary, but have also been collected as far north as Mananara; *subcincta* is found in the region to the west of Toamasina (Tamatave), but then so are *variegata* and *editorum*; *subcincta* is found as far north as the Maroantsetra region, but also as far south as Fenoarivo, but with *variegata* in between; and so on. In the absence of any clear geographic patterning within the huge area of distribution of *Varecia variegata*, it seems more realistic to regard this species as a population embracing several possibly largely discrete pelage coloration patterns, which are probably quite simply genetically determined, than as one that is usefully divisible into discrete geographic subspecies. The conclusion as regards the black-and-white ruffed lemurs thus appears to be variable (in a fashion different from the red ruffed lemur), but monotypic. We cannot concur with Groves (2001) in raising variants of *Varecia variegata* to subspecies status.

CONSERVATION IMPLICATIONS OF *VARECIA* SYSTEMATICS

Earlier we indicated that documentation of a natural hybrid zone would be of great significance in designating geographic priorities for habitat conservation, for captive management, and for lemur systematics generally. Our review of historical documents and taxonomy suggests that the down-ranking of the black-and-white and red ruffed lemurs to subspecies was largely influenced by the substantial number of hybrids produced in captivity. Captive hybridization of lemurs occurred before 1870, and it is highly likely that the taxonomic revisions of *Varecia* in the 19th century were influenced by such breeding practices, whether intentional or not. We now know that black-and-white and red ruffed lemurs have distinct geographic distributions, genetic profiles, and loud calls, and that in sum these distinctions make a strong case for separate species recognition for black-and-white and red ruffed lemurs.

A review of museum holdings and collection records suggests that a natural hybrid zone between black-and-white and red ruffed lemurs occurred north of the Bay of Antongil, extending as far east as the Mahalevona River and as far west as the Vohimara River, a tributary of the Antainambalana (fig. 3). Although hybridization appears to be rare, this hybrid zone is considerably larger than previously thought. Recent surveys have located populations of both the red form and the black-and-white form in this region; degraded habitat may currently prevent the two forms from coming into frequent contact, but it may equally also bring about hybridization at times when contact is made. As with the Antainambalana and Andranofotsy River valleys (Lindsay and Simons, 1986; Hekkala and Rakotonratsima, 1999), the Mahalevona River valley is well populated by humans, especially in its southern reaches (CARE/WCS/PF, 1995). A *subcincta*-like form with reddish brown fur in place of black may exist between the Antainambalana and Andranofotsy watersheds, but this report requires verification. Future surveys should also investigate the Mahalevona watershed, where we have documented an additional hybrid and regions of overlap.

The recently established Masoala National Park was designed to shelter several patches of littoral forest, a considerable, contiguous portion of the Masoala Peninsula, a band of forest running northeast by southwest between the Ambanizana and Mahalevona watersheds, and a small band of forest running east to west between the Mahalevona and Andranofotsy River valleys (fig. 3). These bands of forest in the northernmost reaches of the Masoala National Park are connected to the main body of the Park via three forest corridors which are under active restoration, but are each less than 1 km wide (Holloway, 1997, 2000). The Masoala Peninsula, including the corridors, suffered devastating damage during Cyclone Huddah, which struck on 2 April 2000. Cyclones leave a poignant message behind when they rupture such tenuous links between forest patches. Given our current understanding of the ruffed lemur hybrid zone, forest corridors between intact forest patches will be more critical than ever in maintaining population networks for ruffed lemurs (and other forest-bound taxa) north of the Bay of Antongil. However, to bridge the entire hybrid zone, a protected network of intact forest patches and actively managed forest corridors must extend farther east between the Andranofotsy and Antainambalana watersheds. If we are successful in establishing a network of forest patches and corridors, perhaps we will know again what naturalists may have known long ago; that two distinct variegated lemurs meet in a restricted hybrid zone in northern Madagascar, but that hybridization between them is and was rare. In the longer term, biodiversity in northern Madagascar must be held intact by forest corridors connecting protected areas further north (the Parc National de Marojeje and the Réserve Spéciale d'Anjanaharibe-Sud), farther south (the Parc National de Verezanantoro), and farther east (the Réserve Spéciale de Manongarivo and the Réserve Naturelle de Tsaratanana) (see also Ganzhorn et al., 1996/1997; Goodman, 1999).

ACKNOWLEDGMENTS

We thank many individuals for kindly arranging access to museum holdings and documents, including Richard Thorington and

Linda Gordon (Washington, D.C.), Paula Jenkins and the late Prue Napier (London), Chris Smeenk and A.M. Husson (Leiden), Francis Petter, Michel Tranier, and Roger Saban (Paris), Edi Rutzmoser (Cambridge, Mass.), and Guy Musser, Sydney Anderson, and Chris Norris (New York). Ian Tattersall particularly expresses his appreciation to the late Georges Randrianasolo for so generously sharing his expertise on lemur distributions. We thank George Amato (WCS) and Yael Wyner (AMNH) who made a valuable contribution to the genetics section of this paper. Ken Mowbray of the AMNH helped in many ways, and particularly in preparing the color plate with images furnished by David Haring (DUPC) and Natalie Vasey. Ken Cameron, D.V.M. (Cincinnati Zoo) and Stephen Nash (SUNY, Stony Brook) also helped with visual documentation. Bridget Thomas kindly drafted figures 1 and 2. We would also like to thank the staff librarians at the United States National Museum, the National Zoological Park, the Library of Congress (Washington, D.C.), and the American Museum of Natural History for assistance in locating many documents, including rare illustrations of ruffed lemurs. Thanks also go to Stefan Falke for help with German translation, to Evon Hekkala and Marius Rakontondratsima for access to their unpublished survey report, to David Lees and Russell Thorstrom for help with geo-referencing sites, to Ingrid Porton for providing pedigrees for captive-born ruffed lemurs, and to Andrea Katz and Elizabeth Balko for field identifications from Betampona and Ranomafana/Kianjavato, respectively. We thank Laurie Godfrey, Erik Gunther, Judith Masters, Elwyn Simons, Anne Yoder, and Bob Sussman for their comments on an earlier draft of this paper.

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