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Craniometric Corroboration of the Specific Status of *Lepilemur septentrionalis*, an Endemic Lemur from the North of Madagascar

The disputed taxonomy of the genus *Lepilemur* I. Geoffroy, 1851 has been clarified considerably by cytogenetic techniques, especially analysis of karyotypes. An allopatric species of *Lepilemur*, *L. septentrionalis*, has been created recently on the basis of cytogenetic distinctions (Rumpler & Albignac, 1975). *L. septentrionalis* is shown here to be significantly smaller than the morphologically similar *L. dorsalis* in thirty-four of thirty-seven linear cranial dimensions, but significantly larger in interorbital breadth (lacrimale-lacrimale). Craniometric results therefore reinforce the cytogenetic conclusion that *L. septentrionalis* is a valid species distinct from *L. dorsalis*.

1. Introduction

Taxonomy of the genus *Lepilemur*, the "gentle lemurs", has been very controversial as indicated by successive reclassifications (Petit, 1933; Webb, 1946; Hill, 1953; Petter & Petter-Rousseaux, 1960). The use of cytogenetic data has recently permitted considerable clarification of this dispute (Rumpler, 1974, 1975 and has provided the basis for creation of a new species, *Lepilemur septentrionalis*, with four subspecies (Rumpler & Albignac, 1975). Six additional species are now recognized: *L. leucopus*, *L. ruficaudatus*, *L. rufescens*, *L. dorsalis*, *L. mustelinus* and *L. microdon* (Rumpler, 1975).

The northern part of Madagascar beyond Ambilobe is the known geographical range of *L. septentrionalis*. The southeastern corner of this range is near to, but not overlapping with, the known range for *L. mustelinus*, while the southwestern sector of the range is near the border known for *L. dorsalis* in the Ambanja region and Nosy-Be. These three species are therefore allopatric groups of *Lepilemur*, with *L. mustelinus* easily distinguishable from the other two groups in size and an assortment of morphological characteristics (Petter & Petter-Rousseaux, 1960). However, *L. septentrionalis* is quite similar in proportions, color, and general morphology to *L. dorsalis*, from which it has never before been distinguished (Plate 1).

No consensus exists on procedures and methodology for distinguishing morphologically similar allopatric species. The extreme point of view is taken by Mayr (1964, p. 164) that "no criteria permit satisfactory distinction between species and isolated subspecies." Inherent in this point of view is the concept of species as an actually or potentially interbreeding population or system of populations sharing a common gene pool (Mayr, 1964; Löve, 1964; Rogers & Appan, 1969). Clearly, any additional information concerning possible genetic incompatibility would be relevant to this issue. Rumpler 1975 has stated that the breeding of *Lepilemur* in captivity is exceedingly difficult, and to date it has been impossible to induce breeding between males and females known to be from the same species. The purportedly ideal test of fertility is therefore lacking. Alternative methods for delimiting allopatric species in such cases must be employed in order to arrive at a consistent system of classification; i.e. a formal description and cataloging of organized nature (Sokal & Camin, 1965).

One alternative method which has been employed is the use of cytogenetics to reinforce initial phenetic inferences that two groups are different species (Rogers & Appen, 1969). Discontinuities in phenotypic variation are checked against geographical-ecological discontinuities; cytogenetic data are then analyzed for corroborative evidence of suspected reproductive isolating mechanisms. It is suggested here that when cytogenetic data provide the initial grounds for discriminating between two groups, as in the case of *Lepilemur* (Rumpler & Albignac, 1975), a phenetic test of morphological discontinuities can similarly be useful in the further confirmation of suspected barriers to gene flow. The assumption in both methods is that demonstrated cytogenetic and phenetic distinctions together provide stronger grounds for defining new allopatric species than either type of distinction does alone. The cytogenetic evidence for suspecting reproductive isolation of the species of *Lepilemur* has been presented elsewhere (Rumpler *et al.*, 1972; Buettner-Janusch, 1973; Rumpler 1975). The corroborating evidence of phenetic discontinuities is the focus of this analysis.

2. Materials and Methods

Fifteen adult crania, eight specimens of *L. septentrionalis* and seven specimens of *L. dorsalis*, were prepared and made available by Georges Randrianasolo, Curator at Tsimbazaza Zoological Park. The specimens of *L. septentrionalis* originate from the north of Madagascar, either from the forests of Sahafary, the Andriafiarena chain, or from the Ankarana region. The seven specimens of *L. dorsalis* originate from the Nosy-Be and Ambanja region. Twenty-six linear cranial measurements were taken from standard anthropometric cranial reference points. Homologous reference points were easily determined in *Lepilemur*; only *prosthion* was redefined as the most anterior-inferior point of the premaxilla due to the lack of permanent upper incisors in *Lepilemur*. Six additional measurements were recorded from the mandibulae as well as five measurements on the articulated crania and mandibulae. Average measurement error was less than one percent. The selected parameters are noted in Table 1.

3. Results

Although all specimens except one of *L. septentrionalis* are male and the majority of the *L. dorsalis* specimens are female, the morphometrics clearly demonstrate that *L. dorsalis* is the larger of the two species (Table 1). Of the thirty-seven dimensions, *L. dorsalis* has larger mean values in thirty-four of the cases. Of the remaining three cases, the two groups have essentially identical group means in one case (zygomalare-zygomalare); *L. septentrionalis* is slightly larger in one case (basion-lambda), and is appreciably larger in the final case (lacrimale-lacrimale). This last case, also defined as the interorbital breadth, is especially noteworthy, for despite overall greater cranial size in *L. dorsalis*, it has an absolutely smaller interorbital distance.

A single-tailed *t*-test was employed to test the null hypothesis that *L. dorsalis* is not larger than *L. septentrionalis*. In the thirty-four cases in which *L. dorsalis* was noted larger, the null hypothesis is rejected in twenty-nine instances at the 0.05 level of significance (Table 1). The phenetic differences between the two samples are therefore statistically significant. Of the three cases where *L. septentrionalis* was the larger, the first two cases were not found to be statistically significantly different than *L. dorsalis*

Plate 1. Above, *norma verticalis*.
L. septentrionalis, male, on the
left; *L. dorsalis*, female, on the
right. Below, *norma frontalis*.
Same as above.

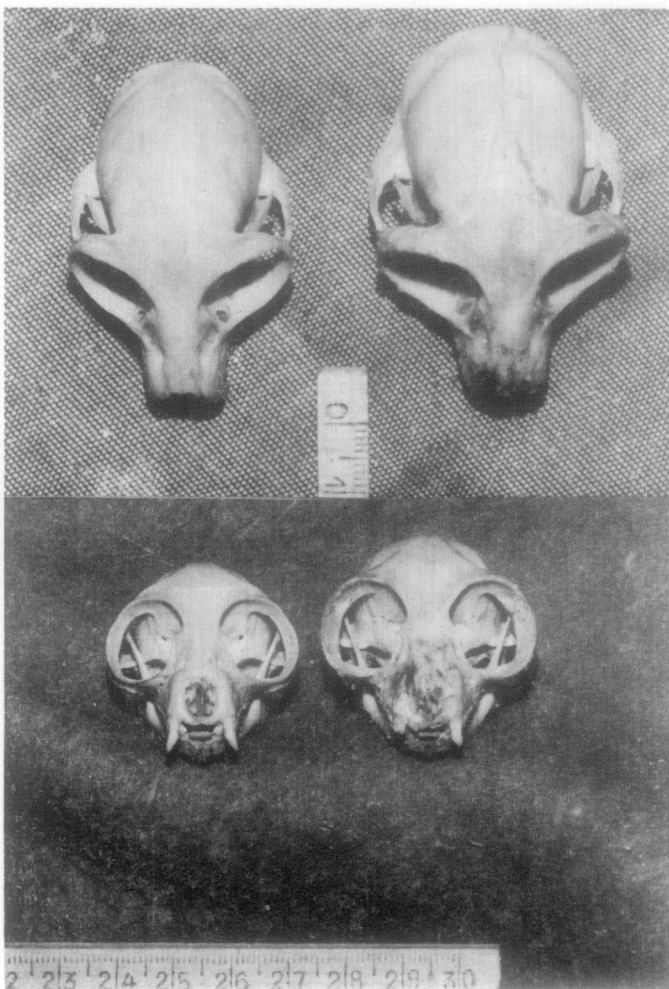


Table 1

Means, standard deviations, and standard errors of the means of thirty-seven cranial dimensions are presented by species for *L. septentrionalis* and *L. dorsalis*

Variable	<i>L. septentrionalis</i>			<i>L. dorsalis</i>			0.05 Level of significance
	\bar{X} (mm)	s.d.	s.e.	\bar{X} (mm)	s.d.	s.e.	
Opistocranium-prosthion	52.4	0.79	0.28	55.7	0.89	0.33	*
Opistocranium-nasion	40.2	0.67	0.23	42.0	1.02	0.38	*
Opistocranium-bregma	23.8	1.11	0.39	25.4	0.90	0.34	*
Basion-lambda	17.6	0.84	0.29	17.5	0.35	0.13	—
Basion-bregma	25.1	0.67	0.23	26.4	1.13	0.42	*
Opisthion-nasion	39.2	0.78	0.27	41.2	0.83	0.31	*
Basion-prosthion	42.2	0.59	0.21	45.9	0.91	0.34	*
Lambda-bregma	16.0	1.30	0.45	17.8	0.81	0.30	*
Lambda-nasion	34.9	1.07	0.37	36.7	1.16	0.43	*
Lambda-prosthion	49.3	0.79	0.28	52.4	0.93	0.35	*
Bregma-nasion	21.7	1.75	0.62	22.0	1.20	0.45	—
Bregma-prosthion	38.6	1.74	0.61	40.5	1.05	0.39	*
Nasion-prosthion	18.2	0.58	0.20	19.8	0.41	0.14	*
Zygion-zygion	35.3	1.04	0.30	36.4	1.59	0.60	*
Zygomalare-zygomalare	25.9	0.90	0.31	25.9	0.33	0.12	—
Outer orbital breadth	34.2	0.93	0.32	36.0	1.41	0.53	*
Lacrimale-lacrimale	9.6	0.35	0.12	8.5	0.26	0.10	*
Left orbital breadth	15.0	0.30	0.10	15.9	0.41	0.15	*
Left orbital height	15.2	0.43	0.13	16.1	0.62	0.24	*
Right orbital breadth	14.9	0.45	0.16	16.0	0.27	0.10	*
Right orbital height	15.1	0.41	0.14	16.1	0.27	0.10	*
Post-orbital constriction	18.1	1.06	0.37	18.4	0.60	0.22	—
Biauricular breadth	26.3	0.73	0.25	28.3	1.09	0.41	*
Euryon-euryon	25.5	0.54	0.19	26.0	0.62	0.23	—
Palate length	18.8	0.91	0.32	20.5	0.44	0.16	*
Ectomalare-ectomalare	17.9	0.35	0.12	18.8	0.62	0.23	*
Gnathion-basion	33.1	1.18	0.41	35.7	1.02	0.38	*
Gnathion-bregma	37.6	1.43	0.50	38.8	1.05	0.39	*
Gnathion-prosthion	13.2	0.47	0.16	14.0	0.54	0.25	*
Gnathion-nasion	22.3	0.62	0.21	23.6	0.62	0.23	*
Gnathion-opistocranium	45.2	1.09	0.38	47.7	0.91	0.34	*
Bicondylar breadth	29.0	0.94	0.33	30.0	1.26	0.47	*
Mandibular height at M_1-M_3	5.7	0.25	0.08	5.8	0.22	0.08	—
Mandibular breadth at M_1-M_3	3.4	0.15	0.05	3.6	0.22	0.08	—
Symphysis length	8.5	0.46	0.16	9.0	0.50	0.19	*
Outer M_2-M_3 breadth	14.8	0.52	0.18	15.8	0.67	0.25	*
Bigonial breadth	18.3	1.27	0.45	21.4	1.46	0.55	*

* Significant at 0.05 level. —, Not significant at 0.05 level.
 \bar{X} , Mean. s.d., Standard deviation. s.e., Standard error of the mean.

at the 0.05 level; however, difference in the group means for the interorbital distance was again significant at the 0.05 level.

Overall skull morphology as reflected by selected craniometric indices is similar in the two species despite the noted morphometric discontinuities (Table 2). It is not the proportions of the crania which serve to distinguish the two groups, but rather the fact that there exist statistically significant differences in the patterns of phenetic variation as well as in the karyotypes of the two groups. The cytogenetic grounds for suspected reproductive isolating mechanisms between the two groups is corroborated by morphometric analysis. Preliminary investigations of the craniometrics of a third morphologically similar species, *L. leucopus*, reinforces the observed trend for species differences in *Lepilemur*, i.e. small but statistically significant morphometric discontinuities in addition to cytogenetic distinctions.

4. Conclusions

Craniometric results corroborate the conclusion based initially on cytogenetics: *Lepilemur septentrionalis* from the north of Madagascar is a valid allopatric species distinct from *Lepilemur dorsalis*.

Table 2

Selected cranial indices of *L. septentrionalis* and *L. dorsalis*. Cranial proportions are very similar despite significant size differences

Cranial index	<i>L. septentrionalis</i>	<i>L. dorsalis</i>
Cranial index $\frac{\text{opistocranium-prosthion}}{\text{biauricular breadth}} \times 100$	50.1	50.8
Total facial index $\frac{\text{gnathion-nasion}}{\text{bizygomatic breadth}} \times 100$	63.1	64.8
Orbital index $\frac{\text{orbital breadth}}{\text{orbital height}} \times 100$	left 98.6 right 98.6	98.7 99.0
Cranial length-height index $\frac{\text{basion-bregma}}{\text{opistocranium-prosthion}} \times 100$	45.3	47.3
Post-orbital constriction index $\frac{\text{post-orbital constriction}}{\text{curyon-euryon}} \times 100$	70.9	70.8

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