

# A Chromosome Arm Number Index and Its Application to the Phylogeny and Classification of Lemurs

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**ABSTRACT** A method is described for assessing the degree to which chromosome evolution via centric fusion has occurred within a taxonomic group, using a numerical index which expresses the average number of major chromosome arms per chromosome in a diploid cell. Index values thus calculated agree with a previously proposed plan of prosimian phylogeny, and substantiate some recently suggested changes in taxonomic groups of the Lemurs, based on karyotypic evidence.

The evolution of the Primates has proceeded by means of a series of adaptations to arboreal and terrestrial ways of life. These adaptations have included changes in behavior and morphology. Accompanying these obvious changes have been less evident, but presumably nonetheless important, alterations in the number and morphology of chromosomes.

Several authors (Chu and Bender, '62; Hamerton, '63) have noted that within the Primates, and especially among the prosimians, species with a high diploid chromosome number have a high number of acrocentric chromosomes, while those with a lower diploid chromosome number have relatively fewer acrocentric and more metacentric chromosomes. These authors have suggested that a major form of karyotype evolution in the Primates has been of the Robertsonian type of centric fusion (Robertson, '16); that is, reciprocal translocations between two acrocentric chromosomes (with 1 major arm) result in the formation of a new metacentric chromosome (with two major arms), plus a chromosome which contains little genetic material and may presumably sometimes be lost without serious detriment to the organism. This could lead to a balanced chromosome polymorphism, as has already been found for at least one population of wild mammals, the common shrew (Ford et al., '57). The new karyotype could become fixed if the animals bearing it enjoyed some selective advantage, either due to the change or coincidental to it.

Judgment of whether such a process has occurred within a taxonomic group depends on a consideration primarily of two measures: the NF or "nombre fondamental," which is the total number of major chromosome arms in a diploid cell (Matthey, '55); and the diploid, or 2N, chromosome number.

It is possible to combine both of these into a single measure, or index, the values of which will express the extent to which chromosome evolution via centric fusion has affected the karyotypes of the species within the group. This might be designated an "Arm Number Index," the values of which are obtained by dividing the number of major chromosome arms by the diploid chromosome number. The values obtained will give the average number of major chromosome arms per chromosome; they will range from 1.0, for species with all acrocentric chromosomes, to 2.0, for species with all metacentric chromosomes.

That is,

$$\text{Arm Number Index} = \frac{\text{NF}}{2N},$$

where  $1.0 \leq \text{AAI} \leq 2.0$ .

The index described here does provide values which are entirely consistent with Chu and Bender's ('62) scheme of prosimian phylogeny based on the evolution of karyotypes, as may be seen from the material summarized in table 1. Where results reported by different investigators do not agree, both determinations have

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TABLE 1

Species	Common name	2N	Chromosomes <sup>1</sup>					NF <sup>2</sup>	NF/2N	Reference
			Autosomal Sex							
			M	S	A	X	Y			
<i>Microcebus murinus</i>	Miller's mouse lemur	66	0	2	64	—	—	68	1.03	Chu and Bender, '61
<i>Cheirogaleus major</i>	Dwarf lemur	66	—	—	64	—	—	68	1.03	Chu and Bender, '61
<i>Haplemur griseus griseus</i>	Gray gentle lemur	54	4	6	42	A	A	64	1.19	Bender and Chu, '63
<i>H. griseus olivaceus</i>		58	2	4	52	—	—	64	1.10	Bender and Chu, '63
<i>Lemur catta</i>	Ringtail lemur	56	6	4	44	A	A	66	1.18	Bender and Chu, '63
<i>L. catta</i>	Ringtail lemur	56	8	6	40	A	A	70	1.25	Egozcue, '67
<i>L. mongoz</i>	Mongoose lemur	60	0	4	54	A	A	64	1.07	Bender and Chu, '63
<i>L. mongoz</i>	Mongoose lemur	58	0	4	52	A	A	62	1.07	Egozcue, '67
<i>L. fulvus rufus</i>	Red fronted lemur	60	0	4	54	A	A	64	1.07	Bender and Chu, '63
<i>L. fulvus albifrons</i>	White-fronted lemur	60	0	4	54	A	A	64	1.07	Bender and Chu, '63
<i>L. fulvus fulvus</i>	Brown lemur	58	0	4	52	A	A	62	1.07	Egozcue, '67
<i>L. fulvus fulvus</i>	Brown lemur	48	10	6	30	A	A	64	1.33	Bender and Chu, '63
<i>L. variegatus</i>	Ruffed lemur	46	14	4	26	M	A	66	1.43	Bender and Chu, '63
<i>L. macaco</i>	Black lemur	44	12	8	22	A	A	64	1.45	Bender and Chu, '63
<i>L. sp. nov.</i>		52	8	4	38	M	A	66	1.18	Bender and Chu, '63

<sup>1</sup> Because of the variability in arm length it is sometimes difficult to designate a particular chromosome as M (metacentric) or S (subterminal), or S or A (acrocentric). The classification made in the original reference cited is used here.

<sup>2</sup> In cases where the X and Y chromosomes have different numbers of arms, the number of arms found in the female has been used here.

been shown. If karyotype evolution has proceeded as Chu and Bender proposed, one would expect the values of the index described here to increase as the 2N chromosome number decreases; as shown in figure 1, they do without exception.

It has been suggested (Chu and Swomley, '61; Bender and Chu, '63) that the Lemurinae, on the basis of their karyotypes, fall into three natural groups, with the *Haplemurs* comprising the first group; the second includes *Lemur catta*, *L. mongoz*, *L. fulvus rufus* and *L. fulvus*

*albifrons*; and the third group is composed of *L. fulvus fulvus*, *L. variegatus*, *L. macaco*, plus an animal morphologically similar to *L. fulvus fulvus* but differing karyotypically, with a 2N chromosome number of 52. (This animal was originally referred to by Chu and Swomley as *Lemur sp. nov.*) These authors noted that the three divisions were tentative, and that relationships could be traced both within and between the divisions.

Recently Egozcue ('67) has suggested some rearrangements of these groups.

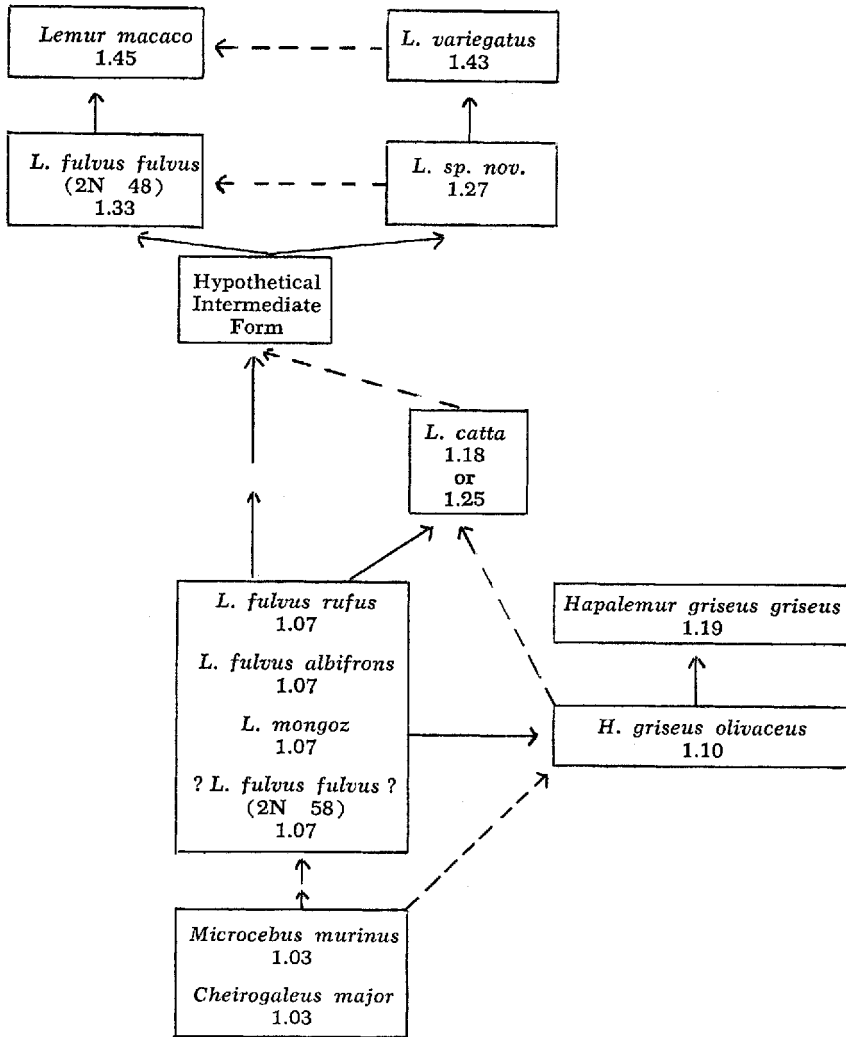


Fig. 1 Lemur phylogeny, with arm number index values.

These involved placing *L. catta* with the *Hapalemurs*, and combining those specimens of *L. fulvus fulvus* having a diploid number of 58 with *L. fulvus albifrons*, *L. fulvus rufus*, and *L. mongoz*. Those specimens of *L. fulvus fulvus* having a diploid number of 48 were left with *L. variegatus* and *L. macaco* (see table 2 for a comparison of the groupings).

Table 2 also shows that index values calculated as described in this paper lend some support for these modifications suggested by Egozcue, as they lead to more consistent values within the groups.

It should be noted, however, that acceptance of the changes suggested does not necessitate revision of Chu and Bender's scheme of prosimian phylogeny based on the analysis of karyotypes, since in this *L. catta* occupied an intermediate position among the groups, and could have been derived from either the *L. mongoz* — *L. fulvus* group or from the *Hapalemurs*, and served as a form plausibly ancestral to the third group which includes *L. macaco*, *L. variegatus*, *L. fulvus fulvus* with 2N of 48, and *L. sp. nov.*

TABLE 2  
Groups within the Lemurinae, based on analysis of karyotypes

Chu and Swomley ('61)	2N	Arm number index	Egozcue ('67)
	52	1.27	<i>Lemur sp. nov.</i> (tentative)
<i>Hapalemur griseus griseus</i>	54	1.19	<i>Hapalemur griseus griseus</i>
<i>H. griseus olivaceus</i>	58	1.10	<i>H. griseus olivaceus</i>
	56	1.25	<i>Lemur catta</i>
<i>Lemur catta</i>	56	1.18	
<i>L. mongoz</i>	60	1.07	
	58	1.07	<i>L. mongoz</i>
<i>L. fulvus rufus</i>	60	1.07	<i>L. fulvus rufus</i>
<i>L. fulvus albifrons</i>	60	1.07	<i>L. fulvus albifrons</i>
	58	1.07	<i>L. fulvus fulvus</i>
<i>L. fulvus fulvus</i>	48	1.33	<i>L. fulvus fulvus</i>
<i>L. variegatus</i>	46	1.43	<i>L. variegatus</i>
<i>L. macaco</i>	44	1.45	<i>L. macaco</i>
<i>L. sp. nov.</i>	52	1.27	

In cases such as this, where a Robertsonian type of chromosome evolution has occurred within a taxonomic group, there will be a decrease in the diploid chromosome number and in the number of acrocentric chromosomes from one species (or group of species) to the next, accompanied by an increase in the number of metacentrics. The NF should nevertheless remain constant throughout the group, unless obscured by other modifications. The index described here summarizes these trends and expresses in a convenient form a relationship between the NF and 2N values which appears to be phylogenetically meaningful.

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