

Metachromism and Its Phylogenetic Implications for the Genus *Eulemur* (Prosimii: Lemuridae)

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Introduction

In 1968, Hershkovitz [1] introduced his 'principle of geographic metachromism' to account for evolutionary change in mammalian tegumentary colors. Based on coat color genetics established by domestic animal breeders [2] and the relationships of coat color to patterns of geographic distribution in mammals, Hershkovitz proposed that irreversible changes in the melanin banding patterns of hair could be used to assess phylogenetic affinities among closely related mammalian taxa. His principle asserts that the ancestral configuration of melanin deposition in mammalian hair results in a cryptic 'agouti' pattern, comprising alternating bands of eumelanin (black/brown) and pheomelanin (reddish/yellow) pigment granules. As populations evolve, these alternating bands can be lost but, importantly, *not regained*. Loss of eumelanin bands eventually produces a reddish (pheomelanin-saturated) hair, whereas loss of pheomelanin

bands produces a black (eumelanin-saturated) hair. The only modification of a hair shaft's pigmentation occurs through 'bleaching' or a decrease in the amount of pigment present. Bleaching and loss of bands are processes that can function together or independently. Along the eumelanin pathway, pigment fades as black-brown-drab-gray-white; along the pheomelanin pathway, pigment fades as red-gold-yellow-cream-white. Albinism, the absence of pigment, is the end point for both pathways. Switching from one pathway to the other is possible, and several bands or levels of pigment concentration can be lost in single 'jumps'. Any melanin-containing tegument, such as skin and eyes, follows the same course of bleaching. Metachromism has been examined previously in hair banding/color patterns, as well as in color patterns of piliary fields (i.e. pelage 'patches') [1, 3–7].

According to Hershkovitz [1, 3], metachromism applies to all mammals, regardless of their habits. Since its inception, no data

have been demonstrated to run counter to the principle of metachromism [4, 7]. The principle is, nevertheless, a 'rule' that requires sources of empirical support. To date, few studies have compared proposed phylogenetic assessments based on metachromism with those resulting from analyses of other characters. One exception is a phylogenetic study of subspecific variation in facial morphology of *Saguinus fuscicollis*, the saddle-back tamarin [8]. Previously, Hershkovitz [1, 3] had used metachromism to reconstruct the evolutionary radiation of this group and proposed that geographic proximity was less reliable than metachromism for assessing the phylogenetic affinities of its members. The recent finding that facial morphology was correlated significantly more strongly with metachromism in *S. fuscicollis* subspecies than with their geographic relationships [8] supports the application of metachromism to questions of phylogeny.

Although the concept of shared, derived characters has indisputable value for phylogeny reconstruction, maintaining that taxa always diverge dichotomously from an ancestor – which immediately ceases to exist and which can never be recognized – is unrealistic [7]. In contrast, the principle of metachromism has been applied fruitfully to the systematics of living primates largely in terms of anagenesis or linear ancestor-descendent sequences [1, 3, 5–7]. Caution must be exercised, nevertheless, when drawing conclusions from comparisons of hair banding patterns in taxa *above the subspecies level*. Once gene flow among populations of a species ceases, each population follows its own course of metachromatic evolution – much of which, due to the postulated unidirectional nature of metachromism, is expected to occur in parallel. In addition, not

only may different environmental pressures select for different *rates* of metachromatic evolution among taxa (e.g. advantages of being cryptic, thermoregulation), different tegumental characters within the same taxon may evolve at different rates (e.g. hair color vs. eye color). Under such conditions, the value of metachromism as an indicator of phyletic affinities could be compromised. Though unstated by Hershkovitz [1, 3], it is for this reason that metachromism lacks power as a character on which explicit phylogenetic hypotheses should be founded [1, 3, 5–7]. Rather, the strength of metachromatic analysis lies in its ability to *rule out* certain phylogenetic hypotheses.

With these caveats in mind, we report below a study that examines the phylogenetic implications of metachromism in the lemurid genus *Eulemur* [9]. Our primary source of comparative data is the number of pheomelanin bands present in hair from species and subspecies comprising this genus. Other metachromatic characteristics, such as facial coloration and hypertrichy (conspicuously lengthened regions of hair) supplement the primary data. Finally, we compare our results to those of Groves [7, pp. 90–92, his fig. 4.3], who also used metachromism in postulating phylogenetic affinities among *Eulemur* and other primate taxa.

Methods

Nomenclature

As the generic name '*Eulemur*' is a recent taxonomic designation (i.e. 1988) and is not yet fully incorporated into the literature, a brief explanation of its use here seems warranted. According to nomenclatural convention, if the type species of a genus is removed from that genus, the generic name is retained by the type, and a new name must be supplied to the remaining taxa. The recent formal recognition

that *Lemur catta* and species of the genus *Hapalemur* share several anatomical and behavioral traits that neither shares with other *Lemur* taxa [9, 10 and citations therein] prompted the removal of *L. catta* from the genus *Lemur*. As *L. catta* was the type species of the genus, it retained the generic name, and a new name was needed for the remaining ‘*Lemur*’ taxa. Although several possible generic names were entertained, publication date priority established *Eulemur* [9] as the generic name for ‘*Lemur*’ taxa other than *L. catta* [11 and I. Tattersall, pers. commun.].

Sampling and Analysis

Between June 1989 and March 1990, we gathered hair samples periodically from *Eulemur* species and subspecies housed at the Duke University Primate Center (DUPC, Durham, N.C., USA). Only two of the twelve recognized taxa were unavailable for study (table 1). A pinch of hair was taken from the mid-back region of donors, without causing obvious discomfort, while each was being distracted by offerings of raisins. The mid-back was chosen as the location for hair extraction because it appears to be the most metachromatically conservative portion of the pelage in lemurs, as has been shown for some other primates [3]. A typical representative of each sex was chosen for each *Eulemur* taxon. Hair from a hybrid male offspring of an *E. rubriventer* female and *E. fulvus sanfordi* male cross also was sampled. If any doubt arose as to the taxon-representative characteristics of the sample obtained, a verification sample was taken from a different donor. Second samples taken from *E. fulvus collaris*, *E. fulvus fulvus* and *E. macaco macaco* confirmed the results of the original samples: in no case did banding patterns differ between same-sexed individuals of a given taxon.

Each sample was analyzed by selecting 15 hairs randomly and mounting them for microscopic examination. The total length of each hair was measured, as was the width of each eumelanin and pheomelanin band. For each hair, bandwidths were converted to percentages of total hair length. Mean values were calculated for the group of 15 hairs for absolute and relative (i.e. percent) lengths of each band.

Saturation of pigment also varies among *Eulemur* taxa and between the sexes. We chose not to quantify saturation (using a photospectrometer), however, because color is a continuous variable having limited value as a phylogenetic character (i.e. character state delineations would be largely arbitrary).

Table 1. Taxa comprising the genus *Eulemur*

Species	Subspecies
<i>E. fulvus</i>	<i>fulvus</i> <i>rufus</i> <i>sanfordi</i> <i>albifrons</i> <i>collaris</i> <i>albocollaris</i> ¹ <i>mayottensis</i> ¹
<i>E. macaco</i>	<i>macaco</i> <i>flavifrons</i>
<i>E. mongoz</i>	–
<i>E. coronatus</i>	–
<i>E. rubriventer</i>	–

From Simons and Rumpler [9].

¹ Not available at the DUPC for study.

General Patterns of Facial Coloration, Hypertrichy and Other Tegumentary Traits

All *E. fulvus* subspecies are sexually dichromatic and exhibit sexually dimorphic facial hypertrichy (i.e. sex-specific differences in dimensions of ear tufts, facial ruffs and beards), whereas ‘non-*fulvus*’ taxa in this genus show only sexual dichromatism (fig. 1).

The least sexually dichromatic subspecies is *E. fulvus fulvus*, in which the male (fig. 1a) exhibits a black face and a whitish beard consisting of hairs that retain some evidence of ‘agouti’ banding. The ears are tipped with short white hairs. The female is similar, although the face is less eumelanin saturated and the beard is less developed than the male’s.

The face of male *E. fulvus rufus* is cream colored with a broad, black stripe running between the eyes from the crown to the nose (fig. 1b). The beard is golden-red, the crown rusty-red, and cream-colored patches are found above the eyes. In the female, cream is replaced by grayish white, and the crown is black. The facial ruff of the female is less developed than that of the male.

Both sexes of *E. fulvus collaris* exhibit an orange beard, which in the male is slightly larger and which sometimes becomes increasingly cream colored with proximity to the face (fig. 1c). The male exhibits the

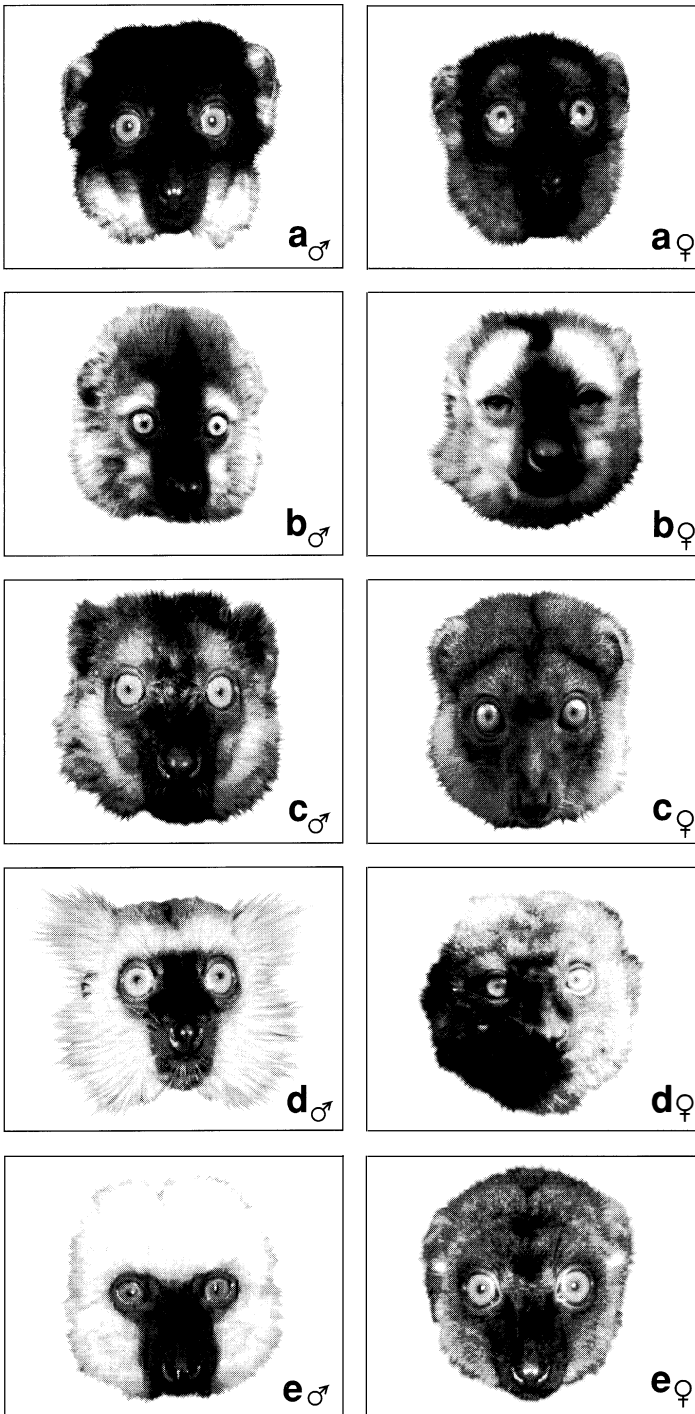


Fig. 1. Faces of representative males and females of *E. fulvus* subspecies. **a** *E. fulvus fulvus*. **b** *E. fulvus rufus*. **c** *E. fulvus collaris*. **d** *E. fulvus sanfordi*. **e** *E. fulvus albifrons*.

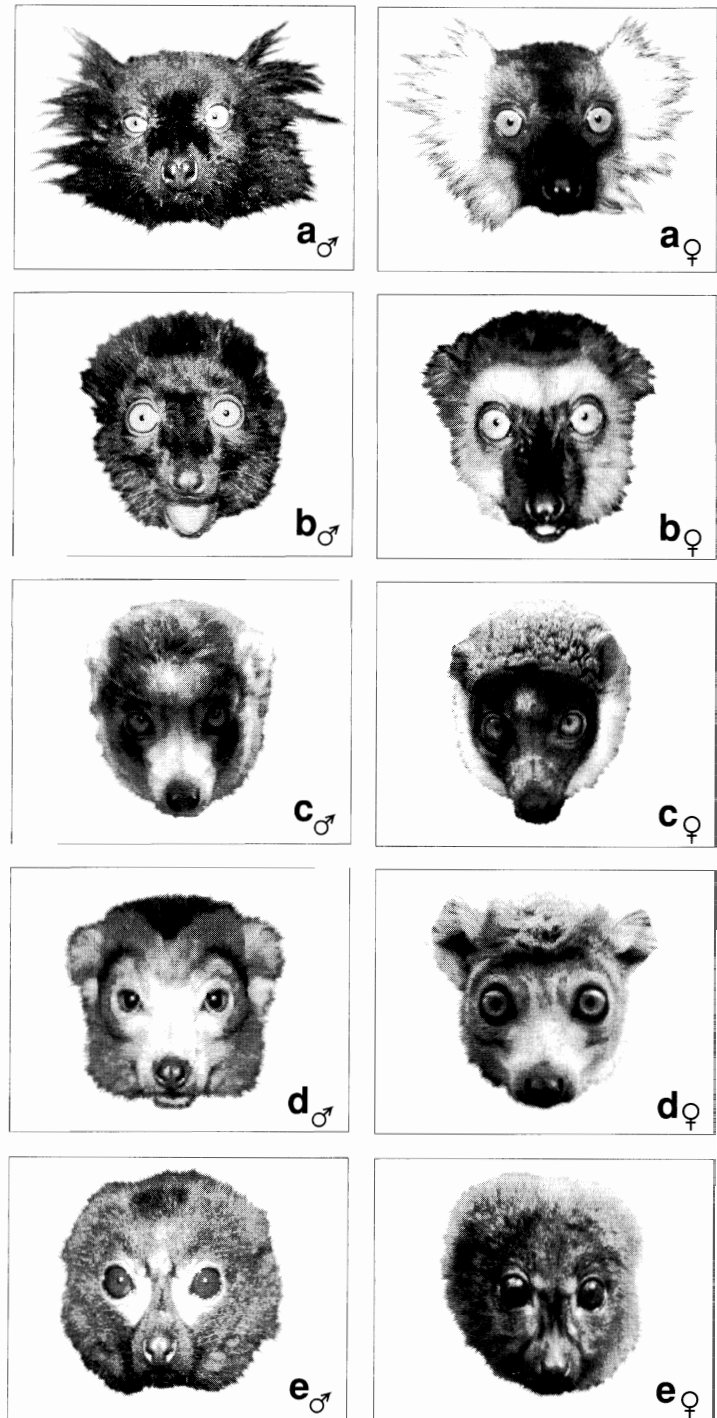


Fig. 2. Faces of representative males and females of *Eulemur* taxa other than *E. fulvus*. **a** *E. macaco macaco*. **b** *E. macaco flavifrons*. **c** *E. mongoz*. **d** *E. coronatus*. **e** *E. rubriventer*.

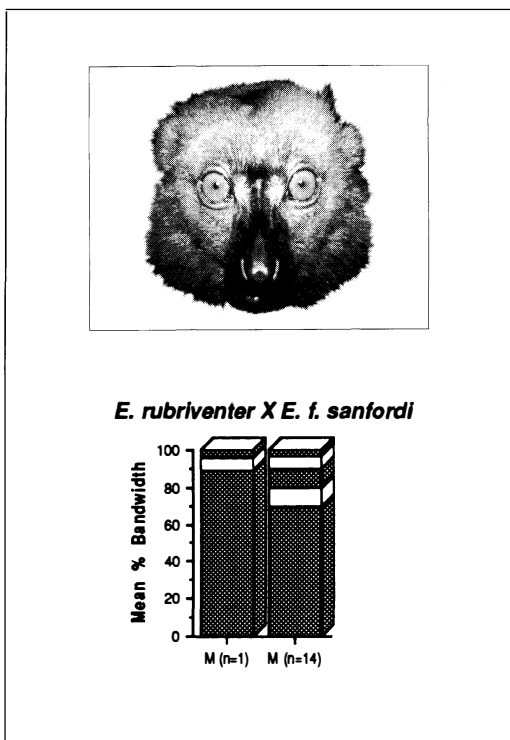


Fig. 3. Face of male hybrid from female *E. rubriventer* X male *E. fulvus sanfordi* mating, and the eumelanin (hatched) and pheomelanin (open) banding patterns observed in his hair sample; m = male; n = number of hairs exhibiting that banding pattern from a total of 15.

wide eumelanin-saturated stripe of fur between the eyes seen in *E. fulvus fulvus* and *E. fulvus rufus*, which in the female is largely grayish.

Male *E. fulvus sanfordi* exhibit long pale ear tufts (fig. 1d) and a pale ring of fur surrounding the face, whereas male *E. fulvus albifrons* possess a luxuriant white facial ruff (fig. 1e). Females of both subspecies have dark gray faces and lack any form of hypertrichy.

In both *E. macaco* subspecies, male are entirely black (fig. 2a, b), and females are dark reddish to pale yellowish gold in body color. Female *E. macaco macaco* (fig. 2a) exhibit the black forehead stripe seen in some *E. fulvus* subspecies, whereas female *E. macaco*

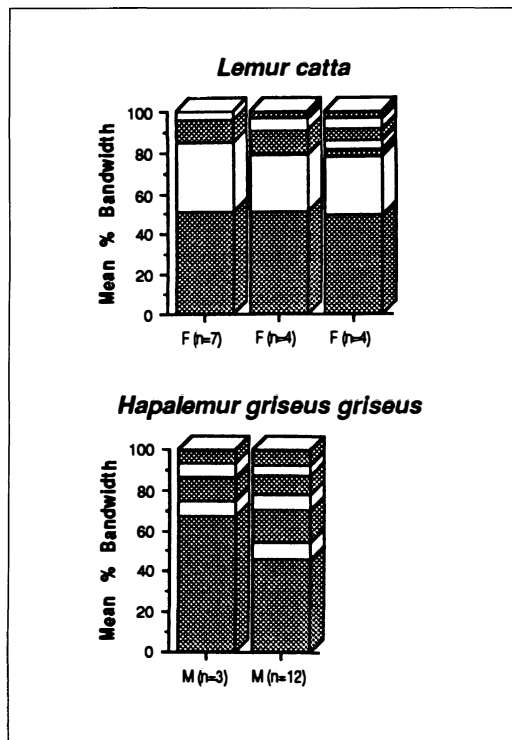


Fig. 4. Eumelanin (hatched) and pheomelanin (open) banding patterns in hair samples from sexually monochromatic lemurs: *L. catta* and *H. griseus*; M and F = males and females; n = number of hairs exhibiting that banding pattern from a total of 15 for that sex.

flavifrons (fig. 2b) exhibit the pale ring of facial fur seen elsewhere in *Eulemur* only in male *E. fulvus sanfordi*. Both sexes of *E. macaco macaco* exhibit equally extravagant facial ruffs that incorporate long ear tufts (as seen in *E. fulvus sanfordi* males), but this trait is absent in both sexes of *E. macaco flavifrons*. The eye color of *E. macaco macaco* is orangish brown, which is typical of the genus, but in *E. macaco flavifrons* eye color is bleached and ranges from pale blue or green to turquoise.

In *E. mongoz*, both sexes possess a white muzzle, and the ears appear small and are covered with short whitish hair (fig. 2c). Males exhibit a reddish beard; females have a white beard.

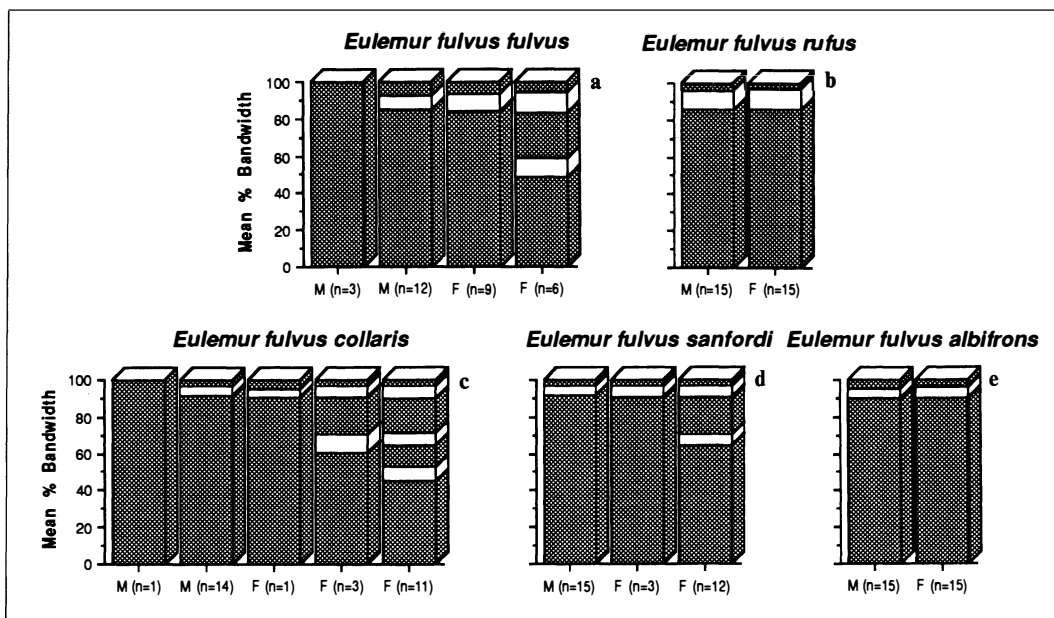


Fig. 5. Banding patterns in hair samples from *E. fulvus* subspecies; details as in figure 4.

E. coronatus is similar to *E. mongoz* in that males tend toward a reddish gray body coloration whereas females are more grayish. The faces of males are white, and in females the white gives way to gray on the cheeks and around the eyes (fig. 2d). In males, the crown is black, and the face is framed with reddish orange hair. In females, the crown and areas in front of the ears are gray, with a narrow, chevron-shaped band of reddish orange hair at the front of the crown giving the appearance of a tiara. The ears of *E. coronatus* are conspicuously large, and are covered with short white hair.

In *E. rubriventer* (fig. 2e), both male and female are a dark chestnut-red, though the female exhibits a yellowish white ventrum. The male has a white 'tear-drop' marking extending a short distance down the rostrum from the medial corner of each eye. The ears are small and are covered with the same reddish-colored hair that surrounds and largely obscures them.

The coloration and hypertrichy patterns exhibited by the male *E. rubriventer* × *E. fulvus sanfordi* hybrid (fig. 3) were most like those of *E. rubriventer*, although the hair was more orangish. The hybrid exhib-

ited a degree of albinistic facial skin around and between the eyes, but this was less conspicuous than is characteristic of *E. rubriventer* males.

Results

A maximum number of three pheomelanin bands occurs in the hair of *Eulemur* species, as well as in the closely related *L. catta* and *Haplemur griseus* (fig. 4), suggesting that three pheomelanin bands is the primitive state for this character in the Lemnidae. In *E. fulvus collaris*, *E. fulvus fulvus* and *E. fulvus sanfordi*, banding patterns differed between the sexes, with males being more derived in possessing fewer bands than females (fig. 5). Banding patterns were sexually monomorphic in *E. fulvus rufus* and

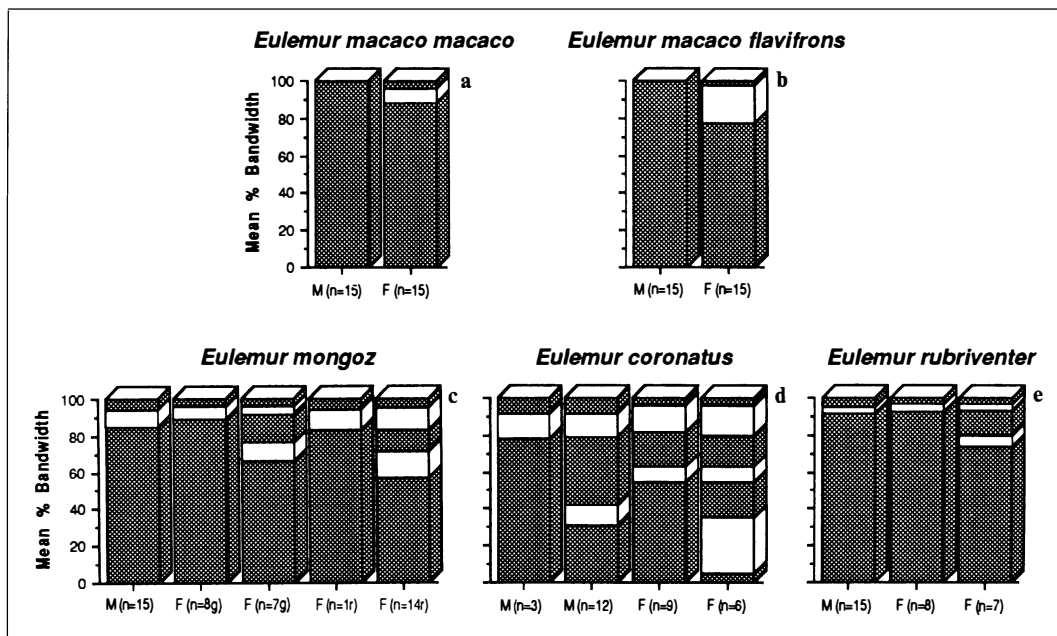


Fig. 6. Banding patterns in hair samples from *Eulemur* taxa other than *E. fulvus* subspecies; details as in figure 4. Note: the letters 'g' and 'r' in *E. mongoz* represent samples from adjacent gray and red regions of the mid-back in females of this species.

E. fulvus albifrons. Because females proved to be metachromatically more conservative than males, we consider females to be more phylogenetically informative for this character. The sequence from the most primitive (numerous, broad bands) to the most derived (few, narrow bands) pattern of banding observed in females was: *E. fulvus collaris* – *E. fulvus fulvus* – *E. fulvus sanfordi* – *E. fulvus rufus* – *E. fulvus albifrons*. Males of all *E. fulvus* subspecies were found to possess at most a single pheomelanin band (fig. 5). The sequence from the most primitive to the most derived banding pattern observed in females of other *Eulemur* taxa was: *E. coronatus* – *E. mongoz* – *E. rubriventer* – *E. macaco flavifrons* – *E. macaco macaco* (fig. 6).

In the male *E. rubriventer* × *E. fulvus sanfordi* hybrid, 14 of the 15 hairs measured exhibited two pheomelanin bands (fig. 3). This is striking in that males of both parental taxa possess a single pheomelanin band only.

Discussion

Given the tenet that melanin bands in hair cannot be regained once lost [1, 3, 4], our results suggest the following: (a) neither *E. fulvus rufus* nor *E. fulvus albifrons* could be ancestral to *E. fulvus collaris*, *E. fulvus fulvus* or *E. fulvus sanfordi*; (b) no subspecies of *E. fulvus* could be ancestral to *E. fulvus col-*

laris; (c) neither of the *E. macaco* subspecies could be ancestral to *E. mongoz*, *E. coronatus* or *E. rubriventer*, and (d) no *Eulemur* taxon could be ancestral to *E. coronatus*. These conclusions can be compared with Groves' [7] proposal that there must have been at least three separate anagenetic lines of descent in *Eulemur*: (1) *E. fulvus fulvus* to *E. fulvus sanfordi* to *E. fulvus albifrons*, with a side-branch from *E. fulvus fulvus* to *E. mongoz*; (2) *E. fulvus fulvus* to *E. fulvus collaris* to *E. fulvus albocollaris*, and (3) *E. fulvus fulvus* to *E. fulvus rufus* to *E. rubriventer* to *E. macaco*, with a side-branch from *E. fulvus rufus* to *E. coronatus*. Results of the present study do not contest the first of these proposed lines of descent, but they do argue against the other two.

Our results conflict with Groves' [7] proposed *E. fulvus fulvus* – *E. fulvus collaris* – *E. fulvus albocollaris* sequence, because the triple-banded hairs of female *E. fulvus collaris* could not have been derived from the double-banded hairs of female *E. fulvus fulvus*. Note, however, that although we chose to quantify melanin bands in hair sampled from the mid-back region, we did find that *E. fulvus fulvus* was unique among *E. fulvus* subspecies in that hairs of the beard exhibited multiple bands. In this characteristic, then *E. fulvus fulvus* is the most metachromatically primitive of the *E. fulvus* subspecies. Also, if the 'common equals primitive' rule of thumb [7] is viewed in light of the rarity of sexual dichromatism in lemurs (i.e. it is appreciable only in *Eulemur*), the fact that *E. fulvus fulvus* is the most sexually monochromatic of the *E. fulvus* subspecies supports the proposition that this is the most primitive member of the species. In addition, female *E. fulvus collaris* exhibit facial fur coloration and patterning that is much

like that of the clearly derived *E. fulvus sanfordi* and *E. fulvus albifrons*. Thus, if *E. fulvus fulvus* advanced metachromatically more rapidly in mid-back pelage than had *E. fulvus collaris* since the time of their separation, Groves' [7] proposal that *E. fulvus fulvus* is the stem taxon of the *E. fulvus* subspecies would be supported. Although *E. fulvus albocollaris* was not available for our study, Groves' hypothesis that the orange-bearded *E. fulvus collaris* gave rise to the white-bearded and parapatric *E. fulvus albocollaris* [7, 12] is in keeping with the principle of metachromism.

Our data challenge Groves' [7] proposed *E. fulvus fulvus* – *E. fulvus rufus* – *E. rubriventer* – *E. macaco* sequence in that the double-banded hairs of female *E. rubriventer* could not have been derived from the single-banded pattern seen in *E. fulvus rufus*. Our results are not at odds, however, with the other components of this ancestor-descendent sequence. Finally, our data conflict with Groves' proposed *E. fulvus fulvus* to *E. coronatus* sequence, as the triple-banded hairs of female *E. coronatus* and double-banded hairs of male *E. coronatus* could not be derived from the single-banded hairs of *E. fulvus fulvus*.

With regard to the male *E. rubriventer* × *E. fulvus sanfordi* hybrid, Hershkovitz [3] pointed out that the 'irreversibility' of metachromatic change may not hold in the case of intertaxon hybridization. Although it is unknown if this interspecific hybrid is reproductively viable (other *E. rubriventer* × *E. fulvus* hybrids [sexes not noted] have been found to be sterile [13]), the atavistic appearance of two pheomelanin bands in the male offspring of parental taxa whose males exhibit only a single pheomelanin band raises an interesting point: were a *Eulemur* taxon

to have arisen as the product of natural hybridization between two species or subspecies [14], the hair banding patterns of this taxon potentially could result in a misreading of its derivation.

A further source of conflict may arise when different tegumentary traits have evolved at different rates between two subspecies. For example, the subspecies *E. macaco macaco* and *E. macaco flavifrons* each are highly derived for different metachromatic features: extreme aural hypertrichy in the former and bleached iris color in the latter. Nevertheless, metachromism permits the possibility to be ruled out that one of the *E. macaco* subspecies was directly ancestral to the other, at least as given their present appearance.

In sum, our results suggest that some (but not all) of the ancestor-descendent sequences postulated by Groves [7] for the genus *Eulemur* are improbable. These results suggest also that *E. fulvus collaris* may be the most primitive *E. fulvus* subspecies and *E. coronatus* the most primitive *Eulemur* species. Analyses of other characters are needed to check the conclusions drawn here from patterns of metachromism in *Eulemur*.

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Addendum

As this paper was going to press, Tattersall and Schwartz [1] published a phylogenetic analysis of the 'Lemur group' based on craniodental characters. In that study, the authors questioned the taxonomic legitimacy of *Eulemur* on the grounds that their craniodental data did not support a *Hapalemur* sp./*Lemur catta* sister group relationship and the concomitant distinction of *Eulemur* as a genus apart. Tattersall and Schwartz [1] proposed further a return to a pre-1980s view of lemurid taxonomy, which subsumed *L. catta*, *Varecia variegata* and those taxa currently assigned to *Eulemur* within the genus *Lemur*. We take issue with this recommendation on several grounds, the least of which is that the resolution of lemurid phyletic affinities provided by the craniodental data is, as the authors point out [1], inconclusive. The lack of craniodental support for a *Hapalemur* sp./*L. catta* clade does not, in our view, constitute a strong argument against the existence of such a clade, particularly given the support provided for it by certain other characters [2, 3]. Taxonomic revisions should be made on the basis of evidence, rather than on the lack of it.

Tattersall and Schwartz [1, 18] have suggested that the taxa under consideration here comprise an 'apparently monophyletic group [which] is structurally so close-knit that it is extremely difficult to establish relationships within it ...'. It therefore is noteworthy that in a previous paper, Tattersall [4] argued that stereotyped patterns of behavior, such as vocal and olfactory displays, may be useful phylogenetic indicators when the taxa of interest are closely related, as in the current case. In the same paper, Tattersall [4, 123] rightfully lamented that 'at this point ... we know rather little even about the gross vocal repertoires of most strepsirhines, and know virtually nothing at all about subtle differences in auditory signals between closely related species or populations'.

Fortunately, this situation is changing. We now can add to the pioneering surveys of vocal communication in lemurs conducted by Andrew [5] and Petter and Charles-Dominique [6] a study of vocal communication in the ruffed lemur (*V. variegata variegata*) [7] and a detailed analysis of the ring-tailed lemur (*L. catta*) vocal repertoire [8]. Even closer to the issue at hand is work in progress that follows Tattersall's [4] advice directly: a comparative study of vocalization structure in the Lemuridae [Macedonia and Stanger, in preparation]. In contrast to the craniodental evidence [1], pre-

liminary comparison of lemurid call structure ([5]; Macedonia and Stanger, in preparation) supports the notion of a *Hapalemur* sp./*L. catta* clade (as does also, it may be noted, stereotypy in scent-marking behavior [3, 9]), although a similar statement that bears directly on the question of *Eulemur* monophyly would seem, at present, premature. Thus, to avoid exacerbating current uncertainties in lemurid systematics, we suggest the continued recognition of the genus *Eulemur* until the time when, if ever, compelling evidence to the contrary is brought to light.

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