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### ► To cite this version:

Jeanne Emma Miarisoa, Herimalala Raveloson, Blanchard Randrianambinina, Sébastien Couette. Deciphering the mandibular shape variation in a group of Malagasy primates using Fourier outline analysis.. *American Journal of Biological Anthropology*, 2023, 182 (3), pp.372-387. 10.1002/ajpa.24832 . hal-04274135

HAL Id: hal-04274135

<https://u-bourgogne.hal.science/hal-04274135v1>

Submitted on 3 Apr 2024

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Journal:	<i>American Journal of Biological Anthropology</i>
Manuscript ID	AJPA-2022-00192.R1
Wiley - Manuscript type:	Research Article
Date Submitted by the Author:	n/a
Complete List of Authors:	MIARISOA, Jeanne Emma; University of Mahajanga; Ecole Pratique des Hautes Etudes, Dijon; UMR6282, Biogéosciences Raveloson, Herimalala; University of Mahajanga Randrianambinina, Blanchard; University of Mahajanga Couette, Sébastien; Ecole Pratique des Hautes Etudes; UMR6282, Biogéosciences
Key Words:	Lemuridae, mandible, Fourier analysis, Geometric Morphometrics
Subfield: Please select 2 subfields. Select the main subject first.:	Primate biology [behavior, ecology, physiology, anatomy], Paleontology

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**Deciphering the mandibular shape variation in a group of Malagasy primates using Fourier outline analysis.**

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**Short title :** Lemuridae mandibular shape variation

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Number of Tables : 3

Number of Figures : 7

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**Abstract**

**Objectives :** Among extant Malagasy primates, the family Lemuridae has previously been recognized as presenting a higher mandibular morphological variation than other families. We conducted a quantitative analysis of mandibular size and shape within the five genera (*Lemur*, *Eulemur*, *Hapalemur*, *Prolemur* and *Varecia*) associated with a set of covariables that could explain this variation.

**Materials and Methods :** We used Fourier outline analysis on the left hemimandible of 182 specimens covering the Lemuridae family. The influence of the phylogeny but also of seven covariables (genus, diet, sex, sexual behavior, mating system, ecoregion and forest type) on mandibular variation was examined using multivariate statistics and models selection.

**Results :** Our results indicate that the high level of morphological variation within the family, associated with a phylogenetic effect and differences in diet, is due to a strong distinction between the genera *Prolemur* and *Hapalemur* and the other genera of the family. A second analysis, correcting this strong effect, indicate that mandibular shape variation is influenced not only by the phylogeny and the diet but by a combination of all the covariables.

**Discussion :** The analysis of morphological variation is a powerful tool with major applications, both for the estimation of biological diversity and for the understanding of the fundamental parameters of a species' ecology. Our work indicates that, if mandibular shape variation is mainly driven by dietary adaptation, other variables describing ecology and habitat should be considered and taken into account for an integrative understanding of species resources and the establishment of conservation measures.

**Keywords:** Lemuridae, mandible, Fourier analysis, Geometric Morphometrics.

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**Introduction:**

Madagascar is one of the world major hotspot of biodiversity, with about 3.2% of the world's endemic plants and 2.8% of endemic vertebrates (De Wit, 2003; Tattersall, 2006). In mammals, the endemism is observed in the orders of Chiroptera (eight endemic families), Carnivora (one endemic family), Afrosoricida (one endemic family) and Primates (five endemic families). This endemic biodiversity, as the entire biodiversity of Madagascar, is threatened with extinction, due to the continuous decrease in habitat size and quality (e.g. Campera et al. 2014; Herrera & Dávalos, 2016) and 90% of Madagascar's species are forest dependent (Allnutt et al., 2008). This is especially the case for the Malagasy primates that combines threats from habitat loss due to agriculture which affects about 90% of the species population, logging and wood harvesting (50%), cattle ranching (25%) and mining (18%) (Harper et al., 2007; Estrada et al., 2017; Vieilledent et al., 2018; Morelli et al., 2020; Eppley et al., 2020) but also threats from poaching, hunting for trade or domestication which affects about 65% species (Estrada et al., 2017; Reuter & Schaefer, 2017; LaFleur et al., 2019). Thus, it has been estimated that 87% of Malagasy primates species are nowadays threatened and that 100% of these species have declining populations (Estrada et al., 2017). Factors threatening primates are dynamic and interact with each other at local, regional, and national scales, leading to a reduction in population sizes and, a probable extinction (Estrada et al., 2017). Previous studies have shown that morphology covaries with ecological parameters in Malagasy primates (e.g. Ravosa, 1990; 1991; 1992; Raveloson et al., 2005; Ross et al., 2012; Meloro et al., 2015; Pitirri & Begun, 2019, 2020; Andrews et al., 2020) but also that the mandible is too variable to be useful in understanding taxonomic relationships (e.g. Schmittbuhl et al, 2007; Humphrey et al., 1999; Pitirri & Begun, 2020; Taylor & Groves, 2003) as well as in understanding diet adaptation (Ravosa, 1990; Raveloson et al., 2005; Meloro, 2015; Ross et al., 2012; Marcé-Nogué, Püschel, & Kaisr, 2017). In addition, morphology (phenotype) also clearly carries a phylogenetic signal (Fleagle et al., 2010; 2016; Masters et al., 2014; Masters & Couette, 2015; St Clair & Boyer, 2016).

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3 Lemuriforms is a monophyletic group that diverged from the loriforms, between 50 and 70  
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5 Ma on the basis of calibrated molecular phylogenies (Yoder and Yang, 2000; Perelman et al.,  
6  
7 2011; Pozzi et al., 2014a; Kistler et al., 2015). Resolving the phylogeny of lemuriforms using  
8  
9 molecular data alone has proven difficulties (Yoder and Yang, 2000; Springer et al., 2012).  
10  
11 The placement of extinct giant lemurs in the phylogeny was originally based on the  
12  
13 morphometric affinities of extinct lemurs to living species (e.g. Jungers et al., 1991; 1997;  
14  
15 Herrera & Dávalos, 2016). Among the lemuriforms, the family Lemuridae is among the most  
16  
17 studied Malagasy primates. It is also considered to be a monophyletic group, as evidenced by  
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19 the many phylogenies published over time, in which the relationships between taxa of this  
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21 family are well resolved. (e.g. Simons & Rumpler, 1988; Tattersall & Schwartz, 1991; Yoder et  
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23 al., 1996; Stanger-Hall, 1997; Randria, 1999; Yoder & Irwin, 1999; Wyner, DeSalle & Absher,  
24  
25 2000; Delperio et al., 2001). The Lemuridae is the most taxonomically diverse of the five  
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27 lemuriform families (Yoder et al., 1996), this specific biodiversity associated with a large  
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29 variation of morphological characters, of diets, of behaviors and ecology, but also a large  
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31 variation of distribution over the island.  
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35 In primates, the craniofacial complex and teeth have been the subject of several studies (e.g.  
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37 Fleagle et al., 2010; Perez et al., 2011; Bennett & Goswami 2012; Baab et al., 2014; Dumont,  
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39 1997; Sauther et al., 2001; Cuzzo, 2012; Scott, 2012) focusing on morpho-functional  
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41 adaptation or taxonomy. Concerning the mandible, previous studies have shown that  
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43 mandibular morphology of primates is influenced by several factors or parameters, including  
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45 diet, allometric scaling, sexual dimorphism, geographical distribution, behavior, growth and  
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47 phylogeny (Daegling & Grine, 2006; Daegling & Jungers, 2000; Guy et al, 2008; Humphrey,  
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49 Dean & Stringer, 1999; Ravosa, 1991; Ross et al., 2012; Schmittbuhl et al., 2007; Meloro et  
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51 al., 2015; Pitirri & Degun. 2019). However, in Malagasy primates, the mandible has been less  
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53 studied than the skull, as attested by the few numbers of articles on this subject, among which  
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55 the ones of Ravosa,1990; Raveloson et al., 2005; Viguier & Tort, 2000; Ross et al., 2012;  
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57 Meloro, 2015 or even Marcé-Nogué et al., 2017. Most of these studies have focused on one  
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3 or another factors and parameters influencing the mandibular morphology (e.g. diet, or sexual  
4 dimorphism, or phylogeny, etc.), but rarely on a set of factors. The distinction of folivorous  
5 species from the frugivorous ones is one of the most reported result explaining mandibular  
6 variation in Lemuridae (e.g. Tattersall & Schwartz, 1974). Other studies have been conducted  
7 in order to understand the functional role of each mandibular parts in jaw movements for  
8 chewing and biting actions (see Vinyard et al., 2007 for a review). Differences in diet between  
9 species are linked to morphofunctional adaptations of the mandibule muscular forces and  
10 strains that could lead to bony differences in size and shape (Ravosa, 1991). The mandibular  
11 stress pattern is dependent on the fusion of the symphysis (never present in Lemuridae) and  
12 of the bony morphology of the temporomandibular joint (Beecher, 1977; Hylander, 1979;  
13 Ravosa, 2000; Terhune et al., 2022). In Lemuridae, the main functional differences between  
14 species are related to the ingestion of leafs, and especially highly fibrous or hard items  
15 (Hylander et al., 2005). It concerns several species of the genus *Eulemur*, *Varecia variegata*,  
16 *Lemur catta* for the consumption of young leaves and *Hapalemur* and *Prolemur* for the  
17 consumption of bamboo shoots and mature leaves (Mittermeier et al., 2013). However, these  
18 factors covary and it seems important to decipher the covariation of each of these factors, and  
19 their interactions with the morphology of the mandible.

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21  
22 The family Lemuridae is composed of species that have very contrasted diet, that inhabit  
23 different habitats, present different behaviors. An integrative knowledge of the covariation  
24 between shape (here mandibular shape) and other variable describing ecology and behaviour  
25 is necessary to establish conservation measures (Estrada et al., 2017). Ours study aims to  
26 identify the main factors controlling morphological variation, thus highlighting the links between  
27 individuals' morphology, their ecology and their environment. We hypothesized the fact that  
28 mandibular variation could be under the influence of a combination of variables rather than a  
29 single one or a couple. We established several models that we compared to test this  
30 hypothesis. Such information is necessary to make decisions and develop the good strategies  
31 in the framework of biodiversity conservation and sustainable remediation.

## Materials and methods :

### Sample

We studied 182 specimens belonging to 12 living species including *Eulemur fulvus*, *Eulemur rufus*, *Eulemur albifrons*, *Eulemur coronatus*, *Eulemur macaco*, *Eulemur mongoz*, *Eulemur rubriventer*, *Lemur catta*, *Varecia variegata*, *Hapalemur griseus* and *Prolemur simus* of the Lemuridae family (Table 1, Figure 1). These specimens (dry hemi-mandibular bones) come from the osteological collections of the Muséum national d'Histoire naturelle (MNHN) in Paris, France. All the specimens have fully erupted teeth on the mandible and on the maxillary, and are thus considered as adults.

### Data collection

Morphological data acquisition consists of representative 2D images from 3D mandible shape bones. Each hemi-mandible was placed on a black background to obtain a contrast between the light-coloured spot representing the object of interest and was illuminated by two lamps (on both sides) with a voltage variator diffusing a homogeneous light (Figure 2).

The focal axis of the camera was placed perpendicular to the plane parallele to the long axis of the hemi-mandible, and then centered on the left lower first molar. We used a Nikon D750 camera equipped with a Nikon 105 mm macro lens. All the focusing of the shots was set and controlled from the computer using the DigiCamControl v 2.1.4.0 software (Duka István, 2018). Our acquisition protocol is consistent with the one described by Raveloson et al. (2005). All the images of our sample were newly taken (they were not coming from Raveloson et al. study) by one of us (J.E.M.). As tooth shape variation was not the aim of our study, and as many mandibles had missing teeth, we kept the parts of the pictures related to the mandible and removed manually the parts related to the teeth, first because our study was not focusing



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3 on teeth and second because several specimens had missing teeth. We thresholded the  
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5 images to remove teeth using Adobe Photoshop CS6 (version 13.0, Thomas & John (2012)).  
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7 Then with this same software, we converted the images in grayscale and the images were all  
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9 reduced to the same size to avoid potential differences in image resolution.  
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## 11 12 **Outlining**

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15 We used the Elliptic Fourier Analysis (EFA) method to quantify the mandible shape and size.  
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17 This method is one of the Geometric Morphometrics methods that can be used for the  
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19 characterization of biological objects shape and their quantification by continuous quantitative  
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21 variables. EFA consists of approaching the outline of the mandible by a sum of ordered  
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23 trigonometric functions (harmonics), each harmonic participating in the reconstruction of the  
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25 original outline, adding complexity (see for instance Kuhl & Giardina, 1982; Zelditch, 2012;  
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27 Claude, 2008). Elliptic Fourier is used to quantify closed contours whatever their degree of  
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29 morphological complexity. With this method, we can keep the fixed position of the mandible  
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31 and we can quantify all angles. However, with 3D landmarks, it is a point to point (anatomical  
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33 points). Our study is complementary to the one published by Raveloson et al. in 2005. We  
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35 used a similar protocol, based on EFA (rather than 3D landmarks) in order to facilitate the  
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37 comparison of results.  
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42 Outline of the hemi-mandibles were produced by the TPS series of software, and especially  
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44 the tpsDIG2 version 2.31 and tpsUtil (Rohlf, 2015). The outlines are automatically calculated  
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46 after the definition of a starting point. In our protocol, all the outlines were aligned along the  
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48 axis of elongation, we defined a reference direction of rotation for outline opening  
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50 (anticlockwise) and we placed the starting points at the same place on every outline  
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52 (Figure 3). The power of reconstruction of the original outline is calculated and used to make  
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54 a decision about the harmonics number to retain. Four coefficients are associated with each  
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56 harmonic and used for shape characterization. Harmonic coefficients are used in multivariate  
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58 analysis for shape comparisons (Rohlf & Archie 1984; Crampton, 1995; Renaud & Michaux,  
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2003). The outline analysis was performed with the Momocs Package v 1.1.0 (Bonhomme et al., 2016) on R v. 3.2.5 (R Core Team, 2021). A quantification of outline size (centroid size) is obtained with the same package, calculated as the magnitude of the semi-major axis of the first fitting ellipse (Claude, 2008).

We estimated the measurement error by measuring twice a subsample of 10 specimens of the same species. We estimated the variance within replicates, the variance between replicates and thus estimated the effect of replication using F statistics. A percentage of measurement error can also be calculated based on the variance values, following the method explained by Bailey and Byrns (1990).

### **Phylogeny:**

We used the phylogeny proposed by Herrera & Dávalos (2016) to estimate the phylogenetic structure of our morphological results and to establish the phylomorphospaces (Figure 4). This phylogeny is one of the most complete analyses for strepsirrhines, and is based on a combination of 421 morphological characters and 5,767 base pairs from two mitochondrial and four nuclear loci. We selected the branches corresponding to the Lemuride family among the majority rule consensus tree. We use two versions of the phylogeny, a first version with the 12 taxa of our sample (Figure 4A) and a second version with a reduced sample on which we removed the species *Prolemur simus* and *Hapalemur griseus* (Figure 4B).

### **Covariables**

We investigated the covariation of mandibular shape with seven variables possibly related to mandibular morphological variation.

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3 We tested the covariation of the groups (here the genera) with the shape of the mandible. The  
4 family Lemuridae constitutes five genera of which: *Eulemur*, *Lemur*, *Varecia*, *Hapalemur* and  
5 *Prolemur* (Mittermeier et al., 2010).  
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10 We tested the covariation of diet with lemurids mandibular shape. Three diet categories were  
11 defined with specimens classified as folivore/frugivore for the species of *Eulemur*,  
12 frugivore/folivore for *Lemur catta* and *Varecia variegata* and folivore or feeding on hard objects  
13 (bamboo shoots, bamboo culm, sugar cane, etc.) for *Hapalemur griseus* and *Prolemur simus*.  
14 We based this classification on data summarized in previous studies on primate dietary  
15 adaptation (e.g. Wright & Willis, 2012; Winchester et al., 2014; Coiner-Collier et al., 2016;  
16 Steffens, 2020; Eronen et al., 2017, St. Clair et al., 2018; Andrews et al., 2020).  
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26 We also investigated the influence of sex, sexual behavior and mating system on mandibular  
27 shape variation, hypothesizing that mandibular shape would express a sexual dimorphism,  
28 would vary depending on dominant and non-dominant specimens and over different mating  
29 systems. Indications for specimen sex were collected from collection labels. We used the  
30 shape of the mandible to evaluate the extent of sexual dimorphism in Malagasy prosimians.  
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37 For sexual behaviour, females are most of the time social dominant (coded "Dominant" for  
38 females and "Non-dominant" for males) in Lemuridae (e.g. Mittermeier et al., 2006, 2010;  
39 Sauther, 2012). However, in *Prolemur simus*, the males are socially dominant over females  
40 (Roulet, 2012). We also hypothesized the covariation of mating system with mandibular  
41 shape and tested this hypothesis by coding both mating systems polygynous (also including  
42 multimale-multifemale system) and monogamous for the different species composing our  
43 sample.  
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53 The covariations of mandibular shape with ecoregions and forest types have been tested.  
54 Lemurs are distributed in the forested zones remaining around the periphery of Madagascar  
55 (Mittermeier, 2010). In order to test these hypotheses, we coded Madagascar's ecoregions  
56 and habitat (Figure 5). Madagascar can be divided into several bioclimatic or  
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3 phylogeographical domains depending on latitude, altitude, temperature, rainfall, seasonality  
4 and vegetation (Battistini, 1996; DuPuy & Moat, 1996). Ecoregions were defined following  
5 climatic (Cornet, 1974) and vegetation criteria. Forest types are defined on the basis of their  
6 belonging to one of the ecoregions (Vieilledent, 2018; Harper, 2007): the central plateau is  
7 temperate, with marked wet and dry seasons, is characterized by mid-altitude montane  
8 rainforest and by sclerophyllous forest at the highest altitudes. The moist forest with dense  
9 evergreen lowland rainforest is located in the east of the island where *H. griseus*, *P. simus*,  
10 *V. variegata*, *E. fulvus*, *E. rubriventer* are distributed and in south-east where *E. collaris*, *H.*  
11 *griseus* and *E. rubriventer* are distributed. *E. collaris* are also distributed in the tropical  
12 rainforest if the south-east. The west of the island is characterized by distinct seasons, with  
13 deciduous forests. The climate becomes drier from the north to the south, where *E. fulvus*, *E.*  
14 *mongoz*, *E. rufus* and *E. coronatus* are distributed. The southern domain is hot and semiarid,  
15 with subarid thorn scrub and gallery forest where *L. catta* are distributed. The dry forest is  
16 present in Mayotte, where *E. fulvus* are distributed (species introduced by humans). Finally,  
17 some specimens of our sample come from parks and zoos.

### 34 35 **Statistical analyses**

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40 We applied a Principal Component Analysis (PCA) on harmonic coefficients in order to  
41 compute the morphospace. The inverse transformation, done on the harmonic coefficients  
42 extracted from every outline, allowed a reconstruction of mandibular shapes describing the  
43 variation expressed by each PCs. Size differences between taxonomic groups are calculated  
44 using the ANOVA method and multivariate morphological differences were tested using  
45 MANOVAs with the help of the package MASS (Venables & Ripley, 2002).

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53 We tested the structure of the morphospace explained by the phylogenetic hypothesis using a  
54 phylogenetic test available on the Geomorph R package (Adams & Otárola-Castillo, 2013;  
55 Adams, 2014). Then, we plotted the phylogeny onto the morphospace, producing a  
56 phylomorphospace, using the package R v. 3.2.5 (R core Team, 2021). For this analysis we  
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3 computed the mean shape for each species (as we have only one observation per group in  
4 the phylogeny), computed the morphospace from these mean shapes and projected the  
5 observations in the morphospace. We obtained a graphic in which the phylogeny and the  
6 morphological variation within each group can be associated.  
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12 We then tested the effects of covariables on mandibular shapes using a linear model. We built  
13 nine different linear models considering mandibular shape variation in function of:  
14

- 15 • Null model
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- 17 • Phylogeny
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- 19 • Phylogeny + Diet
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- 21 • Phylogeny + Sex (covariables sex, sexual behaviours and mating system)
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- 23 • Phylogeny + Habitat (covariables ecoregion and forest type)
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- 25 • Phylogeny + Diet + Sex
- 26
- 27 • Phylogeny + Diet + Habitat
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- 29 • Phylogeny + Sex+ Habitat
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- 31 • Phylogeny + Diet + Habitat + Sex
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37 The robustness of each model is estimated by verifying the distribution and homogeneity of  
38 variances of the residuals. We also detected the presence of potential outliers.  $R^2$  values of  
39 each model is given in tables 2 and 3. We used AICc (corrected Akaike Iteration Criterion)  
40 values for model comparison (Burnham & Anderson, 2004). The model with the lower value of  
41 AICc was considered as the one that best describes the data structuration. We compared the  
42 models with the function aictab of the R package AICmodavg (Mazerolle, 2020). Same models  
43 were tested on centroid size.  
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53 **Result:**  
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58 **Measurement error**  
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3 The measurement error is lower than 2% and results from the MANOVA indicate that the effect  
4 of the replicates is not significant (Pillai = 0.15,  $p=0.81$ ).  
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### 8 **Morphological variation in lemurids**

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11 The morphospace composed of the two first PCs, accounting for 55.5 and 16.9% of total  
12 variation, clearly separates specimens of the genera *Hapalemur* and *Prolemur* from the  
13 specimens of the genera *Eulemur*, *Lemur* and *Varecia* (Figure 6). This distinction occurs mainly  
14 along PC1 that describes mandibles with high coronoid processes, with tips arched posteriorly,  
15 high vertical ramuses and shallow angles but developed and low angular processes on positive  
16 values of the axis (illustrated by *Hapalemur griseus*). Negative values of PC1 (illustrated by  
17 *Eulemur rufus*) describe mandibles with pronounced symphyses, bodies with convex ventral  
18 edges, moderately angular processes, ramuses with marked grooves between the angular  
19 processes and the condyles, marked sigmoid notches and almost vertical coronoid processes.  
20 The variation along this first axis is important between genera (as presented previously) but  
21 also within some genera (especially in *Hapalemur*, *Prolemur* and *Eulemur*). PC2 describes  
22 mandibles with thin bodies, low symphyses and vertical ascending ramus with vertically  
23 developed coronoid processes on positive values (illustrated by *Lemur catta*). The mandibles  
24 described by the negative values of this second axis (illustrated by *Eulemur fulvus*) have thin  
25 bodies, with marked symphysis, moderately developed ascending ramus with marked angles,  
26 condyles and coronoid processes directed posteriorly more than vertically. Shape variation  
27 along this axis is also important. The amount of variation seems homogeneous between  
28 genera and thus only describes differences within genera. The mandibular shape differences  
29 described on the two first PCs is also true when considering the entire variation. The results of  
30 the MANOVA calculated on all the PCs indicate a significant distinction of mandibular shape  
31 between genera (Pillai = 3.57,  $p<0.001$ ). The difference in mandibular shape between genera  
32 is accompanied by a difference in mandibular size (ANOVA results:  $F = 7.18$ ,  $p<0.01$ ), with the  
33 mandibular centroid size in *Prolemur* being significantly higher than mandibular centroid size  
34 in the other genera.  
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3 The mandibular shape difference between the genera *Hapalemur*, *Prolemur* and the other  
4 genera of the lemuridae family also reflects the phylogenetic signal, as presented by plotting  
5 the phylogenetic tree onto the morphospace (Figure 6) but also as established by the results  
6 of the phylogenetic test (K statistics = 1.27,  $p = 0.03$ ). The high difference between  
7 *Hapalemur/Prolemur* and the other genera of the family is so high that it is not easy to  
8 understand the morphological structure of mandibular shape variation in the genera *Eulemur*,  
9 *Lemur* and *Varecia*.

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19 In order to investigate this phylogenetic variation, we ran a new analysis on a subsample  
20 composed of the specimens of these three genera. Results are presented on Figure 7. The  
21 two first PCs account for 49.25 and 23.88% of total variation respectively. Shape variation  
22 along PC1 describes, for negative values, mandibles with thin bodies, developed ascending  
23 rami, with high and vertical coronoid processes, marked mandibular (sigmoid) notches, low  
24 condylar neck but developed condyles, and small angular processes. Positive values of PC1  
25 describe mandibles with thin bodies and small symphyses, low ascending rami with coronoid  
26 processes developed posteriorly, shallow condyles and small angular processes (Figure 7).  
27 PC2 describes mandibles, for negative values, with relatively low coronoid processes, with tips  
28 directed posteriorly, the condyle is marked but without necks, and the angles and the angular  
29 processes are low. Positive values of the second PC describe mandibles with marked  
30 symphyses, developed ascending rami, with high coronoid processes, protruding condyles and  
31 marked necks, and developed angular processes. Specimens of the different taxonomic  
32 groups are overlapping on this morphospace but all the specimens of the genera *Varecia* and  
33 *Lemur* have positive values on PC1 when specimens of the genus *Eulemur* are more widely  
34 distributed along this axis. Within the genus *Eulemur*, specimens of the different species are  
35 also overlapping showing a high amount of shape variation in comparison to the variation  
36 expressed by the specimens of the two other genera. When projecting the phylogeny onto the  
37 morphospace, we can see that the shape variation in this subsample is not structured by the  
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3 phylogenetic signal. This is reinforced by the non significant result of the phylogenetic test (K  
4 statistics = 0.64,  $p = 0.08$ ).  
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## 8 **Analysis of covariations**

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### 10 **covariations with mandibular shape**

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14 We calculated the AICc values for the nine tested models. Results are presented on Table 2.  
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16 Our first analysis was made on the entire sample, but, regarding the high distinction of the  
17 specimens of the *Hapalemur* and *Prolemur* genera, we conducted a second analysis, removing  
18 these specimens. AICc values are here computed as the sum of the AICc relative to the first,  
19 second and third PC axes. We considered the three first PCs as they cumulated more than  
20 90% of total variation in both PCA analyses.  
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28 Models on shape of the entire dataset were all significant (except the null model), with high  
29 values of  $R^2$ . The most likely model being the one with the lowest AICc value, it is noticeable  
30 that the two first models (Phylogeny and Phylogeny + Diet) can be selected to describe the  
31 interactions between covariables and mandibular shape. These models are similar as the two  
32 genera *Hapalemur* and *Prolemur* are also the only ones of the sample having a folivorous diet.  
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34 Our results also indicate that the phylogenetic signal (here the difference in mandibular shape  
35 between genera) associated with the diet signal is predominant and that the other covariables  
36 do not appear as relevant in this situation.  
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46 Results for mandibular shape variation (Table 3) are very different when considering  
47 the reduced sample (i.e. the sample without *Hapalemur* and *Prolemur* specimens). In this case,  
48 all the models, except the null model, were significant but the  $R^2$  values were different from  
49 one model to another. The most likely model is the one considering the covariables Phylogeny,  
50 Diet, Habitat and Sex. If we decipher the different covariables of this model responsible for  
51 mandibular shape variation, Diet still plays a significant role ( $F=131.7$ ,  $p<0.001$ ). For Habitat  
52 covariables, mandibular shapes are different between Ecoregions ( $F=3.617$ ,  $p<0.001$ ) but they  
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3 are not different between forest types. Mandibular shapes are not different between males and  
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5 females nor between the two types of sexual behaviours expressed in our sample (dominant  
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7 females or dominant males). However, mandibular shapes are significantly different between  
8  
9 the two different types of mating systems (monogamous and polygynous). Then, we also found  
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11 a difference of mandibular shape between the three genera included in this analysis ( $F=18.5$ ,  
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13  $p<0.01$ ).  
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#### 15 16 17 - Covariations with mandibular size

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20 The most likely models to explain mandibular size variation are the one with the phylogeny  
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22 and diet as covariables, for the full sample (Table 2). In the case of the full sample analysis,  
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24 the effect of Diet on mandibular size variation is highly significant ( $F=12$ ,  $p<0.001$ ), the effect  
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26 of the phylogeny is also significant but with lower values ( $F=3.4$ ,  $p=0.031$ ). In the case of the  
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28 reduced sample, if the best models are the same as with the entire sample, the AICc values  
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30 are very similar and the  $R^2$  values are low and not significant. In this case, size variation is  
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32 probably too low to be explained.  
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#### 38 Discussion

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41 Our results illustrate the high level of mandibular shape variation in the family Lemuridae. This  
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43 high variation is mainly driven by the fact that the specimens of the genera *Prolemur* and  
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45 *Hapalemur* have different mandibular morphologies than the other genera of the family. Such  
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47 differences are likely explained by a phylogenetic effect combined with an adaptation to  
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49 folivory. As specimens of the genera *Hapalemur* and *Prolemur* are the only folivorous of our  
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51 sample, it is not possible, in this case to explain the differences in mandibular shape from the  
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53 other genera by a phylogenetic effect or by a difference in diet. Specimens of these genera  
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55 indeed present mandibular shapes with very robust and short mandibular bodies, with deep  
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57 mandibular symphysis, even deeper and wider than those of the great apes (Taylor, 2003;  
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59 Ravosa, 1991), and a large muscular insertion on the ascending ramus. This is certainly an  
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3 adaptive specialization to their diet, which in *Hapalemur* is based on bamboo (Wright & Willis,  
4 2012; Grassi, 2006). The difference has been located not only in the choice of food variety but  
5 also in the choice of food qualities (Tan, 1999; Grassi, 2006). Indeed, *Hapalemur griseus* has  
6 been exploiting mainly shoot stems and young bamboo leaves (Rabarivola et al., 2007) while  
7 *Prolemur simus* also feeds on hard leaves, also requiring high bite strength (Vinyard et al.,  
8 2008).

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17 Among most living prosimians (with the exception of *Daubentonia* and the Indriids), it  
18 is inferred that the mandibular corpus is probably not powerfully bent during biting along the  
19 anterior dentition since their anterior teeth, which are either absent or are quite gracile and not  
20 firmly rooted, are poorly adapted to withstand powerful axial and bending stresses (Kay &  
21 Hylander, 1978). Leaf chewing species probably requires a larger average biting force than  
22 frugivorous species, and the leaf chewing species spend a greater amount of time chewing  
23 food compared to the frugivorous (Hylander, 1979).

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32 In this case, *Prolemur simus* has an even deeper and wider body and mandibular  
33 symphysis and a higher ascending ramus than *Hapalemur griseus*. Such developed structures  
34 imply, on the coronoid process, larger insertions of the muscle *temporalis* and of the  
35 sphenomandibular ligaments (along the lingula of the mandible), responsible for an optimal  
36 elevation of the mandible, maximal leverage and accurate contractile strength for hard item  
37 consumption (Pick & Howden, 1977). Developed ascending ramus combined with developed  
38 angular processes allow large insertions of the muscles *masseter* (deep and superficial),  
39 *zygomatico mandibularis* and *medial pterygoid* also responsible for elevation of the mandible  
40 during mastication movements. A developed symphysis rather indicates developed insertions  
41 for the muscles *digastric*, *stylo-hyoid*, *mylo-hyoid* and *genio-hyoid*, all depressors of the  
42 mandible. These large insertions indicate large and powerful muscles with higher leverage and  
43 thus higher chewing strength (Pick & Howden, 1977).

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3 In contrast, in the *Eulemur*, *Lemur* and *Varecia* genera, the mandible reflects a  
4 longitudinal development, a long aspect of the articular condyle and a long and shallow  
5 mandibular body and symphysis with short ascending rami. These traits are explained by a  
6 rather soft diet (frugivorous), composed essentially of leaves, flowers and fruits. The  
7 masticatory apparatus, that is to say, the surfaces of muscular insertions on bones and the  
8 volume of muscles, is less developed with lower chewing strength (Raveloson, 2007; Ravosa,  
9 1991). The mandibular shape differences between genera within lemurids can also be  
10 explained by the manner of food processing employed by the animals. For instance,  
11 specimens of the species *Varecia variegata* use the anterior teeth to grasp and move the  
12 feeding objects (Raveloson et al., 2005). As a result, much of the stress flow is reported to the  
13 anterior part of the jaw (Chivers et al., 1984; Preuschoft & Witzel, 2005), biting forces being  
14 higher on the anterior parts of the mandible (at incisors, canine and premolar) rather than on  
15 the posterior part (Marcé-Nogué et al., 2017). The chewing movement of the mandible has  
16 been reported by previous authors working on chewing movements (Ross et al., 2009). They  
17 identified the peculiar length of lemurids mandible (especially in *Eulemur*, *Lemur* and *Varecia*  
18 species), comparatively to mandibular mass and body mass, that is out of the range of a  
19 general primate model. The authors conclude that the lemurids use their gracile and long  
20 mandibles in faster chewing cycles than the primates, reinforcing the idea of singularity for the  
21 group.  
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44 Such variation within the lemurids and the high difference between folivorous and non  
45 folivorous species have already been reported on cranial shape (e.g. Andrews et al., 2020  
46 work on palate shape variation) as well as on mandibular shape. For instance, in the work  
47 published in 2005 Raveloson et al., highlighted this difference, and separated their analysis in  
48 two sub analyses, with and without the folivorous specimens (all classified as *Hapalemur* in  
49 their case). The aim of Raveloson et al. 2005's work was to evaluate the method and separate  
50 the mandibular morphologies of the genera composing the sample. Our work has different  
51 aims but could be seen as complementary to Raveloson's earlier work. Our results support  
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3 Raveloson et al. 2005's conclusions of a great mandibular shape variation within the family.  
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5 This high variation was also suggested by other authors, based on the morphometric analysis  
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7 of the mandibular shape (Viguiet, 2004 ; St Clair et al., 2018, Oh et al., 2019). Here, we also  
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9 report an high level of variation with the genera. Such variation was also reported by Raveloson  
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11 et al., 2005 but for *Hapalemur* only. The authors explained this variation by differences in  
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13 dietary compositions between species. Our results indicate that the high level of variation for  
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15 each genera composing our sample, not only for *Hapalemur*. The direct correlation between  
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17 mandibular shape variation and dietary shifts could explain such variation. However, the direct  
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19 link between mandibular shape variation and diet specialization is questionable. It is quite clear  
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21 that the folivorous species have a particular mandibular morphology but one could think that,  
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23 in the case of a selective pressure driven by a morphofunctional adaptation, the expected level  
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25 of variation should be low (Futuyma & Moreno, 1988). This is not the case for the folivorous  
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27 species of our sample. The difference in diet could explain the mandibular shape morphology  
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29 for the folivorous but some other covariables could explain the intra generic shape variation.  
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31 Some previous studies have mentioned the fact that other covariables than diet could have an  
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33 effect on mandibular shape variation in strepsirrhines. For instance, in 2018, Fabre et al. have  
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35 quantified the covariation between mechanical and architectural properties of the mandibular  
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37 muscles and the mandible shape variation. The level of covariation found by these authors led  
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39 them to the conclusion that, because it was difficult to identify the biomechanical patterns  
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41 associated with diet, the mandible could reflect other non-dietary systems that permit it to vary.  
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43 An assumption of mandibular random shape variation was even formulated. Our results  
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45 indicate a true covariation of mandibular morphology with diet, but also with other covariables  
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47 non-dietary covariables.  
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53 Another important result is the position of the ring-tailed lemurs in the morphospace.  
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55 *Lemur catta* is frugivorous/folivorous but its mandibular morphology is highly different from the  
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57 other frugivorous/folivorous species. *Lemur catta* became frugivorous/folivorous or even  
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59 opportunistic because of the destruction of its habitat and the insufficiency of food. The species  
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3 shifted its diet secondarily and managed to eat seeds and leaves of the tamarind species  
4 *Tamarindus indica* (Jolly et al., 2006; Yamashita et al., 2015). Given the hardness of this fruit,  
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6 the shift in food items is related to the increase in the ascending branch of their mandible by  
7 exerting masseter muscular forces during mastication relatively long (Vinyard et al., 2006). The  
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9 consumption of tamarind leaves also has consequences. As the dietary shift is relatively  
10 recent, the adaptation process of the mandible shape is probably still incomplete. Dental  
11 pathologies, mandibular wear are observed (Sauter & Cuzzo, 2009) and unconsumed part  
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13 of leaves are found in fecal matters (Yamashita, 2003). In that case, dental and masticatory  
14 morphologies are not fully adapted to processing these foods items and thus a mismatch is  
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16 observable between diet of *Lemur catta* and mandibular morphology (Yamashita et al., 2012).  
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25 In our study based on the reduced sample (without *Hapalemur* and *Prolemur*), the most likely  
26 model is the one considering the entire set of covariables with significant effect of mating  
27 system and ecoregions when the variables sex, sexual behaviour and type of forest were not  
28 covarying with mandibular shape. It is well known that sexual dimorphism is low in  
29 strepsirrhines and probably not correlated with body weight, or canine size (Kappeler, 1989,  
30 1990, 1991; Kappeler & Heymann, 1996; Jenkins & Albrecht, 1991; Thorén et al., 2006). It is  
31 thus not very surprising that we did not find significant differences in mandibular shape  
32 between sexes (even if few studies focused on mandibular shape variation). Sexual behaviour  
33 does not covary with mandibular shape. Here again, several authors have previously  
34 expressed that the lack of sexual dimorphism was probably related to the dominance of  
35 females over males (Richard, 1987; Richard & Nicoll, 1987). Female dominance could diminish  
36 the competition between males and, as a consequence, reduce the level of sexual dimorphism  
37 (Jenkins & Albrecht, 1991). Our results indicate that the mating system of lemurids has a  
38 significant effect on mandible shape variation. Several authors have reported the fact that  
39 intrasexual competition is higher in polygynous species. The male-male competition and  
40 agonistic behaviors can be observed for female access during mating season as described in  
41 *Lemur catta* (Mittermeier et al., 2010). Moreover, the availability of food for each individual in  
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3 a group also depends on the number of individuals in the group, and the monogamous mating  
4 system provides an advantage over the polygynous one on this point (Kling & Wright, 2018).

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6 Intergroup agonistic behaviors are also described for food access in *Eulemur macaco* (Bayard  
7 & Simmen, 2005). It is known that the availability of food for each individual in a group depends  
8 on the number of individuals in the group and that, on this point, monogamous groups have  
9 more advantages than multimale-multifemale groups (Kling and Wright, 2018). Our results  
10 suggest that inter individual competition in large groups has an effect on mandibular shape  
11 variation, possibly in modifying the musculature. Several authors have shown that in  
12 strepsirrhines, canine size is not a sexually dimorphic trait and that canine size is not covarying  
13 with the mating system (Kapeller 1990, 1996). Very little is known about the mandibular shape  
14 variation and we think that it would be important to focus on this anatomical part.

15  
16 Our results indicate that mandibular shape does not vary with types of inhabited forests. We  
17 expected a significant covariation of these variables mainly because the type of forest is  
18 supposed to describe the type of available food items and thus to correspond in a way to the  
19 dietary categories. Our results do not show such interaction. Two conclusions can be  
20 expressed: the first one is that the possible covariation between the type of forest and the  
21 mandibular shape variation is indeed not significant. The second is that the possible  
22 covariation between the type of forest and mandibular shape exists but the method to classify  
23 the forests is not optimal to categorize the animal's habitats. Previous authors have shown that  
24 forest classifications are difficult to homogenize (Humbert, 1954; Faramalala, 1995; Moat,  
25 1996). Then, the Madagascar landscapes are more structured by the biogeographic regions  
26 rather than by a classification of the forest types (Ganzhorn et al., 2006; Mittermeier et al.,  
27 2014).

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29 Our results indicate a significant covariation of mandibular shape with ecoregions. Covariations  
30 of primate morphology with geographical distribution (taking ecoregions as great categories of  
31 distribution) are known for many years (Albrecht, 1990; Albrecht & Miller, 1993). These studies  
32 mainly focused on cranial size variation. Albrecht et al. (1990) explained the pattern of  
33 ecogeographical size difference by the fact that larger animals are found in wetter and more  
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3 productive habitats than smaller ones. Moreover, other works reported that western species in  
4 the tropical forest or dry forest are smaller compared to eastern species in rainforest (Eppley  
5 et al., 2017). The ecogeographical difference is not only visible on size (cranial size in the case  
6 of Viguier, 2002), but also on cranial shape variation (in this case). Our results on the mandible  
7 support these results considering the entire sample, but not considering the reduced one were  
8 size variation was not explained by the covariables.

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16 The natural forest of Madagascar has suffered a great loss of forest cover inhabited by  
17 lemurs (Vieilledent et al., 2017; Ganzhorn et al., 2000). Habitat loss, habitat fragmentation due  
18 to anthropogenic activities or climate change have a negative impact on primates (Almeida-  
19 Rocha et al., 2017). Madagascar is a hotspot of biodiversity but it is also one of the most  
20 threatened areas with almost half of its forest cover lost since 1953 (Vieilledent et al., 2017;  
21 Kling et al., 2019). Landscape fragmentation mainly causes a decrease in lemur species  
22 richness (Ganzhorn, 1998; Ganzhorn et al., 2000). Our results illustrate the fact that multiple  
23 factors can act simultaneously on the morphological variation. These biotic and abiotic  
24 confounding factors are highly important to identify the true effects of environmental changes  
25 and their consequences. Such results are important in the context of conservation and  
26 sustainable remediation, and contribute to a good knowledge of biodiversity.

## 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 **Conclusion**

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44 A quantitative estimation of the morphological variation, using 2D geometric morphometric  
45 methods have been proposed. Our results illustrate the high level of mandibular variation within  
46 the family Lemuridae. We have highlighted a strong phylogenetic effect in this family, with the  
47 clear separation of the genera *Hapalemur* and *Prolemur* from the other genera of the family.  
48 This result was already stated in previous studies. Our results showed that diet was not the  
49 only factor interacting with mandible shape variation, which, rather is influenced by a complex  
50 signal with a combination of factors. These findings are important for the understanding of  
51 variation and diversity and should be taken into account for instance for conservation plans.

**Acknowledgements :**

The authors are grateful to Jacques Cuisin and Aurélie Verguin for the access to specimens from the collections of Anatomie Comparée, MNHN, Paris. Visit of collection was funded by the AP program of École Pratique des Hautes Études.

**Conflict of interest:**

The authors do not have conflicts of interest to disclose.

**Data Availability Statement :**

Data are available upon request to the authors

**Authors contribution :**

**Miarisoa Jeanne Emma:** Investigation ; writing-original draft ; writing-review and editing.

**Raveloson Herimalala:** writing-review and editing. **Randrianambinina Blanchard:** writing-review and editing, **Sébastien Couette:** Conceptualization ; formal analysis ; writing-original draft; writing-review and editing.

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5 **TABLE 1** Specimens of the Lemuridae family composing the sample  
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7 **TABLE 2** Model selection for the mandibular shape and size variation response variables  
8 calculated on the entire sample. Significant values of  $R^2$  are indicated in bold. Akaike  
9 Iteration criterion (AICc) and differences between the lower AIC value (best fitted model) and the other  
10 models are given for shape and size variation.  
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12 **TABLE 3** Model selection for the mandibular shape and size variation response variables  
13 calculated on the reduced sample. Significant values of  $R^2$  are indicated in bold. Akaike  
14 Iteration criterion (AICc) and differences between the lower AIC value (best fitted model) and  
15 the other models are given for shape and size variation.  
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20 **FIGURE 1** Illustration of the mandibular morphology of the species composing the sample.  
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22 **FIGURE 2 Data acquisition and outlining.** 1 : Acquisition of mandible images in lateral  
23 view; 2: Standardisation of the images; 3: Outlining of the object of interest by the tpsDIG2  
24 version 2.31 software; 4 : Step by step reconstruction of the mandibular outline using  
25 Momocs R package, here reconstruction by the two first harmonics.  
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27 **FIGURE 3** Representative of *Prolemur simus* outlines (outlines are centered, starting point for  
28 the outline opening are indicated by arrows.)  
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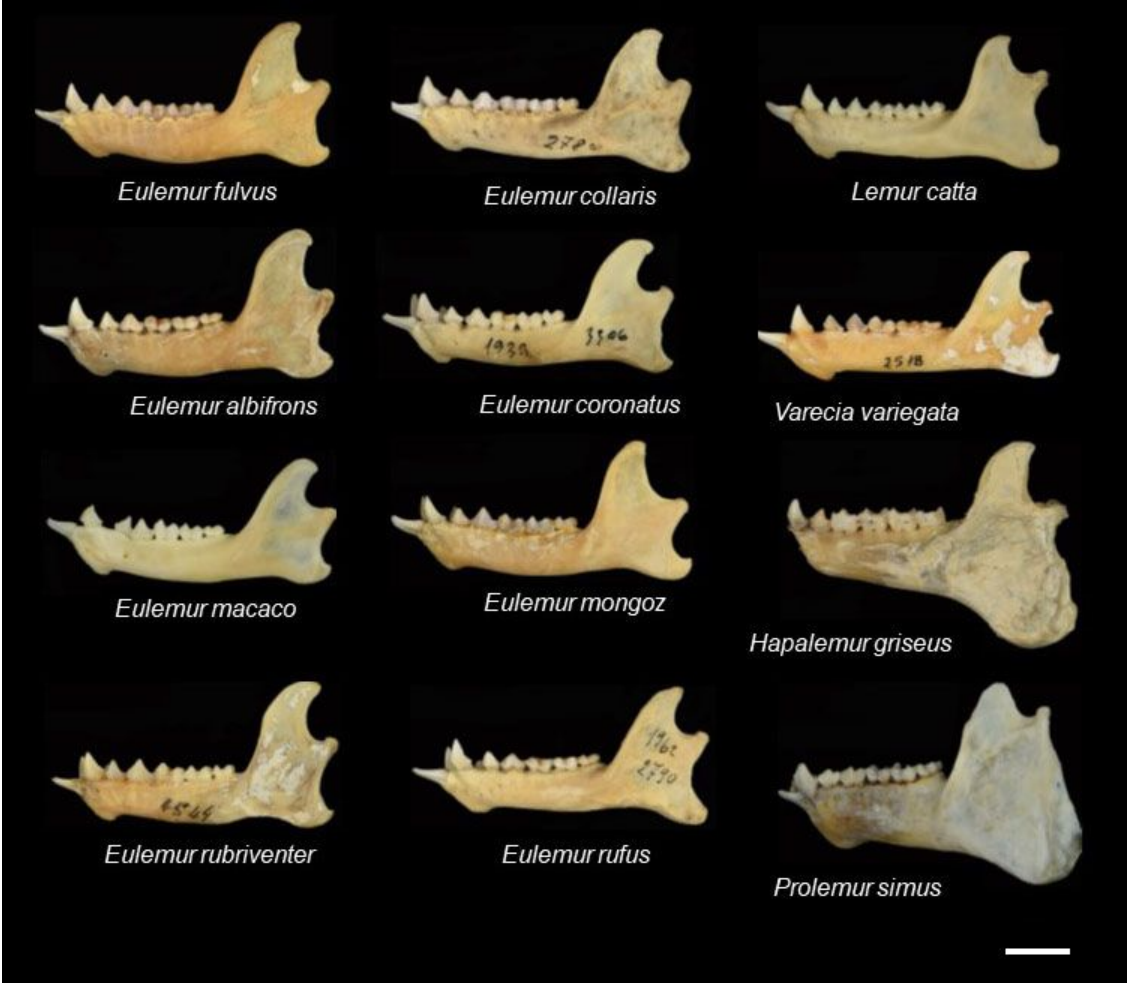
30 **FIGURE 4 A)** Phylogenetic tree of the entire sample, obtained from Herrera & Dávalos (2016),  
31 B) Phylogenetic tree of the reduced sample  
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33 **FIGURE 5** Map of the ecoregions used for the analysis (Source: Kathrin H. Dausmann, 2015.  
34 Modified in 2022)  
35

36 **FIGURE 6** Phylomorphospace of the entire sample computed on the genera. Larger symbols  
37 represent the group centroids. Numbers on the phylogenetic tree correspond to the nodes of  
38 the tree on figure 4. The outline of a specimen of *Eulemur rufus* illustrates the negative values  
39 of PC1, the outline of a specimen of *Haplemus griseus* illustrates the positive values of PC1;  
40 The outline of a specimen of *Eulemur fulvus* illustrates the negative values of PC2, the outline  
41 of a specimen of *Lemur catta* illustrates the positive values of PC2.  
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46 **FIGURE 7** Phylomorphospace of the reduced sample computed on species. Species group  
47 centroids are illustrated by the small circles at the tip of the branches of the tree presented on  
48 figures 5. The outline of a specimen of *Eulemur rubriventer* illustrates the negative values of  
49 PC1, the outline of a specimen of *Lemur catta* illustrates the positive values of PC1; The outline  
50 of a specimen of *Eulemur mongoz* illustrates the negative values of PC2, the outline of a  
51 specimen of *Eulemur albifrons* illustrates the positive values of PC2.  
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**FIGURE 1**

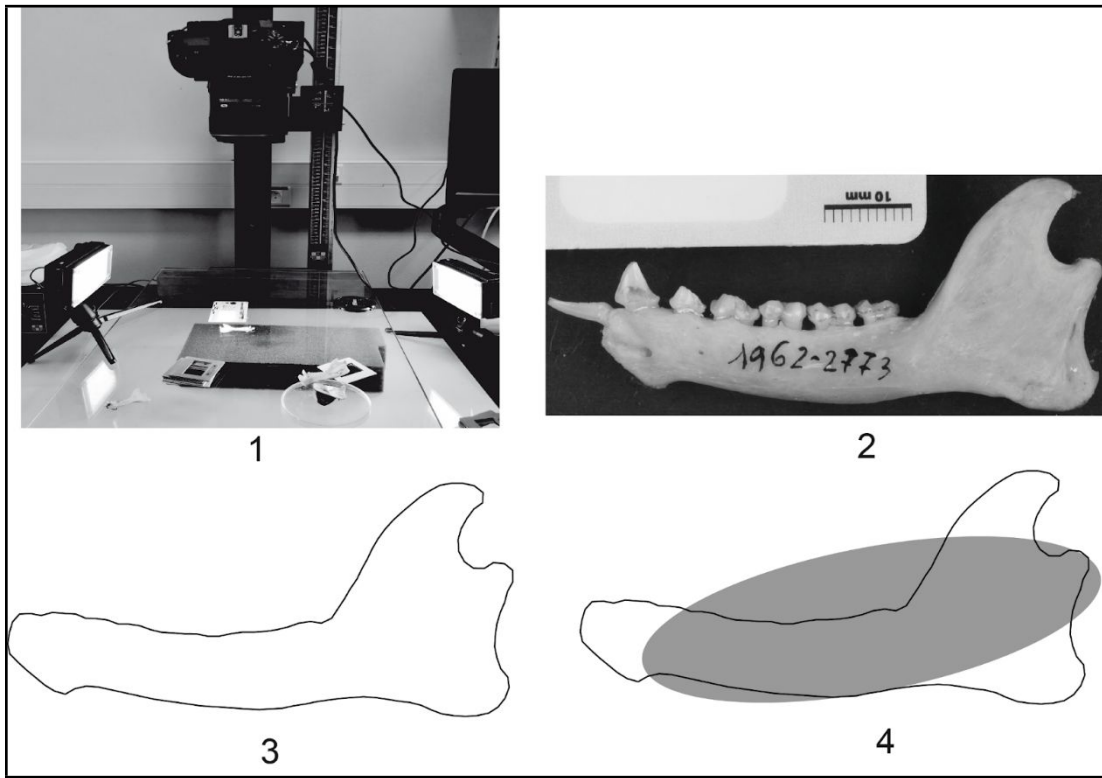


FIGURE 2

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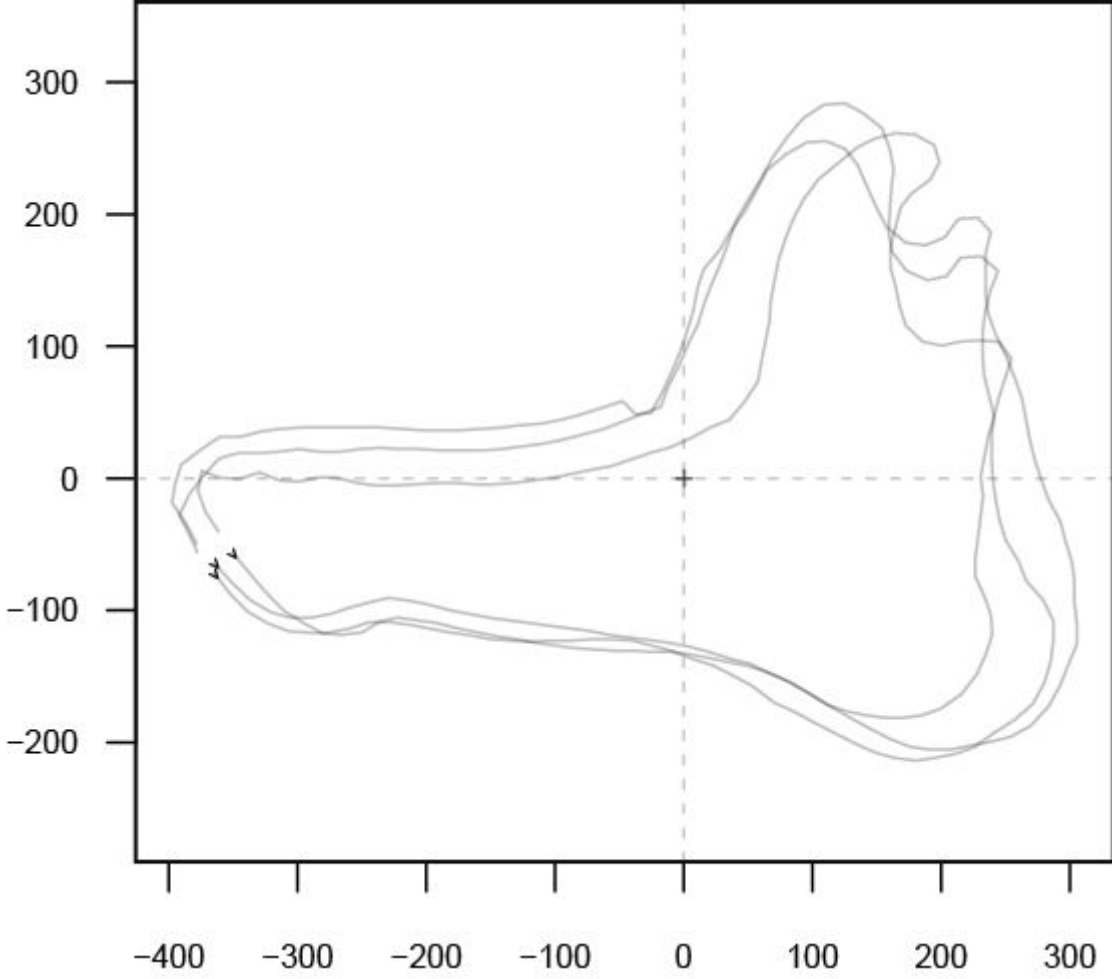
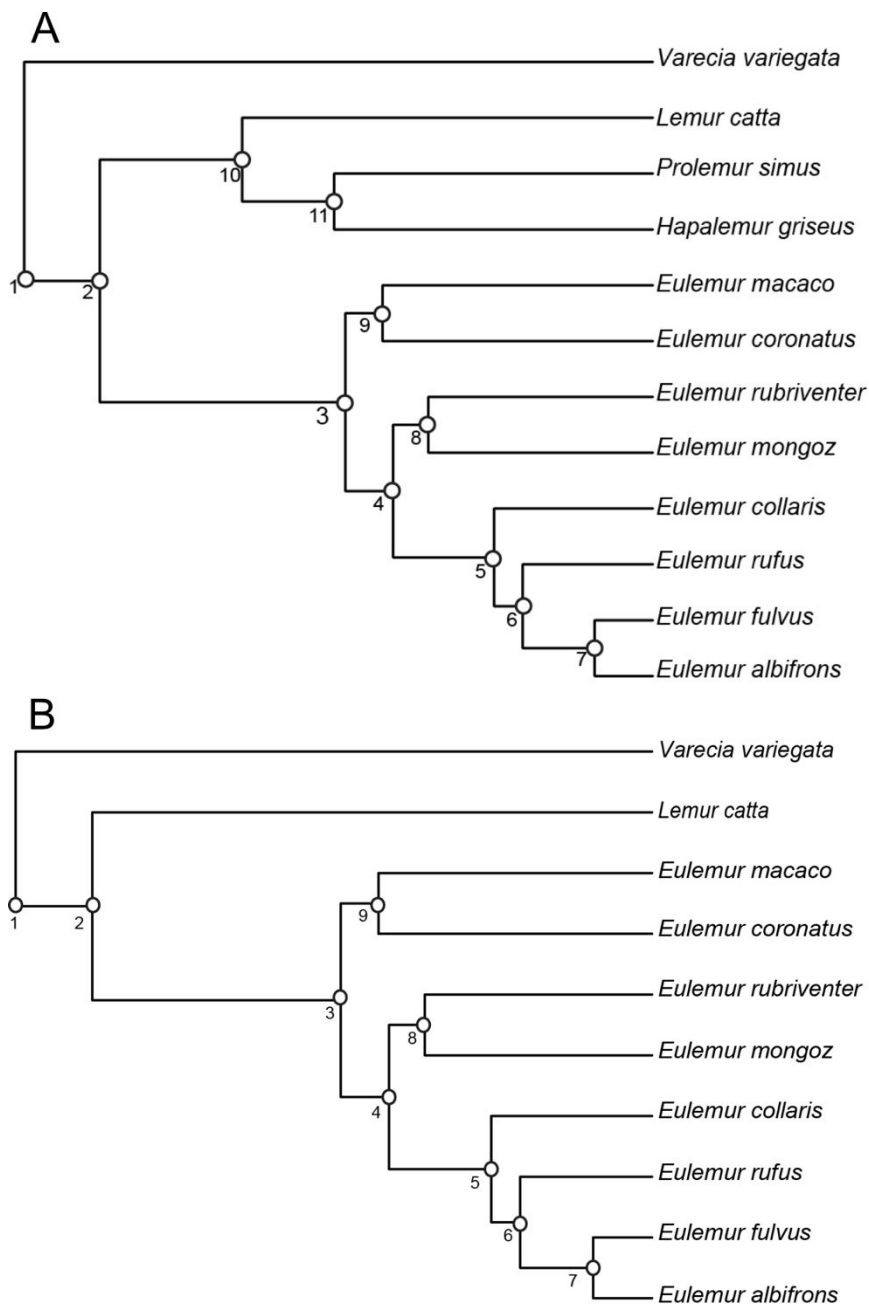
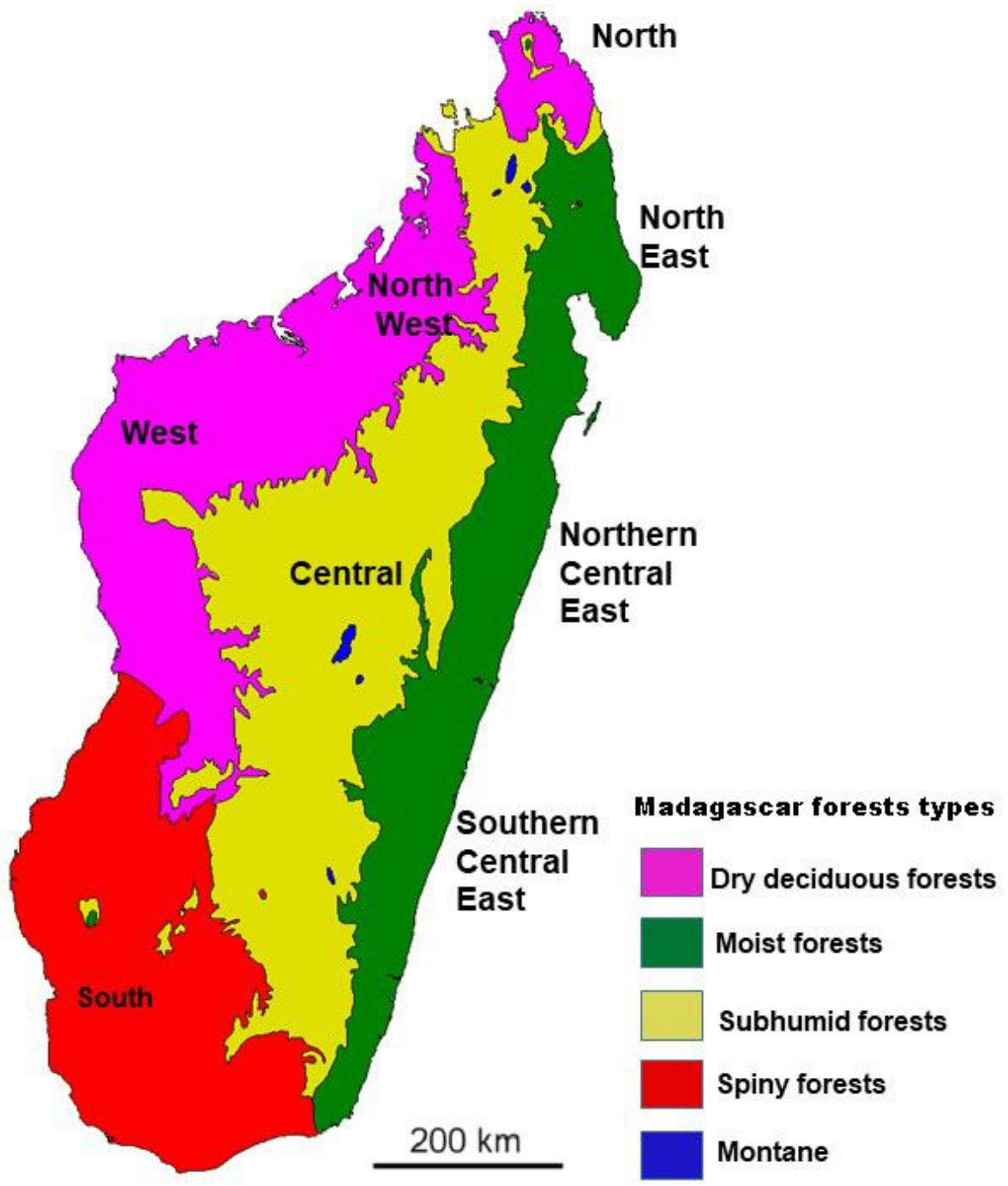


FIGURE 3



**FIGURE 4**

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**FIGURE 5**

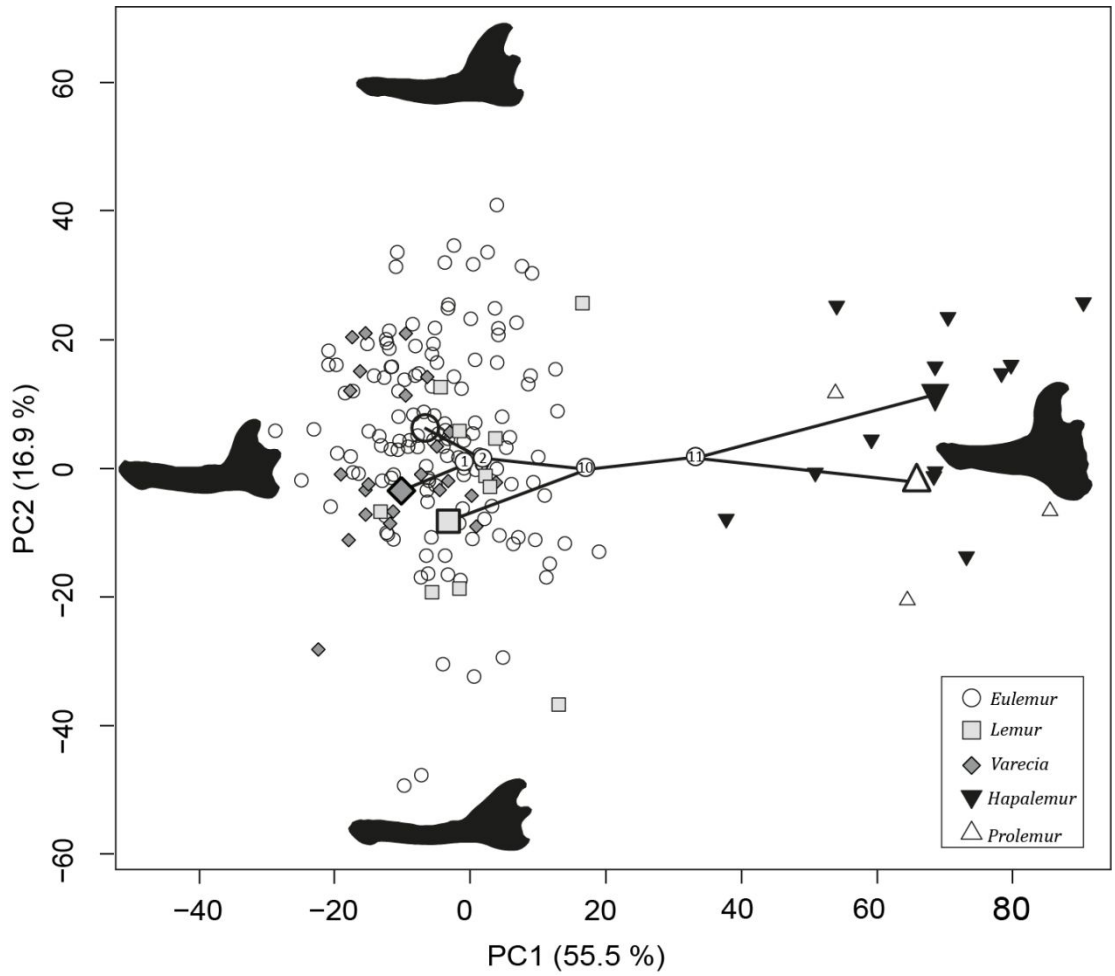


FIGURE 6



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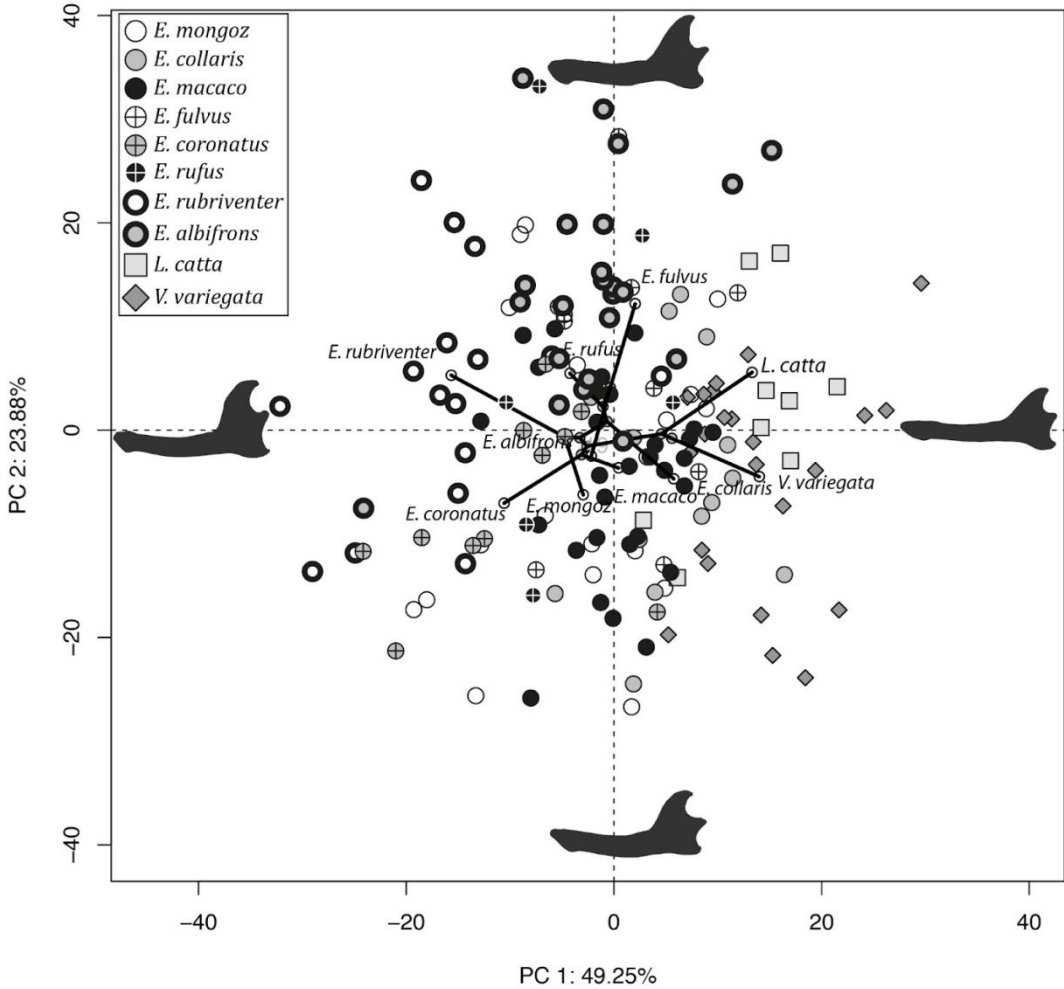


FIGURE 7

Genus	Species	Male	Female	Sex undetermined	Total
<i>Eulemur</i>	<i>E. fulvus</i>	8	4	0	12
	<i>E. collaris</i>	8	6	0	14
	<i>E. mongoz</i>	12	8	0	20
	<i>E. coronatus</i>	10	2	0	12
	<i>E. rufus</i>	5	1	0	6
	<i>E. albifrons</i>	14	9	0	23
	<i>E. macaco</i>	18	13	0	31
	<i>E. rubriventer</i>	10	7	0	17
<i>Lemur</i>	<i>L. catta</i>	6	4	0	10
<i>Varecia</i>	<i>V. variegata</i>	13	10	0	23
<i>Hapalemur</i>	<i>H. griseus</i>	7	4	1	11
<i>Prolemur</i>	<i>P. simus</i>	2	1	0	3
TOTAL					182

TABLE 1

<b>Models (entire sample)</b>	<b>R<sup>2</sup> Shape</b>	<b>AICc Shape</b>	<b>ΔAICc Shape</b>	<b>R<sup>2</sup> Size</b>	<b>AICc Size</b>	<b>ΔAICc Size</b>
Null model	0	4547.55	357.24	0	2494.82	1147.95
Phylogeny	<b>0.846</b>	4190.31	0.00	<b>0.67</b>	1346.86	0.00
Phylogeny + Diet	<b>0.846</b>	4190.31	0.00	<b>0.67</b>	1346.86	0.00
Phylogeny + Sex	<b>0.772</b>	4310.51	120.2	<b>0.609</b>	1398.67	51.81
Phylogeny + Habitat	<b>0.801</b>	4233.42	43.11	<b>0.619</b>	1394.57	47.71
Phylogeny + Diet + Sex	<b>0.817</b>	4226.16	35.81	<b>0.615</b>	1391.17	44.31
Phylogeny + Diet + Habitat	<b>0.836</b>	4209.49	19.18	<b>0.661</b>	1369.37	22.51
Phylogeny + Sex + Habitat	<b>0.826</b>	4220.69	30.38	<b>0.655</b>	1384.85	37.99
Phylogeny + Diet + Habitat + Sex	<b>0.867</b>	4206.58	16.27	<b>0.662</b>	1361.47	14.61

**TABLE 2**

<b>Models (reduced sample)</b>	<b>R<sup>2</sup> Shape</b>	<b>AICc Shape</b>	<b>ΔAICc Shape</b>	<b>R<sup>2</sup> Size</b>	<b>AICc Size</b>	<b>ΔAICc Size</b>
Null model	0	3848.96	90.48	0	2287.84	1049.37
Phylogeny	<b>0.531</b>	3819.19	60.71	0.152	1238.46	0.00
Phylogeny + Diet	<b>0.531</b>	3819.19	60.71	0.152	1238.46	0.00
Phylogeny + Sex	<b>0.557</b>	3793.14	34.66	0.176	1248.72	10.26
Phylogeny + Habitat	<b>0.693</b>	3782.96	24.48	0.091	1249.59	11.13
Phylogeny + Diet + Sex	<b>0.659</b>	3783.83	25.35	0.162	1249.47	11.01
Phylogeny + Diet + Habitat	<b>0.847</b>	3765.74	7.26	0.219	1249.39	10.93
Phylogeny + Sex + Habitat	<b>0.833</b>	3775.62	17.14	0.182	1250.33	11.87
Phylogeny + Diet + Habitat + Sex	<b>0.869</b>	3758.48	0.00	0.336	1245.78	7.31

**TABLE 3**

## EIC COMMENTS

As part of your resubmission package, please provide a description addressing how you handled the points raised by the editorial board member, reviewers, and me in your revised manuscript. Please provide this description by clicking on the Resp. to Reviewers button. Additional comments, such as your response to the Editor-in-Chief letter, can be provided by clicking the Author Comments (if any) button, or in your cover letter (file) submitted to accompany the resubmitted manuscript file.

Please also revisit the "Guide for Authors" (see either the July, 2007, AJBA or the AJBA web page). In your revisions, take a look at the guide again and make all modifications that may be necessary (including those involving figure specifications, e.g., minimum resolution - 300ppi for photos and 600ppi for line graphics, inclusion of each figure as a separate file, formatted as TIF or EPS). This is one area that can delay perfectly sound manuscripts, placing them farther behind in the publication process.

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Please also note that the American Journal of Biological Anthropology and its publisher, Wiley, have recently implemented a data sharing policy. Officially, AJBA now expects, but does not absolutely require, that all data be publicly available. Authors are required to include a Data Sharing Statement in their manuscript stating whether the data underlying the manuscript are publicly available or not, and if so, where. Explicit instructions are now part of the Instructions for Authors. Any manuscript submitted or resubmitted to AJBA will now be required to follow these procedures. They will be incorporated into the Manuscript Central submission protocols as well.

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Thanks for considering the AJBA in publishing your research. I look forward to seeing your revised manuscript. Should you have any questions, do feel free to contact me. Please complete your revisions within eight weeks, no later than 21-Oct-2022. If I receive your manuscript after that date, it will be considered a new submission.

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4 We recognise that the impact of the COVID-19 pandemic may affect your ability to  
5 return your revised manuscript to us within the requested timeframe. If this is the case,  
6 please let us know.  
7

8  
9 Sincerely,  
10 Trudy Turner  
11 Editor-in-Chief  
12 American Journal of Biological Anthropology  
13

14 Editorial Board Member's Comments to Author:  
15

16 Associate Editor: 1  
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18 Comments to the Author:  
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20 I thank the authors for their submission, which has now been assessed by two  
21 Reviewers and the Editorial Board Member (EBM). All are positive about the study and  
22 think the topic of mandibular functional morphology in lemurs (but not the conservation  
23 framework) is relevant to readers of the AJBA. However, all reviewers raise several  
24 important concerns about the overall framing of the paper, requiring more information  
25 about the sample, morphology and function, as well as justification of the methods  
26 used (vs. 3D geometric morphometrics). I agree with this assessment and think major  
27 revisions are needed to get this manuscript to the standard suitable for publication in  
28 AJBA. Both reviewers offer detailed, helpful reviews, including specific comments in a  
29 separate PDF by R2. If the authors follow these constructive suggestions, including  
30 those from the EBM, I think the manuscript will be very much improved. I offer some  
31 additional comments below. I look forward to seeing the revised version.  
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36 We really want to thank the editorial board of AJBA for considering our manuscript and  
37 for giving us an extra month to allow us to revise our manuscript. We also want to thank  
38 the two editors that commented on the manuscript as well as both reviewers. The  
39 comments are very constructive and really helped us to rework our manuscript and  
40 improve it. We think that the manuscript is now really enhanced and hope that we will  
41 have the great pleasure to see it published in AJBA as we took each of the comments  
42 into consideration. A detailed answer is given below.  
43  
44  
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46 Title (and throughout the manuscript), 'Malagasy' should be capitalised. **DONE**  
47

48 Abstract: the 'Objectives' to not actually state what morphology is to be  
49 quantified/assessed (i.e the mandible). This needs to be clarified. It is also unclear  
50 what is meant by 'interactions of the variation with biotic and abiotic factors' in this  
51 context.  
52  
53

54 We reworked the abstract taking this comment, as well as others into consideration.  
55  
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58 Introduction: Currently, the Introduction begins and ends with a review of lemur species  
59 conservation. The authors make a strong link to conservation but it is not clear how  
60 this link is supported when the study is about shape variation in one side of the

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3 mandible. Although conservation of lemurs is certainly important, AJBA is not a  
4 conservation journal and the link between conservation and mandibular morphology is  
5 tenuous.  
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- We really understand that AJBA is not a conservation journal and the aim of this manuscript is not focused on conservation. To us, the conservation aspect of the manuscript is a necessary opening. We have seen that AEs and reviewers stated that this conservation point was too developed. We removed the point about conservation in the first paragraph and the first part of the last paragraph, also focusing on conservation. We linked directly the former paragraph to the study objectives, making clearer the end of the introduction.

17 'World' should not be capitalised. **DONE**

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19 More information about the sample is needed. The species should be listed in the text,  
20 not just Table 1. Information about sex for each taxon would be helpful.

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- We added informations about the number of specimens for each species, including the number of males, females and specimens for which sex is undertermined. It appears in a new version of table 1. Moreover, we listed the species in the material part of the Material and Methods section (first paragraph of this section: "We studied 182 specimens belonging to 12 living species including *Eulemur fulvus*, *Eulemur rufus*, *Eulemur albifrons*, *Eulemur coronatus*, *Eulemur macaco*, *Eulemur mongoz*, *Eulemur rubriventer*, *Lemur catta*, *Varecia variegata*, *Hapalemur griseus* and *Prolemur simus* ")

31  
32 Please thoroughly proofread the revised version prior to submission, as there are  
33 numerous typos and grammatical errors in this original submission.  
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- We really thank EB1 for these comments. We actually realized that the sent manuscript was not our final version. We really apologize about that and are grateful to the EBM and reviewers for their kindness and patience.

44 Editorial Board Member: 2

45  
46 Comments to the Author:

47 Thank you for submitting the AJBA. This article was reviewed by two individuals, and  
48 both find the topic appropriate for the journal. Both reviewers highlight a number of  
49 major and minor revisions, and I encourage the authors to follow these excellent  
50 suggestions.  
51  
52

53 Both reviewers suggested changes for the introduction. I agree that lemur conservation  
54 is important, the current introduction does not provide enough background information  
55 on mandibular functional morphology to set up the study's aims. I encourage the  
56 authors to address R1's question on justifying the use of elliptical Fourier analyses  
57 rather than 3D geometric morphometrics approaches, and R2's questions on clarifying  
58 of the AIC results.  
59  
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3 We answered every reviewers' comments as requested. Detailed answers are given  
4 below.  
5  
6

7 In order to use linear models in the analyses, the authors need to demonstrate that  
8 the data are linear, homogeneous in variance, and normally distributed.  
9  
10

11  
12 The prerequisites for linear models must be verified, but, to be honest, it is difficult to  
13 test that the quantitative and continuous data are linear (here continuous data are  
14 harmonic coefficients) and normally distributed. For qualitative data, the covariates in  
15 our models, we should verify that the multivariate homoscedasticity (variance  
16 covariance matrix test) is respected and that the groups are independent. This is very  
17 difficult to do on such a dataset and we used a post hoc analysis of the models. Some  
18 tests exist, such as Box M test for variance/covariance matrix homogeneity. As  
19 previously said, in our case, the continuous variables are harmonic coefficients  
20 describing shape and such test is not applicable (or not really relevant). We ran the  
21 analyses and estimated the robustness of the models in a second time. We graphically  
22 verified that the mean of the residuals was close to zero, we tested the normality of the  
23 residuals, we checked the homogeneity of group variances using the residuals and  
24 looked at the leverage of points to detected potential outliers. In other words, we  
25 verified that the models really fitted the data. This cannot really be explained in the  
26 text, especially with a multivariate dataset with several covariates (and is never  
27 explained in publications). However, we understand that the idea of robustness is  
28 needed for each model. We added the R<sup>2</sup> values for each model and added an  
29 information about the statistical significance of each linear models (p values). These  
30 statistics are given in table 2.  
31  
32

33 We added a sentence at the end of the Statistical analysis part of the Material and  
34 Methods section to indicate the fact that the model assumptions were verified ("The  
35 robustness of each model is estimated by verifying the distribution and homogeneity of  
36 variances of the residuals. We also detected the presence of potential outliers. R<sup>2</sup> values of  
37 each model is given in tables 2 and 3. ")  
38  
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41  
42 Given the high number of *Eulemur* samples, this sample may not be normally  
43 distributed, and non-parametric models may be needed.  
44

45 We are not sure to understand EBM 2's comment. What does a sample normally  
46 distributed mean? We understand that variables can or cannot be normally distributed,  
47 but not samples. Moreover, we don't really understand the link between the high  
48 number of *Eulemur* specimens and the distribution. EBM2 is right on one point, an  
49 unbalanced number of specimens between groups (here genus) could slightly bias the  
50 models in multivariate analyses. However, as explained above, we were highly  
51 concerned by the robustness and confidence of our models and are sure that the  
52 sample heterogeneity does not affect our models.  
53  
54

55 I also encourage the authors to revise the discussion to address whether the shape  
56 differences in *Hapalemur* and *Prolemur* reflect phylogenetic differences or those  
57 associated diet and habitat given the study sample.  
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3 We understand EBM 2's comment. However, our results do not allow us to conclude  
4 on this point. *Hapalemur* and *Prolemur* are members of a same phylogenetic cluster  
5 and are the only folivorous of our sample. In this state, it is not possible to discern the  
6 origin of the differences (phylogenetic or diet). EBM2 is absolutely right on the fact that  
7 this point must be discussed, and we added a sentence about it in the first paragraph  
8 of the discussion ("As specimens of the genera *Hapalemur* and *Prolemur* are the only  
9 folivorous of our sample, it is not possible, in our case to explain the differences in mandibular  
10 shape from the other genera by a phylogenetic effect or by a difference in diet").  
11  
12

13 Reviewers' comments to author:  
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19 Reviewer: 1  
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22 Comments to the Author

23 Thank you for the opportunity to review this manuscript. In this study the authors sought  
24 to establish several ecological correlates with the shape of the Lemurid mandible using  
25 elliptical Fourier analysis. The study elaborates on a 2005 Raveloson study that  
26 established a basis of the extent of variation within and among Lemurid genera. This  
27 study takes that method and approach and attempts to relate mandible variation with  
28 specific ecological correlates. I believe with revision that this manuscript could be very  
29 strong  
30

31 Major comments

32 • While I find the results of the EF analysis interesting, the authors need to do a more  
33 thorough job of arguing why it was chosen over landmark-based 3-dimensional GM.  
34 3D GM would allow for the authors to address issues of width of the articulated jaw  
35 and include landmarks that could be meaningful such as the attachment sites of  
36 musculature and/or ligaments.  
37  
38

39 We agree with reviewer 1 that the analysis could be done with other shape  
40 characterization methods such as 3D GM. Here, we made the choice to use EF  
41 method. To us, EF is not better or worse than other morphometric methods, it is just  
42 well adapted to characterize the shape of biological objects such as hemimandibles  
43 (essentially described by two dimensions). Moreover, our analysis is complementary  
44 to the one performed by Raveloson in 2005 and we used a similar protocol (which is a  
45 well-adapted protocol for mandibles).  
46  
47

48 EF may be considered as less trendy than 3D GM but is certainly as powerful. For  
49 instance, the analysis of flower petal shape, tree eaves or fishes otoliths are performed  
50 with standardized protocols relying on EF. For these objects it is very rare the find  
51 publications using 3D GM to characterize the shape variation. In our case, it is true  
52 that some authors (especially in recent articles) use 3D GM rather than EF. However,  
53 we don't think that the choice of one or another method could influence the signal that  
54 we analyzed.  
55

56 We agree that the use of landmarks (in 2D or 3D) would be helpful in order to  
57 characterize and quantify some part of the mandible (such as muscle insertions).  
58 However, our idea was not to focus on peculiar parts of the mandible but rather to  
59 consider the entire structure.  
60

We added a sentence at the end of the first paragraph of the “outlining” part in Material and Methods in order to justify the use of EF rather than 3D GM (“Our study is complementary to the one published by Raveloson et al. in 2005. We used a similar protocol, based on EFA (rather than 3D landmarks) in order to facilitate the comparison of results”).

- The manuscript would benefit from some reorganization. Much of the introduction is dedicated to climate change and reduction of biodiversity in Madagascar. While this is an important issue, the results of this project do not directly address this. It would be much better for the authors to use this section to establish what the outline of the mandible says about total body variation, what correlates have been established, and which correlates still need to be tested. They do this in the discussion, but some of that information needs to set up this study in the introduction.

This comment has been formulated by other reviewers and EB members. We reorganized the introducing, removing parts about conservation and adding parts about mandibular morphology and its understanding.

- Please add a hypothesis section and/or table or graphic explaining the correlates tested and criteria for each classification.

We expressed a hypothesis in the introduction. We added supplementary files containing the covariables. We detailed the different models.

- Please add a discussion of TMJ morphology, mandibular gape, and tree gouging behaviors.

We added a part about morpho-functional analysis of the mandible, TMJ, condyle morphology and chewing movements in the introduction. We did not find anything about gouging in the lemurs.

- Please add a summary table of correlates tested with significance values.

We reworked tables 2 and 3 giving more details (R<sup>2</sup>, significant values) and reworked the text.

- Please have someone proofread.

Line-by-Line comments

- Page 3 line 8 “hotspot” WC **DONE**

- Page 3 line 11-12 “The degree of endemism is high in several groups of vertebrates such as fishes, birds, amphibians” Either move or remove this, it’s not relevant to your study **We removed it**

- Page 3 line 15 “Mammals” does not need to be capitalized unless you use the proper Mammalia **DONE**

- Page 3 line 15 “noticeable” WC **DONE**

- Page 3 line 53 “numbers” WC **DONE**

- Page 3 lines 53-60, reorganize into 2 or 3 sentences **DONE**

- Page 4 lines 51-60 this paragraph would be better at the beginning

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3  
4 Based on comments from reviewer 1 and other reviewers/EBM, we reorganized the  
5 introduction. This part is now at the beginning of the introduction.  
6

- 7  
8 • Page 4 lines 17-48 Expand this section to include some of the topics discussed  
9 above

10  
11 We added a part in this paragraph to include a part about functional morphology of the  
12 mandible. Our study is not focusing on functional morphology but we agree that such  
13 part was missing in our introduction. We added a part on mandibular forces during  
14 chewing and biting, on the presence or absence of the symphyseal fusion and about  
15 the morphology of the temporomandibular joint. This part was also related to diet,  
16 especially the consumption of leaves and hard items. We nevertheless want to  
17 highlight the fact that many of the cited studies are focusing on haplorrhines rather  
18 than strepsirrhines and that lemurids are very few represented.  
19

- 20  
21 • Page 5 lines 25-32 This seems beyond the scope of this paper. We don't need the  
22 abbreviations, if you want to keep this then move it to the discussion or broader impacts  
23 sections **Sentence removed**  
24

- 25  
26 • Page 6 lines 11-20 Are these the same images that were used for the 2005  
27 Raveloson et al. paper or were new ones taken?  
28

29 We worked on new images that we sampled for this work after visiting museums. We  
30 used a protocol similar to the one employed by Raveloson et al. Some specimens (very  
31 few) are present if both studies.  
32

- 33  
34 • Page 6 lines 33-34 "removed the parts related to the teeth" In photoshop?  
35

36 Yes we did remove the teeth on our images with the help of photoshop, as precised in  
37 the following sentence.  
38

- 39  
40 • Page 6 line 40 Oversampling seems like the wrong word  
41

42 We changed the end of the sentence. The sentence is now "Then with this same  
43 software, we converted the images in grayscale and the images were all reduced to the same  
44 size to avoid potential differences in image resolution "  
45

- 46  
47 • Page 7 lines 1-38

48 o What is the argument for EFA over landmark based 3D GM? It seems that you're  
49 losing data such as muscle markings and 3 dimensional depth/width and I'm not clear  
50 on what you're gaining in a structure as landmark-rich as the mandible.  
51

52 We answered to this comment previously. We don't consider that we are losing  
53 information for our study that is not focusing on muscle marking only, but rather on the  
54 overall shape of the mandible. We don't fully agree that the mandible is a "landmark  
55 rich structure". If some landmarks are easy to locate, many others are located on bone  
56 edges, along curvatures and are very challenging to locate accurately. Actually, this is  
57 a major topic in the GM community (see discussion on Morphomet: [https://www.mail-  
58 archive.com/morphmet@morphometrics.org/](https://www.mail-archive.com/morphmet@morphometrics.org/) on this point). Semilandmarks and  
59  
60

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3 random distribution of pseudolandmarks could be very helpful to cover the shape,  
4 however, to us, an accurate characterization of mandibular shape using 3D landmarks  
5 could remain problematic. We are not criticizing any authors nor any studies but just  
6 describing facts. In our case, as our work is in the framework of the one published by  
7 Raveloson et al. in 2005, we chose to work with the same protocol as long as this  
8 protocol is powerful enough to rigorously characterize mandible shape and size.  
9

- 10 • How do you remove the teeth? Does this introduce more error?

11  
12  
13 We removed teeth because (1) this is not the aim of our study and (2) some teeth are  
14 missing. We thresholded our images on Adobe Photoshop in order to select and  
15 remove the teeth (teeth have a different colour than bone). Our error estimation took  
16 the entire data acquisition/preparation/ analysis into account. This step (teeth removal)  
17 probably introduces some error, as well as the other steps, but this error remains not  
18 significant (as given in the measurement error part of the results section).  
19

- 20 • How did you choose which side of the mandible to do? Were there any criteria  
21 for which you may remove a specimen? Pathology? Age?

22 We have selected adult specimens.

23 We have kept the same position for the mandible ( hemi-mandible left) to have the  
24 same harmonic direction of the contours

25 We chose, by convention, to work on the left hemimandible (following Raveloson et al.  
26 protocol). We removed specimens with broken parts, we selected adult specimens only  
27 (fully erupted and with fused cranial sutures).  
28

- 29 • Page 7 line 51 “This hypothesis is one of the most complete analyses for  
30 strepsirrhines” wording is awkward

31 We changed the “phylogenetic hypothesis” into “phylogeny”.

- 32 • Page 7 lines 47-56 did the authors consider using 10k consensus tree?

33 No, in our case we did not use a 10K consensus tree but the majority rule consensus  
34 tree published by Herrera & Davalos in 2016. from this tree we selected the branches  
35 corresponding to the Lemuridae family. We added this precision in the text.  
36

- 37 • Page 8 lines 18-31 You need a table for your ecological correlates. I would also like  
38 to see a graphic for your ecoregions.

39 We added R2 values for the models and gave an indication of the significance. We  
40 made a figure (figure 5) for the ecoregions.  
41

- 42 • Page 9 line 45 Where do zoo specimens fall in your ecoregion breakdown?

43 We have 16 zoo specimens in our dataset (16/182). We checked that zoo specimens  
44 were not outliers. The we attributed the ecoregion class of wild specimens to the zoo  
45 specimens of the same species.  
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4 • Page 10 lines 32-42 Why did you not do phylogeny + sex? Or phylogeny + diet +  
5 sex?  
6

7 We agree with the reviewer and added the missing models, we are now testing 9  
8 models:  
9

- 10  
11 • Null model  
12  
13 • Phylogeny  
14  
15 • Phylogeny + Diet  
16  
17 • Phylogeny + Sex (covariables sex, sexual behaviours and mating system)  
18  
19 • Phylogeny + Habitat (covariables ecoregion and habitat)  
20  
21 • Phylogeny + Diet + sex  
22  
23 • Phylogeny + Diet + Habitat  
24  
25 • Phylogeny + sex+ habitat  
26  
27  
28  
29 Phylogeny + Diet + Habitat + Sex  
30  
31

- 32  
33 • Page 11 lines 1-7 what measurement error are you measuring here? How many  
34 individuals were included in the study?  
35

36 We chose 10 specimens of the same species randomly. for these 10 specimens, we  
37 applied the complete protocol twice (positioning, picture, image preparation,  
38 outlining). Then, we tested the differences between replicate considering the difference  
39 between specimens (See Bailey and Byrnes 1990).  
40  
41

- 42 • Page 11 lines 12-60 Can you do a partial correlation to control for centroid size?  
43

44 We are not sure to understand this question. In shape analysis, size is removed. size  
45 variation in analysed in a second time. A partial correlation would be helpful to work on  
46 the allometric pattern (which was not analysed here but is one of the perspectives of  
47 the paper).  
48  
49

- 50 • Page 12 lines 9-16 “The high difference between *Hapalemur*, *Prolemur* and the  
51 other genera of the family is so important that it is not easy to understand the  
52 morphological structure of mandibular shape variation in the genera *Eulemur*, *Lemur*  
53 and *Varecia*” Revise for wording, “high” difference between *Hapalemur/Prolemur* and  
54 the other genera? Or are there large differences between *Hapalemur* and *Prolemur*  
55 too? Also “important” are relative terms. **DONE. High difference between**  
56 ***Hapalemur/Prolemur* and the other genera.**  
57

- 58 • Page 12 line 19 “In order to investigate this phylogenetic variation”**DONE**  
59 • Page 12 lines 26-27 “developed ascending rami, with high and vertical coronoid  
60 processes, marked mandibular (sigmoid) notches”**DONE**

- Page 13 lines 11 weird formatting **DONE**
- Page 13 line 23 “accumulate” WC **DONE**
- Page 14 line 10-14 “Coefficients of determination for the covariates of this model are  $R=0.036$  for Diet,  $R=0.09$  for Ecoregion,  $R=0.067$  for Mating system and  $R=0.05$  for Genus.”? Make the formatting for correlation reporting consistent.

These values were wrong. we changed the text of this part. Moreover, we added the coefficient of determination for each model in tables 2 and 3.

- Page 14 lines 1-33 The capitalization of the correlates look a bit odd.

We have chosen to write in capital letters to make them visible in the manuscript but we can change if necessary.

- Page 14 line 47 “differences are likely explained by a” **DONE**
- Page 16 lines 1-33 Some of this information would be good to introduce in the introduction . **We reorganized the introduction and used some of this part in the new version**
- Page 16 line 42 “in the work published in 2005, Raveloson et al. highlighted this difference, and dissociated their analysis” Dissociated WC? **We changed the sentence in “,and separated their analysis in two sub analyses”**

- Page 16 line 51 “prolongation” WC **DONE**
- Page 16 line 51 “Raveloson et al. 2005’s work.” Awkward wording, maybe “elaboration of Raveloson’s earlier work” **DONE**
- Page 16 “Here, we also report an important level of variation with the genera.” Redundant **DONE**
- Page 17 lines 7-15: “The direct correlation between mandibular shape variation and dietary shifts is probably enough to understand such variation. The direct link between mandibular shape variation and diet specialization is questionable.” These two sentences seem to contradict each other. **Reviewer 1 is right. we changed the sentences in “The direct correlation between mandibular shape variation and dietary shifts could explain such variation. However, the direct link between mandibular shape variation and diet specialization is questionable. “ We also linked both paragraph as they develop similar ideas.**

- Page 17 line 15: “Peculiar” WC **DONE**
- Page 17 line 19: “the expected level of variation should be low” Within folivores? **Yes for the other author’s earlier work within folivores (Futuyma & Moreno, 1988) but it is not the case for our folivores sample.**
- Page 17 lines 35-45: Clarify, are you saying that variation in the shape of the mandible due to musculature is independent of diet? **we changed the sentences in “. Our results indicate a true covariation of mandibular morphology with diet, but also with other covariables non-dietary covariables.”**
- Page 18 lines 16-18: “(I have a paper in my office to cite about this point).” I think you meant to change this, please proofread. **Sorry about that. one of our comments was left in the manuscript.**

- Page 18 line 21: Reduced sample – reduced from what?

At the beginning, we analyzed all of the samples (all of the genera study) and then, we removed the genera of *Hapalemur* and *Prolemur* to see the variations between the three genera *Eulemur*, *Lemur* and *Varecia*. So, we talk about the reduced samples by removing the genera *Hapalemur* and *Prolemur* analysis. Reviewer 1 is right, we gave some precisions about it in the text.

- Page 18 line 36: “Sexual behaviour does not covary with mandibular shape.” **DONE**
- Page 19 line 16 “ not a sexually dimorphic trait” **DONE**
- Page 19 line 23-24 “Our results indicate that mandibular shape does not vary with types of forests inhabited.” **DONE, actually we reworked this sentence.**
- Page 19 line 34 “The second is that this covariation” What does “this” refer to?

It refers to the possible covariation between the type of forest and mandibular shape. We reworked this sentence “The second is that the possible covariation between the type of forest and mandibular shape exists but the method to classify ...”

- Page 19 lines 46-50: “Covariations of primate morphology with geographical distribution (taking ecoregions as great categories of distribution) are none for many years (Albrecht, 1990; Albrecht & Miller, 1993).” **Done, we changed “none” by “known”.**
- Page 20 lines 2-5: “The ecogeographical difference is not only visible on size, but also on shape variation (Viguiet, 2002).” Size of what? Body size? Head size? Please expand.

We agree with reviewer 1, this is not clear. We changed our sentences in “The ecogeographical difference is not only visible on size (cranial size in the case of Viguiet, 2002), but also on cranial shape variation (in this case). Our results on the mandible support these findings. “

- Page 20 lines 7-10: “Madagascar’s natural forest suffered a large loss of the forest cover while lemurs are distributed almost in all three of these four ecoregions (Vieilledent et al., 2017; Ganzhorn et al., 2000).” Revise for clarity **DONE.**

We changed the sentence in “The natural forest of Madagascar has suffered a great loss of forest cover inhabited by lemurs “

- Figure 1: Please expand and describe where in the process images 3 and 4 were taken

We added details on the figure caption in order to clarify these points.

- Figure 2: The caption is confusing, the outlines are points?

We gave precisions in the new version of the caption: “**FIGURE 2** Representative of *Prolemur simus* outlines (outlines are centered, starting points for the outline opening are indicated by arrows.)”

- 1  
2  
3 • Figure 5: How were the positive and negative consensus shapes produced?  
4 We added details in the caption indicating the species for which the outlines are used  
5 for PC's variation illustrations. We did the same on figure 6.  
6  
7  
8 • Table 1: how many males and females of each? We added this information in the  
9 revised version of the table.  
10  
11  
12

13 Reviewer: 2  
14

15 Comments to the Author

16 This paper is an interesting application of elliptical Fourier analysis to variation in  
17 mandibles in the Lemuridae. The species in this clade are widespread across the  
18 island of Madagascar, occurring in a range of habitats and varying in diet and aspects  
19 of their behavioral ecology. The authors have demonstrated a clear distinction along  
20 dietary lines in mandibular outline, with the bamboo lemurs convincingly separated  
21 from other taxa, even the closely related Lemur catta. The authors additionally present  
22 analyses excluding the bamboo lemurs in order to investigate morphological variation  
23 among the remaining species without the strong dietary effects from this unusual diet,  
24 and found some indication of other factors that influence mandibular shape.  
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28 In terms of scientific content, I would have liked more detail and discussion on previous  
29 research on mandibular morphology included in the introduction and discussion – the  
30 authors indicate that some studies have been done, but do not discuss their results in  
31 detail. Some attempt in the discussion is made to put the mandibular shape results in  
32 a wider context but this could be expanded further with more specific details on  
33 morphological trends.  
34

35 We thank review 2 for this advice, we reworked our discussion taking R2 comments  
36 into account, as well as the other reviewer and EBMs ones.  
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39 The other major comment I had was that the measurement of size and use of size in  
40 some of the analyses would benefit from more explanation. While the pictures were  
41 apparently taken with a scale, it is not stated explicitly that the images were rescaled  
42 to that standard, so centroid size seems likely to reflect just proportion of area of the  
43 photograph that is occupied by the mandible, which will reflect shape and decisions  
44 made about cropping etc. I may be misunderstanding some part of the methods, but I  
45 think it should be clearer what the “size” actually means. Lemurids have a modest level  
46 of size variation compared to some of primate clades, but if someone wanted to  
47 replicate these analyses with another group this might be a more salient issue.  
48

49 Size standardization is done at several steps of the protocol. First, we used a lens with  
50 a fix focal to avoid zoom effects. Second, a scale was used for each picture. Third, we  
51 set the images to the same dimension (number of pixel in length and width). Fourth,  
52 we used TPSDig2 to extract the outline and each picture was associated with it scale.  
53 Then, the function *efourier* of the package *Momocs* calculates the centroid size as the  
54 magnitude of the semi-major axis of the first fitting ellipse (see Bonhomme et al. 2014).  
55 Bonhomme, V., Picq, S., Gaucherel, C., & Claude, J. (2014). *Momocs: outline analysis*  
56 *using R. Journal of Statistical Software, 56(13).*  
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3 Thus, centroid size is centroid size as it seems to us that we have controlled all the  
4 potential bias.  
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9 The statement in the abstract that all of the covariables influence mandibular shape  
10 variation is a little unclear – while there were significant effects of covariables in various  
11 categories, but some of the seven covariables listed in the abstract were non-  
12 significant if I am understanding the analysis correctly. The AICc analysis could be  
13 better explained and clarified with more details on the methodology provided, and more  
14 consistent terminology when referring to covariables would be helpful..  
15

16  
17 We tried to do so in the new version.  
18

19 The writing could use additional proofreading and there are places where clearer  
20 phrasing or alternate vocabulary would communicate the concepts more clearly. Some  
21 of these have been addressed in my detailed comments but more proofreading and  
22 review would be beneficial. There are also places where some of the text could be  
23 reduced in length or the relevance of that section could be made clearer. For example,  
24 the relevance of the vulnerability to extinction of various fauna in the introduction is not  
25 very clearly linked to the analysis of mandibular morphology.  
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28 Other reviewer and EBMs highlighted these points, we corrected our text and reworked  
29 the abstract, the introduction and the discussion.  
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### 35 Detailed comments

#### 36 Abstract

37 Page 1: Lines 13 and 14 describe the seven covariables as sex, age, body mass, diet,  
38 ecoregion, sexual behavior and habitat. In lines 21 and 22 it is stated that in the second  
39 analysis (removing

40 Hapalemur and Prolemur) all of the covariables influence the morphology. In the  
41 results section on page 13, the text states that forest types, sex, and dominance pattern  
42 do not influence

43 morphology in the sample which seems contradictory to this statement in the abstract.  
44 Also, are ecoregions part of habitat or separate? Why is “forest region” not listed? I  
45 think it would be

46 helpful to clarify the description of the covariables and to increase detail on the analysis  
47 in which they are used throughout the manuscript.  
48

49 We reworked the abstract and hope this new version is clearer.

50 For the second analysis, removing Hapalemur and Prolemur, all covariates are  
51 significant except sex.

52 What is called “habitat” is composed of the covariables “Ecoregion and “Forest type”.  
53 “forest region” does not exist in our text. It appears that our definition of variables is not  
54 easy to understand and work to make it clearer.  
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#### 59 Introduction 60

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3 Page 3: This part of the introduction gives a lot of specific detail on the numbers of  
4 lemur species threatened by various human activities that seems extraneous to the  
5 focus of the manuscript on factors affecting mandibular shape – I think this could be  
6 reduced a great deal or alternatively the relevance of this information to the research  
7 questions of the paper could be explained more clearly to justify the inclusion of this  
8 information. In contrast, while the authors  
9 do list a number of papers that have shown morphological and ecological covariation  
10 in Malagasy primates, including some on page 2 that focus on the mandible, there is  
11 not much  
12 discussion of the morphological findings which might be relevant to readers.  
13  
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15  
16 We removed the part about lemur species threats. We added some details about  
17 morphological findings about mandible, and especially morpho functional indications.  
18 We reworked the introduction.  
19

20  
21 Page 3: Line 44. “Factors acting on primate threat are dynamic...” “Factors threatening  
22 primates” would be a clearer phrasing. **DONE**

23 Page 3: Line 46. “... for this it is necessary” “this” here is ambiguous. For what? Also, I  
24 think this section generally should be expanded to clarify the link between extinction  
25 and studying mandibular morphology. **DONE**

26 Page 5: Line 38. Please expand with more on the way in which studies linking  
27 morphology and ecology will be useful for biodiversity conservation.  
28

29  
30 We reworked this part giving more details on this point.  
31

32 Page 6: Line 14. When you describe the hemi mandibles as being in the sagittal plane,  
33 this seems contrary to the figure of the camera set up (which is a very helpful inclusion  
34 for clarifying the methodology). In anatomical position, the symphysis will be in the  
35 midline and the condyles/ ramus will be more lateral, so a median sagittal plane would  
36 intersect the symphysis and parasagittal planes would intersect the condyles and  
37 intervening portions of the  
38 mandibular ramus, but no sagittal or parasagittal plane can intersect both the condyle  
39 and the symphysis. If the hemimandible is laid flat for photography, then the camera  
40 has to be oriented obliquely relative to the anatomical position of the mandible,  
41 because the mandibular corpus is oriented in an oblique orientation in life. I would  
42 describe your plane parallel to the long axis of the hemimandible, but not as sagittal.  
43  
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45  
46 Reviewer 2 is absolutely right, actually the hemimandibles were positioned in the plane  
47 parallel to there long axes, and not to the sagittal plane. We corrected our  
48 methodological part.  
49

50 Page 7: Line 5. Probably you want to “retain” harmonics rather than “retrain” them. **We**  
51 **corrected it.**  
52

53 Page 7: Line 26. I am confused by how meaningful centroid size will be given the earlier  
54 statement that the images were all reduced to the same size. (Page 6 line 40). See  
55 general comments.  
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59 We agree that it is not clear. After outline characterization by TPSDig2, the outline files  
60 were opened in R, size was extracted and outlines were scaled to analyze shape

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3 variation. All these steps were done automatically by efourier function of the momocs  
4 package.  
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8 Page 7: Line 52. I think the phylogenies could be combined into one same figure- there  
9 is a lot of repeated information in the two figures if kept separate. I would also suggest  
10 adding something to the figure legend about how the node numbers on the phylogeny  
11 match the later figures.  
12

13 We reorganized the figures to have both phylogeny on the same figure. We changed  
14 the text about it. We tried to have the node numbers on figure 6 but it is too difficult to  
15 make them readable.  
16  
17

18 Page 8: Line 6. here you refer to six covariables and in the abstract you said seven. It  
19 would be good to have this clarified. We have seven covariables (phylogeny, diet, sex,  
20 sexual behavior, mating system, ecoregion and forest type). We homogenized it the  
21 number of covariable is now the same in the text and in the abstract.  
22  
23

24 Page 9: Discussion of ecoregions and forest types -it would be helpful to know how  
25 this information was integrated into the analyses. Is each specimen assigned to a  
26 forest type and  
27 ecoregion based on location data (in which case how did you handle captive  
28 specimens?) or are these assigned at the species level (in which case how did you  
29 handle instances where the same  
30 species is present in more than one forest type or ecoregion?)  
31  
32

33 We have localities for a great majority of specimens, and used this information. When  
34 locality was not available, we used the species informations (Animaldiversity.org,  
35 Mittermeier et al. 2006, 2010, 2013). We did the same for zoo specimens and checked  
36 that they were not outliers (but we have few zoo specimens as said previously). None  
37 of the specimens of the same species were attributed to different forest type nor  
38 ecoregions. We agree with reviewer 2 that it could be a problem (that we did not have  
39 to face for this study) and that our categorizations could present some problems. We  
40 tried to categorize each specimen with rigor, avoiding biases.  
41  
42

43 Page 9: Line 35-39. The sentence that ends "where is just the rest place for lemurs" is  
44 pretty unclear- I can't suggest alternate wording because I don't exactly know what is  
45 intended.  
46  
47

48 We agree that this part of the sentence was not clear. We proofread the paragraph  
49 and removed this part.  
50  
51

52 Page 9: line 60. If the size was centroid size, was there any way to scale to actual  
53 size? If I am understanding the methods correctly, centroid size will largely reflect  
54 shape because the shorter deeper mandibles will have more area than the longer  
55 thinner mandibles. I don't see the value of analyzing centroid size to any extent unless  
56 the units are standardized for all the images  
57  
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59 We are not sure to understand R2 comment. Centroid size represents dimensions of  
60 the objects, not only length or width. The distinction between size and shape is the

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3 basis of Geometric Morphometrics in order to avoid to analyse a mixed signal. Centroid  
4 size is not shape, it is everything but shape. However, shape can be dependent upon  
5 size (allometries). Centroid size is the best option to study overall size because it really  
6 reflects the dimensions of the objects regardless the linear measurement used.  
7

8  
9 Page 10: Please describe the methods related to the linear models in more detail,  
10 particularly related to the coding of variables and the interpretation of the models. For  
11 example, how were the categorical variables treated? When you combined different  
12 pieces of information into the model for example combining ecoregion and forest type  
13 as habitat what did that look like in the data set?  
14

15  
16 When we combined covariables in the linear models, we tested the effect of each  
17 covariable and the interactions between these covariables on the dependent variable  
18 (shape, or size). In the example given by reviewer 2 we tested the effect of ecoregion  
19 on shape, on habitat on shape and the effect of the interaction of ecoregion and habitat  
20 on shape. The model considers all these effect (not the effects independently). This is  
21 the reason why we built all the possible models and compared them, using AIC values  
22

23  
24 Page 11: In the discussion of PCA results lines 18- 21 it would be good to state clearly  
25 in the text that which species are on the positive vs negative end of PC1 because it  
26 would be a way of  
27 connecting the morphological shape description to the sample. This information is  
28 available in the plots but would be nice to see in the text also. It would also be nice to  
29 see examples of the  
30 mandibles of different genera in a figure.  
31

32  
33 We added a new figure to illustrate the morphologies, we gave the name of the species  
34 used to illustrate the variation along PCs in the figure caption and in the text.  
35

36  
37 Page 11: Lines 36. I think it would be clearer to refer to the ascending ramus/ rami  
38 rather than the ascending branch here and at other points in the text, as this is the  
39 more typical terminology. Done

40  
41 Page 12: did you run the MANOVA on the reduced sample? It would be interesting to  
42 know if there are still significant differences between genera without Hapalemur and  
43 Prolemur. Also, are the results of this MANOVA included in any tables?  
44

45  
46 We performed the MANOVA analysis on the reduced sample. The difference between  
47 genera is not significant (see table 3), that is to say that the phylogeny only cannot  
48 explain shape variation. Same thing for the phylogeny plus diet. However, it becomes  
49 significant when adding the other covariables and the model that fitted the best the  
50 dataset (and which is significant) if the model with all the covariables. this result  
51 indicates that the analysis of phylogeny or diet is not sufficient to understand the  
52 morphological variation of the mandible.  
53

54  
55 Page 13 : I think the AICc results here need more explanation. For a start, I don't think  
56 the acronym is spelled out anywhere in the paper. It would be nice to have a summary  
57 of what the number indicates.  
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59  
60 AIC is the acronym for Akaike Iteration Criterion and the lower capital c indicates that  
it is corrected for small samples. It is the most often used for model selection. By

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3 calculating and comparing the AIC scores of several possible models, you can choose  
4 the one that is the best fit for the data. The computation of AICc is based on the Log-  
5 likelihood values that describe how likely the model is, given the data. We added a  
6 sentence in the method section about this point.  
7

8  
9 Page 14: I still have the same questions about size in this analysis - it is difficult to  
10 know what the size variation indicates without clarification.  
11

12 We show that size variation is explained by phylogeny or diet (as it is not possible to  
13 separate phylogenetic effect from diet effect) in the entire sample and it is explained  
14 by none of the covariables in the reduced sample.  
15

16  
17 Page 15: Lines 21-23. I would suggest that you phrase this as the leaf chewing  
18 \_species\_ vs frugivorous species rather than “the leaf chewing” and “the frugivorous”  
19 DONE  
20

21  
22 Page 15: Lines 34-35. The temporalis muscles are listed separately from the “pars  
23 temporalis” – I am not sure what the latter refers to if not part of the temporalis.  
24 We corrected it.  
25

26  
27 Page 15: Lines 45-50. There isn't usually much resistance to depressing the mandible/  
28 opening the mouth so I am not sure why larger muscles attaching at the symphysis  
29 would relate to chewing strength. Usually symphyseal dimensions are interpreted more  
30 as related to bending/ wishboning forces of the mandible due to the actions of the  
31 working and balancing side jaw adductors rather than to the size of the digastrics.  
32 We found this information in (Pick & Howden, 1977).  
33

34  
35 Page 16: Line 24. I'm not sure what is meant by the “light aspect of the mandible” –  
36 does this refer to it being relatively gracile in the non-folivorous lemurids? Also I would  
37 suggest using “chewing movements” or “masticatory movements” rather than “chew  
38 movements”.  
39

40 We changed “light” into “gracile”. we changed “chew- movements” in “chewing  
41 movements”.  
42

43 Page 17: Line 23 – the folivorous species rather than “the follivorous” DONE

44 Page 18: Lines 16-18. I think it was intended that an additional citation would be  
45 inserted here. We added the reference

46  
47 Page 18: paragraphs of the discussion starting at line 21 and continuing to the next  
48 page– is there a way to use the AICc analysis to examine what aspects of the  
49 morphology are related to the covariables? I ask because there isn't really a clear  
50 mechanism by which ecoregion or mating system would affect mandibular anatomy,  
51 and understanding which morphological features are showing as associated with  
52 particular covariables might help elucidate this point.  
53

54  
55 We really understand reviewer 2's comment. We cannot answer these questions for  
56 the moment with this analysis but this is our next project.  
57

58  
59 Page 20 line 7 – “while” is an awkward phrasing here. This sentence could use some  
60 clarification to make the intended meaning clearer. DONE

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4 Page 20 line 16 – I think you mean to say that almost half of its forest cover has been  
5 lost since 1953 – it seems like there is something missing as the sentence is currently  
6 written. **DONE**  
7

#### 8 9 Figures and tables

10  
11 As mentioned above, it would be nice to have an additional figure showing an example  
12 of each of the genera included in the analysis to give additional context to some of the  
13 PCA plots I also feel like there are more analyses described in the results than are  
14 presented in the tables.

15  
16 Additional information would be helpful for understanding why some covariables were  
17 considered significant and others were not.  
18

19 **We added supplementary information as asked. Our covariable table is in**  
20 **supplementaries, we added two figures and we reworked our tables as asked.**  
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