

Is the morphological disparity of lemur skulls (Primates) controlled by phylogeny and/or environmental constraints?

BÉNÉDICTE VIGUIER*

CNRS UMR 5561 'Biogéosciences', Centre des Sciences de la Terre, 6 boulevard Gabriel, 21000 Dijon, France

Received 5 July 2001; accepted for publication 10 April 2002

The cranial morphology of *Lemur catta* and of the five species of the genus *Eulemur* is investigated here by landmark identification and Procrustes superimpositions. This geometrical morphometric method makes it possible to describe pure shape differences independent of size effects, and to quantify differences between specimens. The aim of this study is to determine whether the morphological disparity of lemur skulls is constrained by the environment and/or by the group's phylogenetic history. First, Procrustes residuals are analysed by principal component analysis and the scatter-plots interpreted against the geographical distributions of taxa to determine whether morphology is correlated with geography. Then, a morphological distance tree is computed and compared with various cladograms reported in the literature to test for any correlation between morphology and phylogeny. Morphological disparity is found to be closely correlated with geographical distribution but independent of phylogeny. This confirms that the morphological disparity of lemur skulls is associated with a high degree of homoplasy, probably as a result of ecological constraints. © 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2002, 76, 577–590.

ADDITIONAL KEYWORDS: biogeography – geometrical morphometric methods – Lemurs – Madagascar – morphological disparity – Primates – Procrustes superimposition.

INTRODUCTION

Madagascar is a large island with contrasting environments owing to its varied topography and climate. It can be divided into several bioclimatic or phytogeographical domains depending on latitude, altitude, temperature, rainfall, seasonality and vegetation (Humbert, 1955; Paulian, 1961; Battistini, 1996; Du Puy & Moat, 1996). The central plateau is temperate, with marked wet and dry seasons, and is characterized by mid-altitude montane rainforest and even by sclerophyllous forest at the highest altitudes. The east coast is warm and humid, without a dry season, with

dense evergreen lowland rainforest. The Sambirano domain, in the north-west is an enclave of humid rainforest similar to that of the east coast. The west of the island is characterized by distinct seasons, with deciduous forests giving way to xerophytic thickets as it becomes drier from north to south. The southern domain is hot and semiarid, with subarid thorn scrub.

Geographical zones of primate species distribution can be identified (Martin, 1972), whose boundaries coincide with major river or mountain barriers. MacPhee *et al.* (1985) showed that the central plateau was covered by a mosaic of woodlands, bush lands and savannah around 7000–8000 BP (before present). But the central plateau has since been largely denuded of forest and no extant primates (except for humans) are found in this zone. Lemurs are distributed in the forested zones remaining around the periphery of Madagascar. Ecogeographical size variations among primates of Madagascar have been demonstrated by

*Current address: CNRS UMR 8569 'Paléobiodiversité: histoire et dynamique', Laboratoire EPHE 'Evolution des primates', Muséum National d'Histoire Naturelle, 8 rue Buffon, 75005 Paris, France. E-mail: viguiere@mnhn.fr

Albrecht *et al.* (1990). The present study is the first attempt to test for any associated pattern of cranial shape variations.

To test for any correlation between lemur skull shape and geography, species studied need to have the largest geographical distribution as possible and need to cover most of the various environmental domains of the island. Moreover, sample chosen need to consider species closely related in phylogeny and in ecology, in order to limit the number of possible sources of variation that can interact with skull shape. Selected species belong to the Lemuridae family, which includes the most familiar Malagasy primates known as 'true lemurs'. All these forms are medium-sized quadrupeds, with corresponding horizontal body posture. They are mainly diurnal or cathemeral and have a varied diet consisting principally of fruits (Napier & Napier, 1967, 1985; Petter *et al.*, 1977; Ankel-Simons, 1983, 2000; MacDonald, 1984; Tattersall, 1987; Grzimek, 1990; Nowak, 1991; Garbutt, 1999). These species can be distinguished easily by external features (coat characteristics and colouring) but their cranial morphologies are rather similar. They have characteristic long fox-like faces. The skull is elongate and narrow, with a long muzzle and a short brain case. The latter is constricted behind the orbits and broadened posteriorly. The occipital is rounded and produced posteriorly (Hill, 1953; Tattersall, 1982).

Kappeler (1990, 1991) demonstrated that prosimians show more or less sexual dimorphism, but that lemurs are characterized by a general lack of sexual dimorphism and are the less dimorphic prosimians. Jenkins & Albrecht (1991) used skull length to evaluate the extent of sexual dimorphism in Malagasy prosimians. They confirmed the monomorphism of lemurs. As resumed by Tattersall (1993), studied species are characterized by 'the absence of sexual dimorphism either in body size or in the morphology of hard tissues'. The selection of these species permits to avoid influence of sexual dimorphism on skull shape and to isolate the effect of biogeography.

The geographical distributions of the species of the genus *Lemur* and *Eulemur*, excluding *Eulemur fulvus*, are juxtaposed forming a continuum around most of the periphery of Madagascar. A similar situation is observed for the various subspecies of *E. fulvus*, but in a different pattern, although some subspecies are found both in the eastern and western domains. Taxonomic and ecological boundaries do not strictly coincide in either case. This may suggest that the differentiation of taxa is not correlated with the environmental pattern. This particularity of the geographical distribution of these species has already been emphasized by Tattersall (1992, 1993), Tattersall & Sussman (1998) and Albrecht *et al.* (1990).

These species of the Lemuridae are among the most

closely studied of Malagasy primates. It is universally accepted that the Lemuridae constitute a monophyletic family, and many cladograms are found in the literature (Dene *et al.*, 1980; Eaglen, 1983; Dutrillaux, 1988; Groves & Eaglen, 1988; Simons & Rumpler, 1988; Tattersall & Schwartz, 1991; Jung *et al.*, 1992; Crovella *et al.*, 1993; Montagnon *et al.*, 1993; Macedonia & Stanger, 1994; Groves & Trueman, 1995; Purvis, 1995; Yoder *et al.*, 1996; Stanger-Hall, 1997; Randria, 1999; Yoder & Irwin, 1999; Wyner, DeSalle & Absher, 2000; Delpero *et al.*, 2001; Ventura *et al.*, 2001).

These species are therefore a good basis with which to test for (1) any correlation between cranial morphology and biogeography and (2) any link between cranial morphology and phylogeny.

MATERIAL AND METHODS

SELECTION OF TAXA

The specimens were taken from the 'Mammifères et Oiseaux' laboratory collection of the Muséum National d'Histoire Naturelle de Paris. Crania were selected according to the availability of specimens. The study is based on 43 skulls of adult Lemuridae. Table 1 lists the samples used. It was impossible to distinguish between the two subspecies of *E. macaco* from the data in the collection. Five subspecies of *E. fulvus* were included in the study while a sixth one (*E. f. collaris*) was excluded as no specimens were available.

PROCRUSTES SUPERIMPOSITIONS

In this study, the disparity of cranial morphology is depicted using geometric morphometry. This method allows pure shape difference to be described regard-

Table 1. Species studied and number of specimens examined

Species	
<i>Lemur catta</i> (Linnaeus, 1758)	<i>n</i> = 4
<i>Eulemur mongoz</i> (Linnaeus, 1766)	<i>n</i> = 5
<i>Eulemur macaco</i> (Linnaeus, 1766)	<i>n</i> = 5
<i>Eulemur coronatus</i> (Gray, 1842)	<i>n</i> = 5
<i>Eulemur rubriventer</i> (I. Geoffroy, 1850)	<i>n</i> = 4
<i>Eulemur fulvus</i> (E. Geoffroy, 1796)	<i>n</i> = 20
Sub-species of <i>E. fulvus</i>	
<i>Eulemur fulvus rufus</i>	<i>n</i> = 4
<i>Eulemur fulvus fulvus</i>	<i>n</i> = 8
<i>Eulemur fulvus sanfordi</i>	<i>n</i> = 1
<i>Eulemur fulvus albifrons</i>	<i>n</i> = 5
<i>Eulemur fulvus albocollaris</i>	<i>n</i> = 2

less of size, and differences between specimens to be quantified. Skull shapes were compared by Procrustes superimpositions (Sneath, 1967; Bookstein, 1991). The use of the coordinates of the locations of the morphological landmarks is a good reflection of shape variation. Homologous landmarks were chosen to provide a good overall description of skull morphology.

Photographs of the lateral views of the skulls were taken using a digital camera. Sagittal plane of skulls was positioned perpendicularly to the axis of the camera. All the photographs were taken at the same distance from skull to focal point, in order to obtain homogeneous warping of each specimen. The photos were then identically scaled to attain a skull length of 1000 pixels in order to get the same accuracy of measurement. Then the x,y coordinates of the landmarks were digitized using the image analysis software OPTIMAS 6.2. A set of 28 landmarks (Fig. 1) was used to depict the main traits of the skulls. Eight of the landmarks were in the sagittal plane and the remaining 20 were located on the left half of the skull. Table 2 lists the location of the 28 landmarks.

The shapes of the skulls were adjusted by translation, scaling and rotation, using all the points for specimen fitting by the use of a generalized least-squares Procrustes superimposition (GLS) (Gower, 1975; Rohlf & Slice, 1990) and a mean shape, termed the consensus configuration, was determined. Figure 2 shows the plot of the consensus configuration with the 43 specimens superimposed. This approach is based on Procrustes residuals, which are the x,y coordinates of the vectors connecting the landmarks of a specimen to the corresponding landmarks of the consensus configuration. Procrustes residuals were analysed by Principal Components Analysis (PCA) of the covariance matrix, using APS software (Penin, 1999). PCA is likened to a morphological space. Correlation between morphology and geography can thus be analysed by comparing the position of taxa in the morphological space with their respective geographical distribution.

An additive morphological distance tree was computed using the matrix of shape distances between each

pair of configurations of landmarks. This approach is based on the Procrustes distance, which is the square root of the summed squared distances between least-squared superimposed landmarks of two specimens (Bookstein, 1991). Comparisons were made by least-square adjustments with PROCUSTES software (David & Laurin, 1992). The distance matrix was processed and a phenetic tree computed with the FITCH program of PHYLIP software (Felsenstein, 1995). The phenogram obtained was compared with various cladograms found in the literature, to test for any correlation between morphology and phylogenetic history.

Table 2. List of landmarks used

Landmarks	Location
1	Prosthion
2	Top of the median bony process of the maxilla
3	Top of the median bony process of the nasal
4	Nasion
5	Bregma
6	Lambda
7	Opistocranium
8	Opisthion
9	Top of the infra-orbital foramen
10	Anterior jugal contact of alveolar ridge and P2
11	Posterior jugal contact of alveolar ridge and M1
12	Frontolachrymonasal suture
13	Maxillolachrymonasal suture
14	Intersection of orbital ridge and lachrymojugal suture
15	Intersection of orbital ridge and lachrymofrontal suture
16	Lowest point of orbital edge
17	Zygomaxillaire
18	Frontolachrymopalatin suture
19	Top of orbital edge
20	Intersection of the anterior edge of postorbital bar and the frontojugal suture
21	Intersection of the posterior edge of postorbital bar and the frontojugal suture
22	Intersection of the upper edge of zygomatic arcade and the temporojugal suture
23	Intersection of the lower edge of zygomatic arcade and the temporojugal suture
24	Stephanion
25	Frontoparietosphenoidal suture
26	Temporoparietosphenoidal suture
27	Asterion
28	Porion

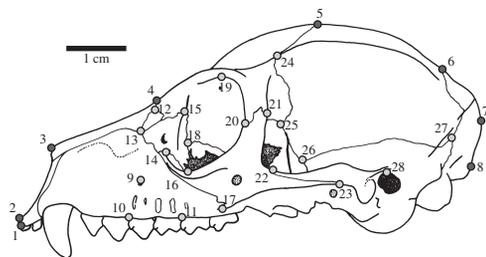


Figure 1. Location of the 28 landmarks measured on the left lateral view of a skull of *Lemur catta*. See Table 2 for the identification of landmarks.

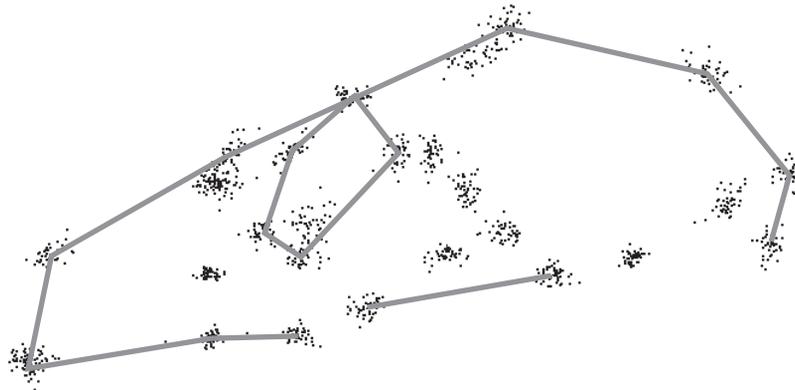


Figure 2. Plot of the consensus configuration and residuals for generalized least-square fit of the whole sample.

RESULTS

MORPHOLOGICAL DISPARITY VS. GEOGRAPHICAL DISTRIBUTION

Figure 3A illustrates the geographical distribution of *L. catta*, *E. mongoz*, *E. macaco*, *E. coronatus* and *E. rubriventer*, and Fig. 4A shows that of the subspecies of *Eulemur fulvus*. The geographical distributions of *L. catta* and the species of the genus *Eulemur*, excluding *E. fulvus*, form a continuum around most of the periphery of Madagascar (Fig. 3A). The range of *E. mongoz* is restricted to the dry deciduous forest in the western domain, south of the Sambirano. *E. macaco* is found in the Sambirano domain in rain forest and in mixed forest just south of this domain. *E. coronatus* is restricted to the drier deciduous forest of the arid Cap d'Ambre and the rain forest of the Mont d'Ambre, both in the western ecogeographical domain. *E. rubriventer* is distributed throughout the rainforest of the eastern domain. *L. catta* is found in the spiny forest, dry scrub, deciduous forest and gallery forest of the arid southern domain.

E. fulvus is the most widespread of the 'true lemur' group. This species is divided into six subspecies with distinct ranges that do not overlap. The geographical distributions of the subspecies of *E. fulvus* also form a continuum around most of the periphery of Madagascar (Fig. 4A). But these taxonomic boundaries do not follow the same pattern as the first set of taxa: some subspecies are found both in the eastern and the western domains, on either side of the central plateau. *E. f. rufus* and *E. f. fulvus* occur both in the eastern evergreen forest and the western deciduous forest of the island. *E. f. fulvus* is also found in the Sambirano domain. *E. f. sanfordi* is restricted to the northern tip of Madagascar. *E. f. albifrons* is found in the north-east of the eastern domain. *E. f. albocollaris* occurs in a small area of central south-eastern Madagascar. *E. f. collaris* is found in the far south-east of the island.

Figure 3B plots the individuals analysed onto the factorial plane PC1–PC2 of the PCA computed with the covariance matrix of Procrustes residuals for *L. catta*, *E. mongoz*, *E. macaco*, *E. coronatus* and *E. rubriventer*. The two first principal components express 37.51% of total variance. Comparison of the distribution of taxa in this morphological space with their geographical distribution (Fig. 3A) reveals that PC1, which accounts for 20.57% of the total variance, corresponds to a transition of species from east to west of Madagascar, while PC2 (16.94% of the total variance) shows a general north–south distribution.

The factorial plane PC1–PC2 of the PCA computed for the subspecies of *E. fulvus* is reported in Fig. 4B. Factorial plane PC1–PC2 expresses 32% of the total variance. The various taxa are less clearly discriminated than in the previous analysis (Fig. 3B): it is subspecies that are compared and not individuals belonging to separate species. Nonetheless, distribution within the morphological space is still correlated with geographical distribution as shown by the map (Fig. 4B). Specimens can be split up into two sets: subspecies with large geographical distribution found both in the western and eastern regions are distinguished from those restricted to the northern and eastern domains by the negative values along PC1.

A third GLS fit was computed for the whole sample (*L. catta*, *E. mongoz*, *E. macaco*, *E. coronatus*, *E. rubriventer* and the various subspecies of *E. fulvus*). Procrustes residuals were analysed by PCA. Figure 5A shows the factorial plane PC1–PC2 that expresses 31.03% of the total variance. Two morphological trends (grey arrows) can be distinguished: (1) along PC1, a transition from subspecies of *E. fulvus* living both in western and eastern regions to species from the north-west and then to forms restricted to the north and then to the east; (2) along PC2, a transition from subspecies of *E. fulvus* living both in western and eastern regions to species restricted to the north-west, and

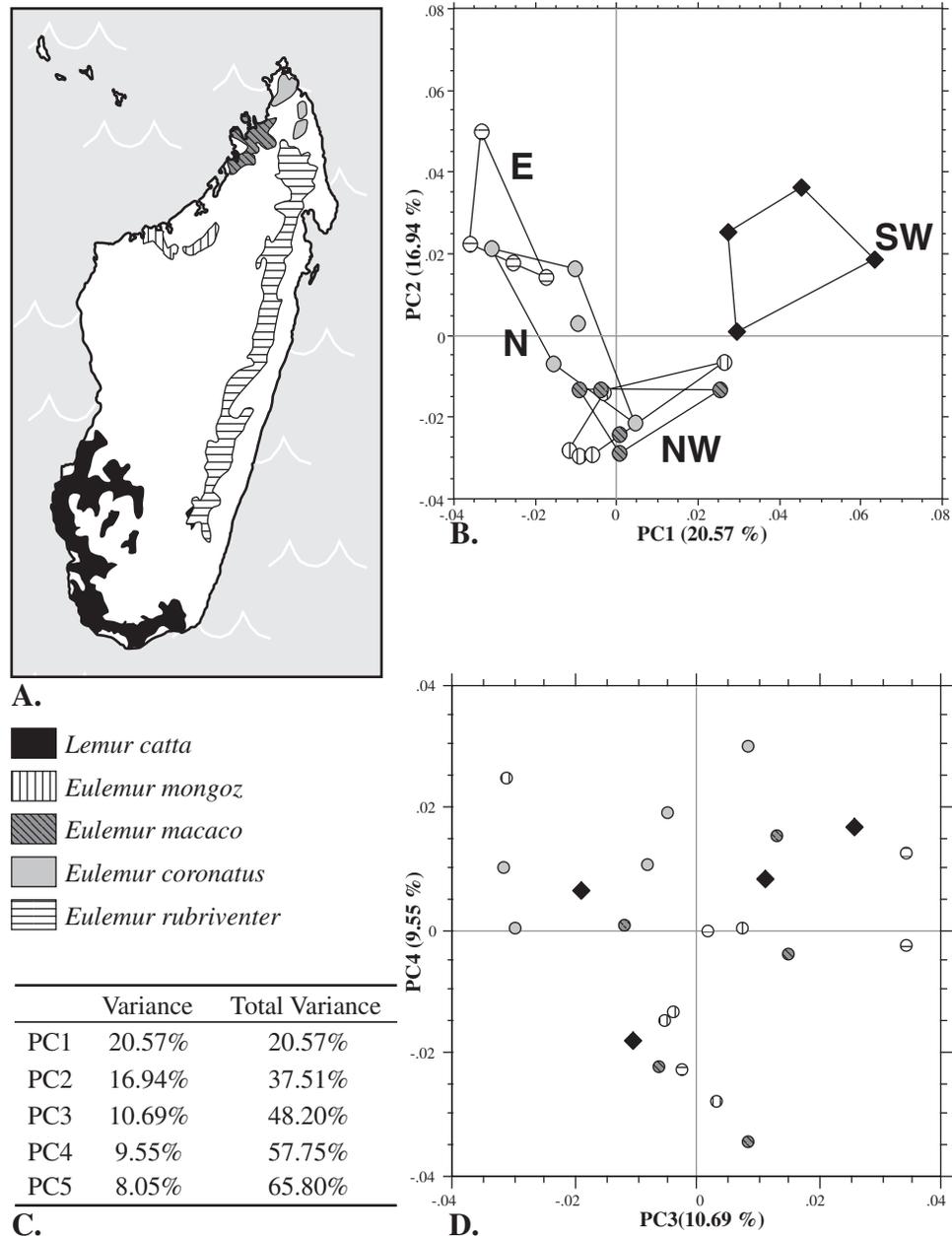


Figure 3. Morphological disparity vs. geographical distribution for *L. catta*, *E. mongoz*, *E. macaco*, *E. coronatus* and *E. rubriventer*. A, Map of Madagascar showing areas of distribution of these species. B, Scatterplot PC1–PC2 of the principal component analysis of Procrustes residuals computed for *L. catta*, *E. mongoz*, *E. macaco*, *E. coronatus* and *E. rubriventer*. C, Proportions of variance reflected in the first few principal axes. D, Factorial plane PC3–PC4.

then isolation of *Lemur catta* (south-west) in the negative values. Therefore morphological disparity is constrained by geography, reflected by a trend towards increasingly humid zones along PC1 and towards increasingly arid environments along PC2.

For every GLS computed, the first few principal axes of the PCA computed with the covariance matrix of Procrustes residuals for *L. catta*, *E. mongoz*,

E. macaco, *E. coronatus* and *E. rubriventer*, for the subspecies of *E. fulvus* or for the entire sample (*L. catta*, *E. mongoz*, *E. macaco*, *E. coronatus*, *E. rubriventer* and the subspecies of *E. fulvus*) support only a low proportion of total variance (Figs 3C, 4C and 5B) and species are more or less superposed on planes PC3–PC4 (Figs 3D, 4D and 5C). There is no significant link between PC-scores along axes 3–4 and

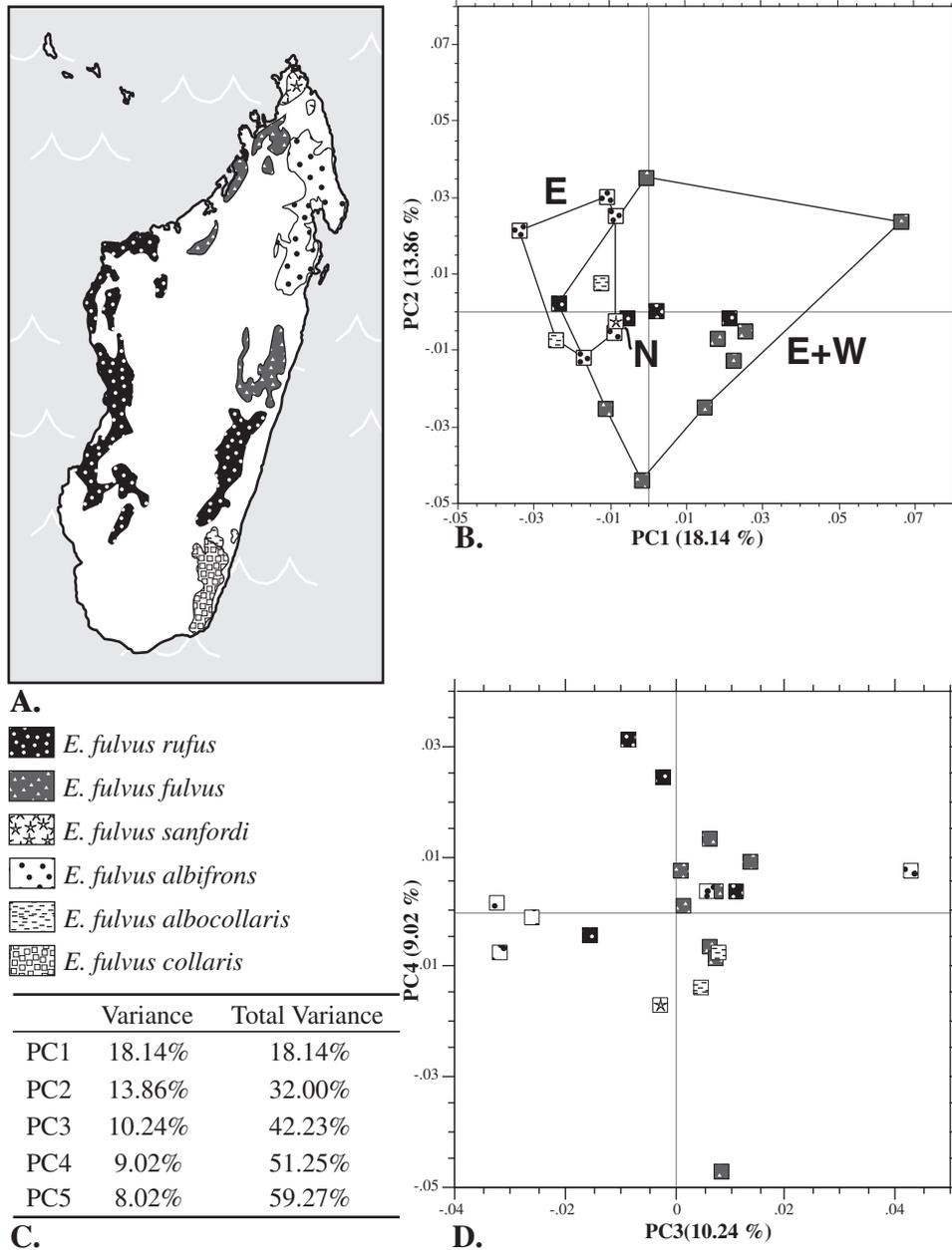


Figure 4. Morphological disparity vs. geographical distribution for the various subspecies of *E. fulvus*. A, Map of Madagascar showing areas of distribution of the subspecies of *E. fulvus*. B, Scatterplot of the factorial plane PC1–PC2 of the principal component analysis of Procrustes residuals computed for the subspecies of *E. fulvus*. C, Proportions of variance reflected in the first few principal axes. D, Factorial plane PC3–PC4.

geographical distribution of species. Such pattern reflects a low level of covariance between variables, which suggests an important noise inherent to the data set since the species studied are very close morphologically and phylogenetically.

A correlation between variations in skull morphology and biogeography has been demonstrated on factorial planes PC1–PC2. Note that this correlation

is expressed whatever taxonomic level is considered. This constraint is expressed both for species and for subspecies, and is also expressed in the same direction for species and for subspecies; for the same taxonomic level (species or subspecies), specimens from the east of the island consistently achieve a lower factorial score on PC1 (Fig. 5A).

The particularity of the geographical distribution of

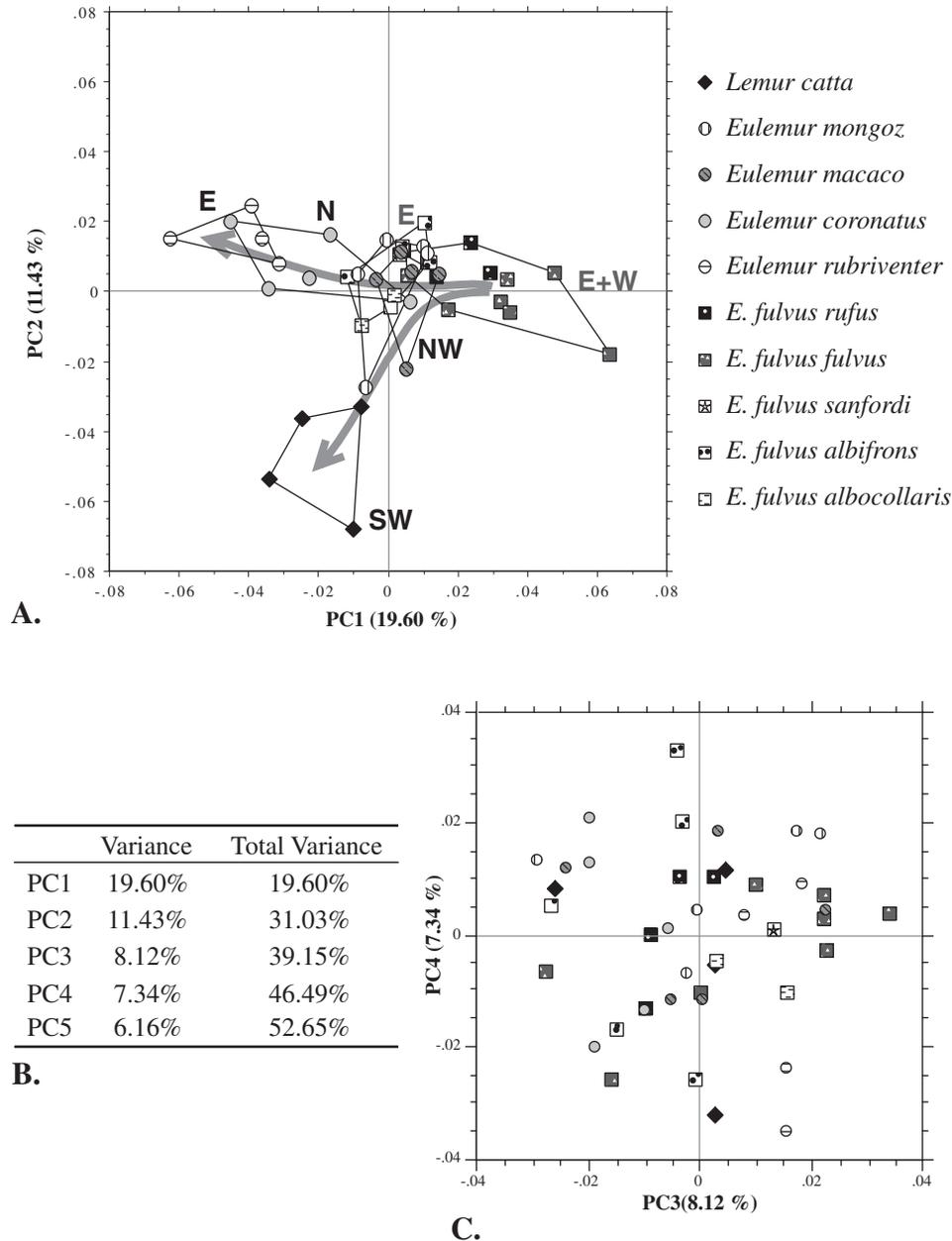


Figure 5. Morphological disparity vs. geographical distribution for the entire sample (*L. catta*, *E. mongoz*, *E. macaco*, *E. coronatus*, *E. rubriventer* and the subspecies of *E. fulvus*). A, Scatterplot of the factorial plane PC1–PC2 of the principal component analysis of Procrustes residuals computed (the grey arrows show the geographical trend associated with the morphological gradient). B, Proportions of variance reflected in the first few principal axes. C, Factorial plane PC3–PC4.

the species of Lemuridae studied here has been reported in the literature (Tattersall, 1992, 1993). Other observers have previously tackled problems of biogeographical variations in primates; see Albrecht & Miller (1993) for a review. This kind of pattern of geographical differentiation has been tested in various groups of Haplorhini, such as New World monkeys, Old World monkeys and apes. Biogeographical vari-

ations have also been described among Malagasy primates. For example, Drenhaus (1975) performs a multivariate analysis of skull dimensions on the seven species of the genus *Lepilemur*, showing that the species are spread over the morphological space in a ring of overlapping distributions strikingly resembling their geographical distribution around the periphery of Madagascar. Albrecht *et al.* (1990) inves-

tigate habitat-related size variations of skull length for all the living Malagasy prosimians and their recently extinct subfossil relatives. Habitat effects on variation in size are shown for nearly all kinds of Malagasy prosimians: '(1) the smallest Malagasy prosimians inhabit the semiarid forests, bush, and thickets of the south; (2) next largest are those from the dry deciduous forests of the west and the humid but seasonal forests of the Sambirano; (3) larger yet are those from humid tropical and secondary forests of the east; and (4) the largest of all are the extinct forms of the central highlands devoid of living prosimians'. This pattern is clearly described for the subspecies of *E. fulvus*, but not for the other species studied here. *E. macaco*, for example, is a contradictory case: this is the largest member of the group that could not be predicted from its distribution in the west. The comparison of the result of Albrecht *et al.* (1990) with the result of this study shows that the pattern of ecogeographical size variation differs from that of shape differentiation. *E. macaco* does not fit the circular pattern of ecogeographical size increase around the periphery of the island demonstrated by Albrecht *et al.* (1990), but fits the pattern of shape differentiation from ubiquitous *E. fulvus* brought out here.

The studies by Drenhaus (1975) and Albrecht *et al.* (1990) are based on dimensions alone. In this study, an attempt was made to see to what extent the pattern of shape variation demonstrated here is linked to size variation. Regression analysis of factorial scores on centroid size and on skull length of each specimen were performed to test for any correlation between shape and size. The results of both analyses (centroid size and skull length) were identical and only regression on skull length is displayed in the present article (see Fig. 5). Skull length is chosen as estimator of size insofar as results can be directly compared with those of Albrecht *et al.* (1990). It appears that the test on the slope of the straight line for PC1 is highly significant

($r^2 = 0.42$, $P < 0.00001$) and that the factorial scores on PC2 are independent of size ($r^2 = 0.07$, $P = 0.08$). The close correlation with size on PC1 suggests that the morphological trend observed along PC1 could be constrained by allomorphy. This is a variation in the shape of organisms at the same development stage (i.e. adult in the present work), concomitant with a change in size (Huxley *et al.*, 1941). On the other hand the morphological trend observed along PC2 seems to render a shape variation that is not linked with size. This might mean that (1) the form variation within the genus *Eulemur* (along PC1 in Fig. 5) is a case of allomorphy, and that (2) the transition to another genus, the genus *Lemur* (along PC2 in the Fig. 5) could be explained by a shape variation independent of size variation. Figure 6 shows that things are not as simple as they appear. The various taxa are aligned on the straight line, except for one that lies below it. This exception is not *L. catta* as expected, but *E. rubriventer*. So it cannot be said that shape variation along PC1 is caused by allomorphy alone. The position of *E. rubriventer* on the plot of Fig. 6 demonstrates that ecogeographical form variation within the genus *Eulemur* is not allomorphy but a shape modification. This relation explains why the pattern of shape variation does not fit the pattern of size variation of Albrecht *et al.* (1990).

Albrecht *et al.* (1990) suggested an interpretation of the pervasive pattern of ecogeographical size differences observed in the prosimian case: larger animals are found in wetter, lush and more productive habitats. This may be an adaptive response to differences in the productivity of the various regions determined by climate and vegetation. The results of the present study show the existence of adaptive shape variations in addition to adaptive size variations.

Albrecht & Miller (1993) describe the linear ordering of *Colobus polykomos* subspecies in the narrow band of forest along the coast of western Africa, the

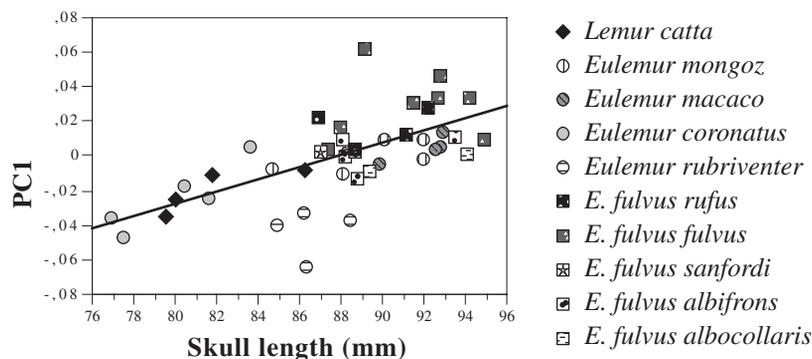


Figure 6. Plot of the regression of factorial scores on PC1 (after GLS for the entire sample: *L. catta*, *E. mongoz*, *E. macaco*, *E. coronatus*, *E. rubriventer* and the subspecies of *E. fulvus*) on skull length (mm). $r^2 = 0.42$, $p < 0.00001$.

divergence of Sulawesi macaques from a central population along the arms of the island, and the ring like distribution of *Lepilemur* around the coastal periphery of Madagascar that 'evolution and dispersal in these groups was strongly shaped by regional geography'. The same is true of the species of the genus *Lemur* and *Eulemur* studied here.

MORPHOLOGICAL DISPARITY VS. PHYLOGENY

Although it is universally accepted that the Lemuridae family is monophyletic, the phyletic relationships between species within this family are far from reaching such a consensus. Despite a wealth of systematic studies dedicated to the Lemuridae, relationships within the family remain unclear. Many different trees are found in the literature and present contradictory branching patterns. Moreover, the absence of a fossil record hampers our understanding of phyletic relationships within the group. Figure 7 displays eight phylogenies taken from the literature and simplified in order to show only the species studied in the morphometric analyses. These phylogenies are displayed in chronological order of their publication. Investigators obtain different results depending on the approach they adopt. Dene *et al.* (1980) consider their distance tree obtained using immunological data to be relevant to phylogeny (Fig. 7A). Not all the species measured in this paper are present on the tree. *E. mongoz* and *E. macaco* are close together, *E. fulvus* is more distant and *L. catta* seems to be the most divergent and most primitive. Eaglen (1983) presents a cladistic analysis of lemurid phylogeny based on 30 morphological and behavioural characters (Fig. 7B). Data include osteological traits of the cranium and postcranial skeleton, dental characteristics, integumental features and highly stereotyped forms of behaviour. This set of characters does not permit the distinction between *E. macaco* and *E. fulvus*, and between *E. mongoz* and *E. coronatus*, which are therefore grouped together in the figure. *L. catta* is the most primitive species. Upward in the tree, the *E. mongoz* group, the *E. macaco* group and *E. rubriventer* are branched successively. Tattersall & Schwartz (1991) carried out a quantitative parsimony analysis of 37 craniodental characters (Fig. 7C). The resulting tree is entirely pectinate, branching from the base to the top: *L. catta*, *E. coronatus*, *E. fulvus*, *E. macaco*, *E. rubriventer* and *E. mongoz*. Crovella *et al.* (1993) have used techniques of hybridization of highly repeated DNA sequences. Comparison of the migration patterns from DNA fragments of the different species has been used to propose a cladogram (Fig. 7D). This cladogram is pectinate and branches, respectively, from the base to the top: *L. catta*, *E. macaco*, *E. mongoz*, *E. fulvus*, *E. rubriventer* and

E. coronatus. Groves & Trueman (1995) performed a cladistic analysis from characters modified from the datasets of Tattersall & Schwartz (1991) and Groves & Eaglen (1988). These are morphological characters (craniodental, postcranial and integumental features). The comb-like cladogram they obtained (Fig. 7E) is identical to the tree of Tattersall & Schwartz (1991) for the species concerned. Purvis (1995) presented a composite tree (Fig. 7F), derived by applying a parsimony algorithm to previously published studies. This analysis is therefore based on morphological, molecular, karyotypic and behavioural data. At the base of the tree, *L. catta* is the sister taxon of the genus *Eulemur*. *Eulemur* species branch with *E. rubriventer* as the most primitive and with two couples of species grouped together in subclades: *E. coronatus* and *E. mongoz* on the one hand, and *E. macaco* and *E. fulvus* on the other hand. Yoder & Irwin (1999) performed an analysis based on three mitochondrial genes and one nuclear gene. Figure 7G shows the tree obtained with just combined mitochondrial and nuclear data or with this genetic data plus morphological and behavioural data taken from Groves & Trueman (1995), Stanger-Hall (1997) and Macedonia & Stanger (1994), in which all characters are equally weighted. In both cases, a similar branching pattern is obtained for the species analysed here. *L. catta* is the most primitive species and the sister taxon of the genus *Eulemur*. *Eulemur* species are organized in a pectinate sequence: *E. mongoz*, *E. fulvus*, *E. macaco* and *E. rubriventer*. Figure 7H shows the tree obtained using the same data as in Fig. 7G, in which genetic characters are differentially weighted according to a priori assumptions of character informativeness, and behavioural and morphological characters are equally weighted. This tree is different from the previous one in the branching order of *Eulemur* species: *E. macaco*, *E. rubriventer*, *E. mongoz* and *E. fulvus*.

In every case, *L. catta* is found to be the most primitive and the sister taxon of the genus *Eulemur*. However, the branching pattern of *Eulemur* species appears to be extremely problematic. Cladograms found in the literature are different from each other, but it is impossible to detect any trend based on the kind of data used. There is no unity for the trees based on molecular data only. Cladograms drawn by analysis of morphological, behavioural and molecular traits differ from each other. Only the trees based on morphological characters look alike for the species concerned, however, the tree in Fig. 7E (Groves & Eaglen, 1988) is partly derived from the data of tree in Fig. 7C (Tattersall & Schwartz, 1991).

Figure 8A displays the morphological distance tree computed in order to compare morphological data with phylogenetic data for the whole sample (*L. catta*, *E. mongoz*, *E. macaco*, *E. coronatus*, *E. rubriventer* and

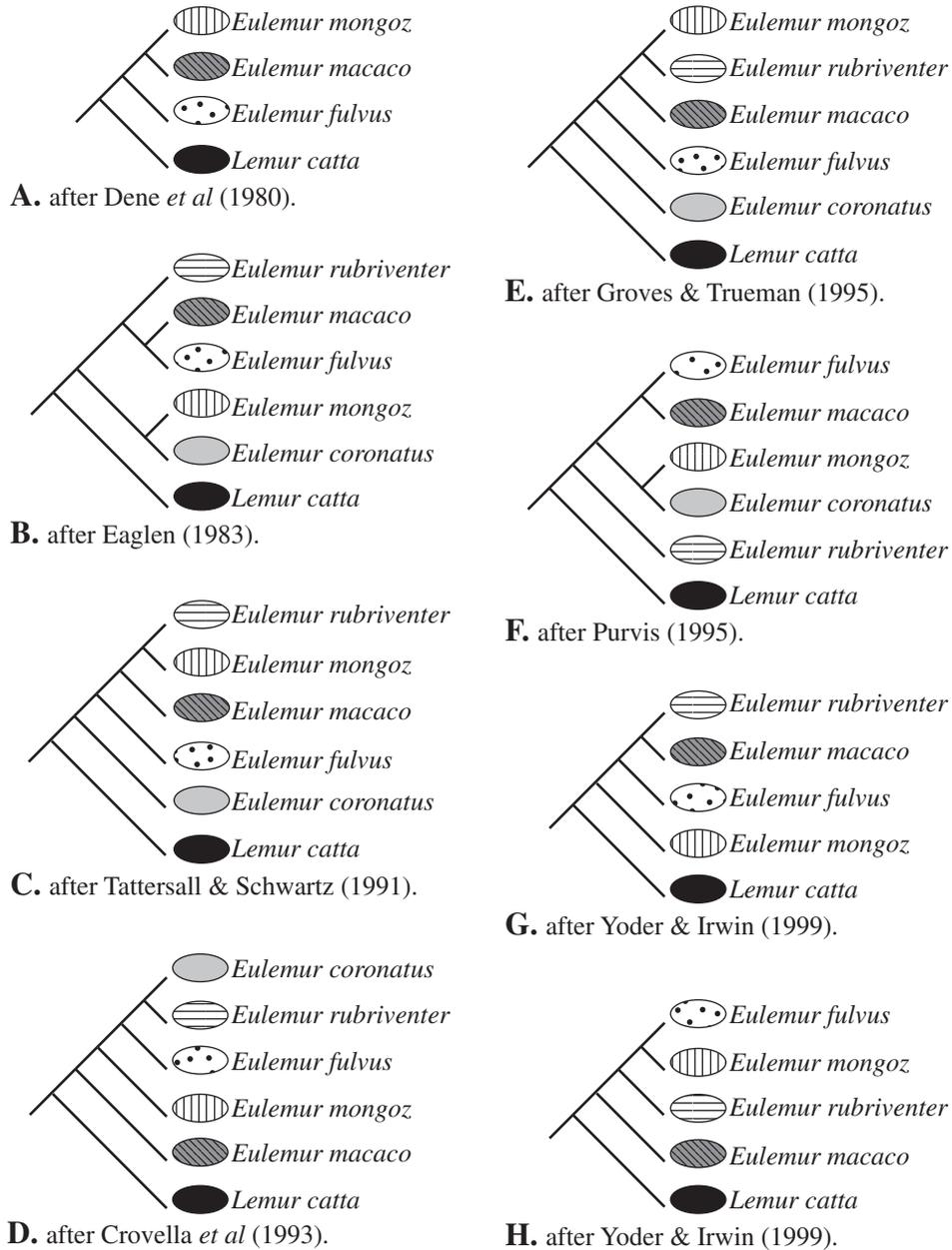


Figure 7. Various phylogenies reported in the literature.

the various subspecies of *E. fulvus*). In the phenogram obtained, the branches are short reflecting the morphological similarity between species. Yet, while some taxa are widely dispersed within the tree, others are clearly differentiated. Remember that morphological differences are expressed solely horizontally and not along the vertical axis. So species at the base of the tree are the most scattered, and species on the topmost branches of the phenogram are the most differentiated.

The different subspecies of *E. fulvus* are at the base

of the phenogram, grouped on the first branch with some specimens also found at the node of the following boughs. *E. mongoz* and *E. macaco* then come close together. In the second part of the tree (after the first black arrow), two branches separate; a first branch with *E. coronatus* and then *E. rubriventer*, then, at the top of the tree, a second branch with *L. catta*. The phenetic tree exhibits a similar pattern to that of the PCA (Fig. 5); subspecies of *E. fulvus* and then species from the dry north-west of the island, followed on the one hand by the taxa from increasingly humid domains

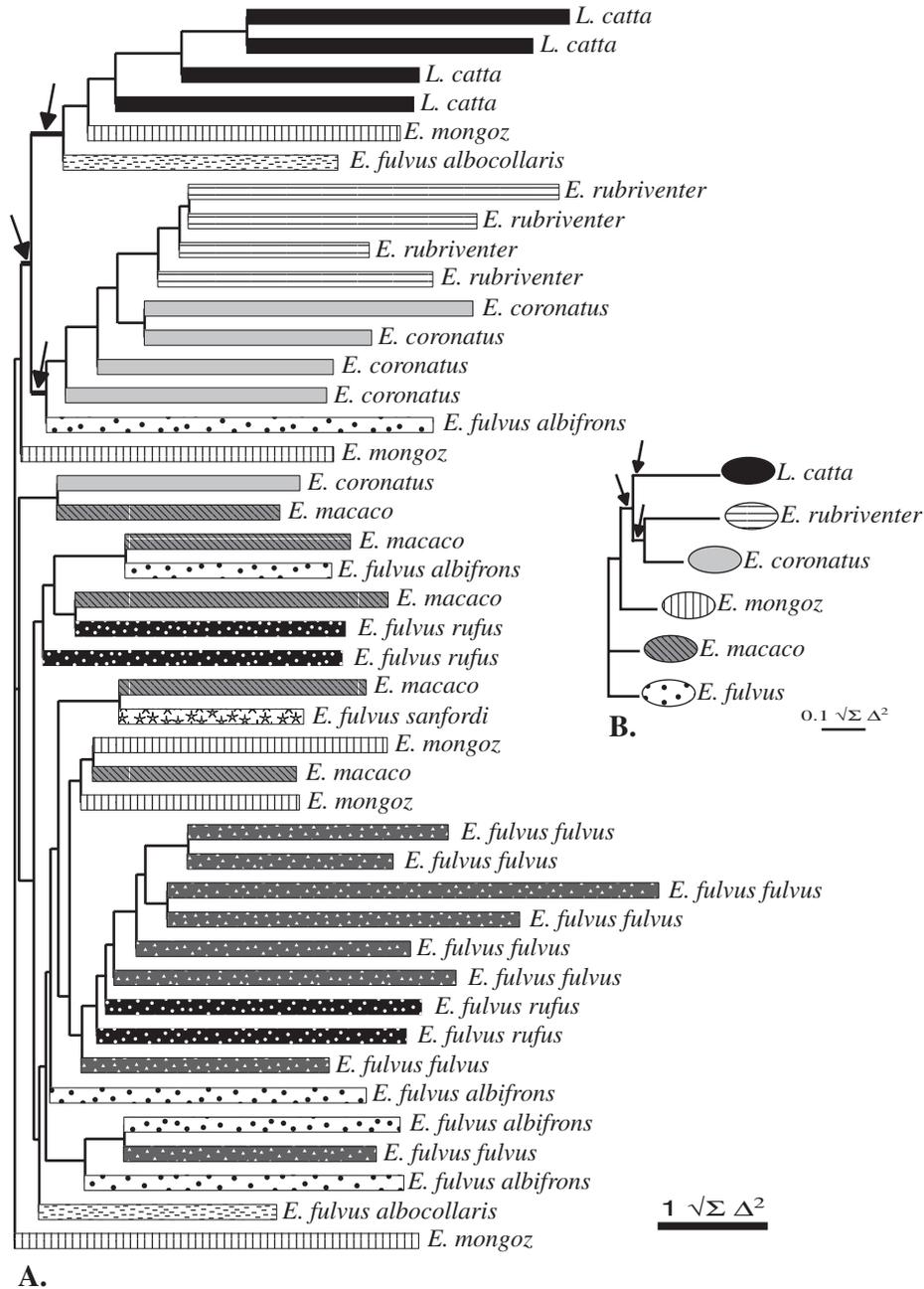


Figure 8. A, Morphological distance tree computed for the entire sample (*L. catta*, *E. mongoz*, *E. macaco*, *E. coronatus*, *E. rubriventer* and the subspecies of *E. fulvus*). B, Simplified phenogram computed for consensus configurations of each species, used for comparisons with the trees of Figure 7. The black arrows show the major dichotomies of the tree.

(north and east), and on the other hand by the forms from increasingly arid regions (south).

This morphological distance tree can be simplified for comparison with the cladograms; Fig. 8B shows the phenogram computed for the consensus configuration calculated for each of the six species. The same pattern is recognizable; *E. fulvus*, *E. mongoz* and *E. macaco*,

followed on the one hand by *E. coronatus* and then *E. rubriventer*, and on the other hand by *L. catta*. It has been seen previously that many cladograms are found in the literature (Fig. 7). Nevertheless, despite an abundance of systematic studies dedicated to the Lemuridae showing that the relationships within the family remain unclear, the phenogram obtained here

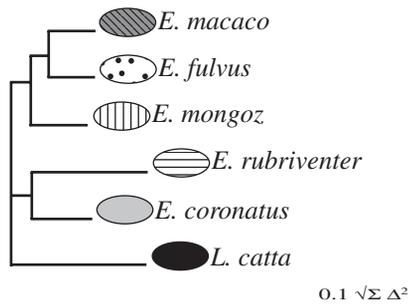


Figure 9. Simplified phenogram computed for consensus configurations of each of the six species, imposing the position of *L. catta* at the base of the tree.

does not fit any of these hypotheses. No convincing relationship can be identified between variations in cranial morphology and phylogeny.

L. catta is the most primitive species in each tree of the Fig. 7. If the morphological distance tree is calculated again imposing *L. catta* at the base (Fig. 9) in keeping with the phylogenetic arrangement, it can be seen that this new phenogram does not fit any of the proposed hypotheses either. Therefore morphological disparity seems to be independent of phylogenetic history.

Despite a proliferation of competing phylogenies, the pattern of morphological variations among the species studied does not fit in with any previous model. The fact that phylogenetic relationships among these species are not well understood (many cladograms are found in the literature) reflects the occurrence of a high degree of homoplasy (convergence, parallelism, or reversals). Some studies (Eaglen, 1983; Groves & Eaglen, 1988; Tattersall & Schwartz, 1991; Stanger-Hall, 1997; Yoder & Irwin, 1999) have referred to this problem. Some specialists in the field have doubted the generic differences between *Lemur* and *Eulemur* (Tattersall & Schwartz, 1991). Despite the lack of consensus across diverse analyses of morphological and ethological characters (Tattersall & Schwartz, 1991; Macedonia & Stanger, 1994; Groves & Trueman, 1995; Stanger-Hall, 1997; Randria, 1999), the use of cytogenetic and molecular methods (Dutrillaux, 1988; Jung *et al.*, 1992; Crovella *et al.*, 1993; Montagnon *et al.*, 1993; Yoder *et al.*, 1996; Yoder & Irwin, 1999; Wyner *et al.*, 2000; Delpero *et al.*, 2001; Ventura *et al.*, 2001) tends to confirm the separation of all *Eulemur* species from the group *L. catta/Hapalemur* proposed by Simons & Rumpler (1988). *Varecia* appears to be basal in the family. *Hapalemur* and *L. catta* are strongly supported as sister taxa and together are the sister group to the genus *Eulemur*. Whereas support for the *L. catta* position is high, the nodes within the genus *Eulemur* are poorly supported. No trends can be seen

even within trees based on the same type of data (e.g. molecular). Yoder & Irwin (1999) suggested that 'internal branches within the *Eulemur* radiation are proportionally too short to provide robust resolution'. Tattersall (1993) confirms this by stating that 'many of the most striking cranial autapomorphies of the various lemur species have also been evolved independently within the complex of *E. fulvus* subspecies'. It has been demonstrated that morphology is correlated with environmental constraints. The high degree of homoplasy might depend in a large extent on ecological constraints, such as the productivity of the various regions, as mentioned by Albrecht *et al.* (1990), and adaptive variation in the masticator apparatus depending on the kind of food available.

CONCLUSION

It has been demonstrated that (1) the cranial morphology of lemurs is clearly linked to their biogeography. This pattern of form variation cannot be explained by single allomorphy but highlight shape variation related to environmental conditions. It has also been shown that (2) any link between variations in skull shape and phylogeny is concealed by a high rate of homoplasy. Shape variation seems therefore apparently independent of phylogeny.

It can therefore be concluded that variations in the cranial morphology of lemurs depend more on environmental factors than on phylogenetic history, and that the high rate of homoplasy that is characteristic of the group is determined largely by ecological constraints through adaptations as well as ecophenotypic variations.

ACKNOWLEDGEMENTS

I thank P. Neige, L. Villier and D. Marchand for their useful comments on the manuscript. I am grateful to J. Cuisin (MNHN Paris) for providing specimens. I also thank C. Suttcliff for his help with the English version. This article is a contribution of the theme 'Signal morphologique de l'Evolution' of the CNRS UMR 5561 'Biogéosciences', Dijon.

REFERENCES

- Albrecht GH, Jenkins PD, Godfrey LR. 1990. Ecogeographic size variation among the living and subfossil prosimians of Madagascar. *American Journal of Primatology* **22**: 1–50.
- Albrecht GH, Miller JMA. 1993. Geographic variation in primates. A review with implications for interpreting fossils. In: Kimbel WH, Martin LB, eds. *Species, species concepts*,

- and primate evolution. New York: Plenum Press, 123–161.
- Ankel-Simons FA. 1983.** *A survey of living Primates and their anatomy*. New York and London: Macmillan and CollierMacmillan.
- Ankel-Simons FA. 2000.** *Primate anatomy*, 2nd edn. San Diego: Academic Press.
- Battistini R. 1996.** Paléogéographie et variété des milieux naturels à Madagascar et dans les îles voisines: quelques données de base pour l'étude biogéographique de la 'région malgache'. In: Lourenço WR, ed. *Biogeography of Madagascar*. Paris: Editions de l'ORSTOM. 1–17.
- Bookstein FL. 1991.** *Morphometric tools for landmark data. Geometry and biology*. Cambridge: Cambridge University Press.
- Crovella S, Montagnon D, Rumpler Y. 1993.** Highly repeated DNA analysis and systematics of the Lemuridae, a family of Malagasy prosimians. *Primates* **34**: 61–69.
- David B, Laurin B. 1992.** *Procrustes: an interactive program for shape analyses using landmarks.*, Version 2.0. Université de Bourgogne.
- Delpero M, Masters JC, Cervella P, Crovella S, Ardito G, Rumpler Y. 2001.** Phylogenetic relationships among the Malagasy lemuriforms (Primates: Strepsirrhini) as indicated by mitochondrial sequence data from the 12S rRNA gene. *Zoological Journal of the Linnean Society* **133**: 83–103.
- Dene H, Goodman M, Pritchard W. 1980.** Immunodiffusion systematics of the primates. IV: Lemuriformes. *Mammalia* **44**: 211–223.
- Drenhaus U. 1975.** *Ein Beitrag zur Taxonomie der Lemuriformes Gregory 1915 unter besonderer Berücksichtigung der Gattung Lepilemur I. Geoffroy 1851*. PhD Thesis Christian-Albrechts-Universität, Kiel.
- Du Puy DJ, Moat J. 1996.** A refined classification of the primary vegetation of Madagascar based on the underlying geology: using GIS to map its distribution and to assess its conservation status. In: Lourenço WR, ed. *Biogeography of Madagascar*. Paris: Editions de l'ORSTOM. 205–218.
- Dutrillaux B. 1988.** Chromosome evolution in primates. *Folia Primatologica* **50**: 134–135.
- Eaglen RH. 1983.** Parallelism, parcimony, and the phylogeny of the Lemuridae. *International Journal of Primatology* **4**: 249–273.
- Felsenstein J. 1995.** *PHYLIP (Phylogeny Inference Package), Version 3.5*. University of Washington.
- Garbutt N. 1999.** *Mammals of Madagascar*. Sussex: Pica Press.
- Gower JC. 1975.** Generalized Procrustes analysis. *Psychometrika* **40**: 33–51.
- Groves CP, Eaglen RH. 1988.** Systematics of the Lemuridae (Primates, Strepsirrhini). *Journal of Human Evolution* **17**: 513–538.
- Groves CP, Trueman JWH. 1995.** Lemurid systematics revisited. *Journal of Human Evolution* **28**: 427–437.
- Grzimek B. 1990.** *Encyclopedia of mammals*, Vol. 2. McGraw-Hill Co.
- Hill WCO. 1953.** *Primates: comparative anatomy and taxonomy. I. Strepsirrhini*. Edinburgh: The University Press.
- Humbert H. 1955.** Les territoires phytogéographiques de Madagascar. Leur cartographie. *Année Biologique* **31**: 195–204.
- Huxley JS, Needham J, Lerner IM. 1941.** Terminology of relative growth-rates. *Nature* **148**: 225.
- Jenkins PD, Albrecht GH. 1991.** Sexual dimorphism and sex ratios in Madagascan prosimians. *American Journal of Primatology* **24**: 1–14.
- Jung KY, Crovella S, Rumpler Y. 1992.** Phylogenetic relationships among lemuriform species determined from restriction genomic DNA banding patterns. *Folia Primatologica* **58**: 224–229.
- Kappeler PM. 1990.** The evolution of sexual size dimorphism in prosimian primates. *American Journal of Physical Anthropology* **21**: 201–214.
- Kappeler PM. 1991.** Patterns of sexual dimorphism in body weight among prosimian primates. *Folia Primatologica* **57**: 132–146.
- MacDonald D. 1984.** *The encyclopedia of mammals: 1*. London: George Allen & Unwin.
- Macedonia JM, Stanger KF. 1994.** Phylogeny of the Lemuridae revisited: evidence from communication signals. *Folia Primatologica* **63**: 1–43.
- MacPhee RDE, Burney DA, Wells NA. 1985.** Early Holocene chronology and environment of Ampasambazimba, a Malagasy subfossil lemur site. *International Journal of Primatology* **6**: 463–489.
- Martin RD. 1972.** Adaptive radiation and behaviour of the Malagasy lemurs. *Philosophical Transactions of the Royal Society of London B* **264**: 295–352.
- Montagnon D, Crovella S, Rumpler Y. 1993.** Comparison of highly repeated DNA sequences in some Lemuridae and taxonomic implications. *Cytogenetics and Cell Genetics* **63**: 131–134.
- Napier JR, Napier PH. 1967.** *A handbook of living Primates*. New York: Academic Press.
- Napier JR, Napier PH. 1985.** *The natural history of the Primates*. Cambridge, Massachusetts: MIT Press.
- Nowak RM. 1991.** *Walker's mammals of the World*, 5th ednEDZ, Vol. 1. Baltimore and London: The John Hopkins University Press.
- Paulian R. 1961.** *Faune de Madagascar. 13: la zoogéographie de Madagascar et des Îles Voisines*. Tananarive-Tsimbazaza: Publications de l'institut de recherches scientifiques.
- Penin X. 1999.** *APS, Version 2.21*. <http://www.cpod.com/monoweb/aps>.
- Petter JJ, Albignac R, Rumpler Y. 1977.** *Faune de Madagascar. 44: mammifères lémurien (Primates, Prosimiens)*. Paris: ORSTOM CNRS.
- Purvis A. 1995.** A composite estimate of primate phylogeny. *Philosophical Transactions of the Royal Society of London B* **348**: 405–421.
- Randria GFN. 1999.** Skeletal morphology and the phylogeny of the Lemuridae. A cladistic analysis. In: Rakotosamimanana B, Rasamimanana H, Ganzhorn JU,

- Goodman SM, eds. *New directions in lemur studies*. New York: Kluwer Academic/Plenum Publishers, 55–68.
- Rohlf FJ, Slice D. 1990.** Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Biology* **39**: 40–59.
- Simons EL, Rumpler Y. 1988.** *Eulemur*: new generic name for species of *Lemur* other than *Lemur catta*. *Comptes Rendus de l'Académie Des Sciences Paris, Série III* (307): 547–551.
- Sneath PHA. 1967.** Trend-surface analysis of transformation grids. *Journal of Zoology* **151**: 65–122.
- Stanger-Hall KF. 1997.** Phylogenetic affinities among the extant Malagasy lemurs (Lemuriformes) based on morphology and behavior. *Journal of Mammalian Evolution* **4**: 163–194.
- Tattersall I. 1982.** *The Primates of Madagascar*. New York: Columbia University Press.
- Tattersall I. 1987.** Cathemeral activity in primates: a definition. *Folia Primatologica* **49**: 200–202.
- Tattersall I. 1992.** Systematic versus ecological diversity: the example of the Malagasy primates. In: Eldredge N, ed. *Systematics, ecology, and the biodiversity crisis*. New York: Columbia University Press, 25–39.
- Tattersall I. 1993.** Speciation and morphological differentiation in the genus *Lemur*. In: Kimbel WH, Martin LB, eds. *Species, species concepts, and Primate evolution*. New York: Plenum Press, 163–176.
- Tattersall I, Schwartz JH. 1991.** Phylogeny and nomenclature in the 'lemur-group' of Malagasy strepsirrhine primates. *Anthropological Papers of the American Museum of Natural History* **69**: 1–18.
- Tattersall I, Sussman RW. 1998.** 'Little brown lemurs' of northern Madagascar. Phylogeny and ecological role in resource partitioning. *Folia Primatologica* **69** (Suppl. 1): 379–388.
- Ventura M, Boniotto M, Cardone MF, Fulizio L, Archidiacono N, Rocchi M, Crovella S. 2001.** Characterization of a highly repeated DNA sequence family in five species of the genus *Eulemur*. *Gene* **275**: 305–310.
- Wyner Y, DeSalle R, Absher R. 2000.** Phylogeny and character behavior in the family Lemuridae. *Molecular Phylogenetics and Evolution* **15**: 124–134.
- Yoder AD, Cartmill M, Ruvolo M, Smith K, Vilgalys R. 1996.** Ancient single origin for Malagasy primates. *Proceedings of the National Academy of Sciences of the United States of America* **93**: 5122–5126.
- Yoder AD, Irwin JA. 1999.** Phylogeny of the Lemuridae: effects of character and taxon sampling on resolution of species relationships within *Eulemur*. *Cladistics* **15**: 351–361.