

## COMPARATIVE STUDY OF LACTATE DEHYDROGENASE IN FIFTEEN GENERA OF NEW WORLD MONKEYS

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### ABSTRACT

Electrophoretic variation of LDH was investigated in 3,200 specimens belonging to 28 species and 15 genera of New World monkeys. A small sample of (Old World) *Cercopithecus aethiops* was also tested for comparison. Variation was observed in seven species, five alleles being detected for both *LDHA* and *LDHB* loci. The frequency of the variant alleles was low in almost all species, the exceptions being *Callithrix kuhli* and *Callithrix jacchus penicillata*, in which the *LDHA\*5* allele showed frequencies of 47% and 60%, respectively. In the monomorphic patterns the B4 and A4 bands were the same in all fifteen genera, but differences were observed in the B3A1, B2A2 and B1A3 hybrid bands. Furthermore, only the B4 band was shared by humans, Old World and New World monkeys. An important marker was found in the genus *Cebus*, which clearly distinguishes the "tufted" and "untufted" groups.

### INTRODUCTION

Lactate dehydrogenase (LDH; E.C.1.1.1.27) is the enzyme responsible for the reversible conversion of pyruvate to lactate in somatic tissues of mammalian species. Upon electrophoresis, LDH is resolved into five isozymes, each of which is a tetramer composed of electrophoretically distinct A and B subunits. By random combination they form the series of isozymes named LDH1 through LDH5 with the following structure: B4 (LDH1, the most anodic band), B3A1 (LDH2), B2A2 (LDH3), B1A3 (LDH4) and A4 (LDH5, the less anodic band) (Markert, 1963). These subunits are under the control of two structural loci (Shaw and Barto, 1970),

named *LDHA* and *LDHB*. A third locus, *LDHC*, active in primary spermatocytes only, has been described in birds and mammals (Goldberg, 1963; Schneider *et al.*, 1983).

In a review published by Roychoudhury and Nei (1988), hundreds of populations with thousands of individuals from different human ethnic groups were analyzed. Variants were detected in 18 and six populations for *LDHA* and *LDHB* respectively. Excluding two populations, the Guaymi from Panama (*LDHB\*GUA1*: 7%) and the Balinese from Indonesia (*LDHA\*Calcutta-1*: 1.3%), all the others presented frequencies of the rarer alleles of less than 1%.

In Old World monkeys, variants have been reported in *Macaca fuscata* (*LDHA* and *LDHB*; Kawamoto *et al.*, 1982), *M. fascicularis* and *M. mulatta* (*LDHA*: Kawamoto *et al.*, 1982) and *M. assamensis* (*LDHB*: Shotake, 1979).

In New World monkeys, electrophoretic variants were described for both loci in *Alouatta belzebul* (Schneider *et al.*, 1991a), and for *LDHA* in *Saimiri sciureus ustus* (Silva, 1990), *Callithrix jacchus penicillata* (Meireles *et al.*, 1992) and *Callithrix kuhli* (Schneider *et al.*, 1991b). *LDHB* variants were detected in *Callithrix humeralifer humeralifer* (Meireles *et al.*, 1992), *Saimiri sciureus sciureus* (Silva, 1990) and *Pithecia irrorata*

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(Sampaio *et al.*, 1991a). Interestingly, in *Callithrix jacchus penicillata* the usually less frequent allele was more prevalent than the form that occurs in higher numbers among the other species.

In this paper we present a comparative study of LDH isozymes performed on 3,200 New World monkeys belonging to 28 species and 15 genera.

## MATERIAL AND METHODS

Information about the species, number of individuals studied and origin of the New World monkeys investigated is shown in Table I. The collecting sites are depicted in Figure 1. For comparative purposes we also studied a small sample of an Old World monkey, *Cercopithecus aethiops* (N=22), which is kept in captivity at the "Centro Nacional de Primatas" (Belém, PA, Brazil).

Blood samples were collected using EDTA as anticoagulant. Plasma was separated by centrifugation and red blood cells were glycerolized and stored at -20°C. Hemolysates were prepared by mixing red blood cells, distilled water and carbon tetrachloride in equal proportions. Electrophoretic patterns of LDH were obtained through horizontal electrophoresis in agarose gel (0.8%: Sigma, Pharmacia and Bethesda), potato starch gel (11%: Sigma) or corn starch gel (12%: Penetrose 30, donated by Fercla Comercial Ltda.). The citrate phosphate (CP) buffer, pH 5.9 (*Tank*: 40x CP: 110 mM monobasic sodium phosphate, 245 mM citric acid, adjusted with 10 M NaOH; *Gel*: 1x CP) was generally used. Staining procedures were those proposed by Harris and Hopkinson (1976). All variants previously reported by our group (Silva, 1990; Sampaio *et al.*, 1991b; Schneider *et al.*, 1991a; Meireles *et al.*, 1992) were compared in the same

Table I - Species, number of individuals studied and origin of the New World monkeys sampled.

Species	No.	Origin <sup>1</sup>	References <sup>2</sup>
<b>Genus <i>Alouatta</i></b>			
<i>A. belzebul</i>	1069	Tocantins	Schneider <i>et al.</i> (1991a)
<i>A. seniculus</i>	16	Jari	Lima <i>et al.</i> (1990)
<i>A. seniculus</i>	14	Porteira	Present paper
<i>A. seniculus</i>	77	Balbina	Present paper
<b>Genus <i>Ateles</i></b>			
<i>A. paniscus</i>	7	Porteira	Sampaio <i>et al.</i> (1991c)
<i>A. chamek</i>	44	Jamari	Sampaio <i>et al.</i> (1991c)
<b>Genus <i>Brachyteles</i></b>			
<i>B. arachynoides</i>	1	Captive (a)	Present paper
<b>Genus <i>Lagothrix</i></b>			
<i>L. lagothricha</i>	8	Captive (b)	Present paper
<b>Genus <i>Pithecia</i></b>			
<i>P. irrorata</i>	143	Jamari	Sampaio <i>et al.</i> (1991a)
<i>P. pithecia</i>	4	Jari	Present paper
<b>Genus <i>Chiropotes</i></b>			
<i>C. satanas satanas</i>	12	Porteira	Sampaio <i>et al.</i> (1991a)
<i>C. satanas utahiki</i>	95	Tocantins	Schneider (1988)
<b>Genus <i>Cacajao</i></b>			
<i>C. calvus</i>	7	Ucayali (b)	Sampaio <i>et al.</i> (1991a)
<b>Genus <i>Aotus</i></b>			
<i>A. azarae</i>	92	Jamari	Barroso <i>et al.</i> (1991)
<i>A. infulatus</i>	71	Tocantins	Schneider <i>et al.</i> (1989)
<i>A. nancymai</i>	92	Marañon	Barroso <i>et al.</i> (1987)
<i>A. vociferans</i>	20	Napo (b)	Barroso <i>et al.</i> (1987)

Continued

Table I - Continued

Species	No.	Origin <sup>1</sup>	References <sup>2</sup>
<b>Genus <i>Callicebus</i></b>			
<i>C. brunneus</i>	166	Jamari	Schneider <i>et al.</i> (1991b)
<i>C. cupreus</i>	33	Maniti (b)	Schneider <i>et al.</i> (1991b)
<i>C. moloch</i>	80	Tocantins	Schneider (1988)
<b>Genus <i>Cebus</i></b>			
<i>C. apella apella</i>	149	Tocantins	Schneider (1988)
<i>C. apella paraguayanus</i>	56	Paraguay (c)	Sampaio <i>et al.</i> (1991b)
<i>C. albifrons</i>	10	Colombia (b)	Present paper
<b>Genus <i>Saimiri</i></b>			
<i>s. sciureus sciureus</i>	108	Tocantins	Schneider (1988)
<i>S. sciureus macrodon</i>	8	Napo (b)	Silva (1990)
<i>S. sciureus boliviensis</i>	66	Santa Cruz (d)	Silva (1990)
<i>S. sciureus peruviansis</i>	44	Marañon (b)	Silva (1990)
<i>S. sciureus ustus</i>	171	Jamari	Silva (1990)
<b>Genus <i>Callithrix</i></b>			
<i>C. humeralifer humeralifer</i>	14	Santarém (e)	Meireles <i>et al.</i> (1992)
<i>C. humeralifer emiliae</i>	85	Jamari	Meireles <i>et al.</i> (1992)
<i>C. jacchus jacchus</i>	35	R.G. Norte (e)	Meireles <i>et al.</i> (1992)
<i>C. jacchus geoffroyi</i>	6	Captive (f)	Meireles <i>et al.</i> (1992)
<i>C. jacchus geoffroyi</i>	34	Captive (a)	Schneider <i>et al.</i> (1991c)
<i>C. jacchus penicillata</i>	10	Captive (g)	Meireles <i>et al.</i> (1992)
<i>C. kuhli</i>	32	Captive (a)	Schneider <i>et al.</i> (1991c)
<b>Genus <i>Leontopithecus</i></b>			
<i>L. chrysopygus</i>	10	Captive (a)	Schneider <i>et al.</i> (1991c)
<i>L. chrysopygus</i>	6	Captive (f)	Present paper
<b>Genus <i>Cebuella</i></b>			
<i>C. pygmaea</i>	7	Captive (e)	Present paper
<b>Genus <i>Saguinus</i></b>			
<i>S. bicolor bicolor</i>	22	Captive (a)	Schneider <i>et al.</i> (1991c)
<i>S. bicolor martinsi</i>	4	Captive (a)	Schneider <i>et al.</i> (1991c)
<i>S. fuscicollis</i>	136	Jamari	Melo <i>et al.</i> (1992)
<i>S. midas midas</i>	13	Porteira	Melo <i>et al.</i> (1992)
<i>S. midas niger</i>	123	Tocantins	Schneider (1988)
<b>Total</b>	<b>3200</b>		

<sup>1</sup> The letters in parentheses indicate the institutions where the samples were collected: (a) Centro de Primatologia do Rio de Janeiro, Rio de Janeiro, Brazil; (b) Proyecto Peruano de Primatologia, Iquitos, Peru; (c) Centro de Educación Médica e Investigaciones Clínicas Norberto Quirno, Buenos Aires, Argentina; (d) Centro Argentino de Primatología, Corrientes, Argentina; (e) Centro Nacional de Primatas, Belém, Brazil; (f) Criadouro Barbuse Leal, Brasília, Brazil; (g) Universidade de Brasília, Brasília, Brazil.

<sup>2</sup> The references give further details about these populations, as well as information about other genetic markers.

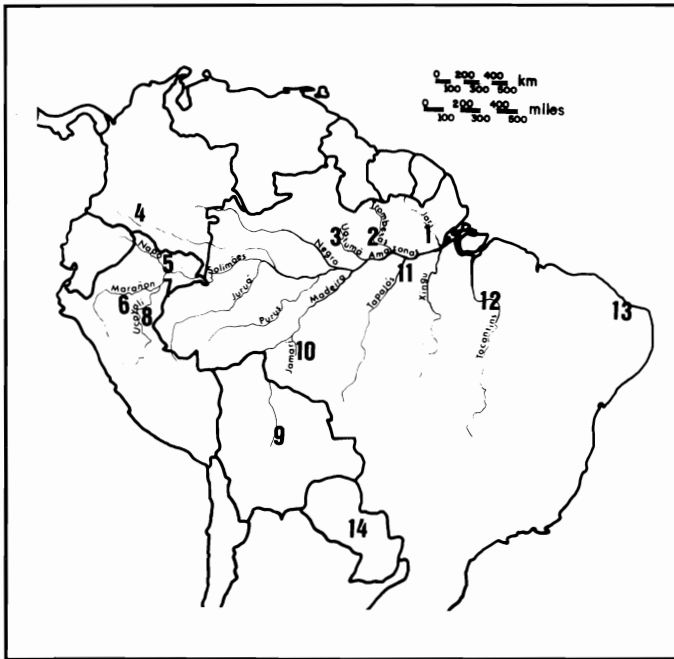


Figure 1 - Map indicating the collecting sites of natural populations of New World monkeys sampled in this study: (1) Jari; (2) Porteira; (3) Balbina; (4) Colombia; (5) Napo; (6) Marañón; (7) Maniti; (8) Ucayali; (9) Santa Cruz; (10) Jamari; (11) Santarém; (12) Tocantins; (13) Rio Grande do Norte; (14) Paraguay.

gel and the alleles renamed. Intergeneric comparisons were also done in various buffers to show differences not detected in CP pH 5.9. These buffers were: CPE pH 6.9 (Tank: 20x CPE: 110 mM monobasic sodium phosphate, 75 mM trisodium citrate, 2.5 mM EDTA adjusted with 10 M NaOH; Gel: 1x CPE); phosphate pH 6.5 (Tank: 10x phosphate: 100 mM monobasic sodium phosphate, adjusted with 10 M NaOH; Gel: 1x phosphate); TC pH 5.5 (Tank: 10x TC: 100 mM Tris, adjusted with citric acid; Gel: 1x TC). Gels were photographed with Agfa 12 ASA film.

Allele frequencies were estimated by gene counting. Observed and expected distributions were tested by chi-square using Yates' correction for continuity.

## RESULTS AND DISCUSSION

Intraspecific electrophoretic variation in the LDH isozymes was observed in *Alouatta belzebul*, *Callithrix humeralifer humeralifer*, *C. jacchus penicillata*, *C. kuhli*, *Pithecia irrorata*, *P. pithecia*, *Saimiri sciureus sciureus* and *S. sciureus ustus* (Table II and III, Figures 2 and 3).

Both loci were variable in *A. belzebul*. Two of the four populations sampled showed variants in LDHA and three in LDHB. *LDHA*\*4 varied from 1% to 2%, and

Table II - LDHA genotype and allele frequencies in New World monkeys.

Species	Genotype	Number		Allele frequencies	
		Observed	Expected		
<i>Saimiri sciureus ustus</i>	1	166	166.0	<i>LDHA</i> *1	0.98
	1-2	5	4.9	<i>LDHA</i> *2	0.02
<i>Pithecia pithecia</i>	1	3	3.0	<i>LDHA</i> *1	0.88
	1-3	1	1.0	<i>LDHA</i> *3	0.12
<i>Alouatta belzebul</i>	1) TWB				
	1	34	34.0	<i>LDHA</i> *1	0.99
	1-4	1	1.0	<i>LDHA</i> *4	0.01
	2) Mixed				
	1	957	956.3	<i>LDHA</i> *1	0.98
	1-4	31	32.5	<i>LDHA</i> *4	0.02
	4	1	0.2		
<i>Callithrix kuhli</i>	1	9	8.9	<i>LDHA</i> *1	0.53
	1-5	16	16.2	<i>LDHA</i> *5	0.47
	5	7	6.9		
<i>C. jacchus penicillata</i>	1	2	2.1	<i>LDHA</i> *1	0.40
	1-5	6	5.7	<i>LDHA</i> *5	0.60
	5	3	3.1		

TWB: west bank of Tocantins River; Mixed: individuals from both the west bank of Tocantins River and Tocantins island.

Table III - LDHB genotype and allele frequencies in New World monkeys.

Species	Genotype	Number		Allele frequencies		
		Observed	Expected			
<i>C. humeralifer humeralifer</i>	1	13	13.0	<i>LDHB*1</i>	0.96	
	1-2	1	1.0	<i>LDHB*2</i>	0.04	
<i>Alouatta belzebul</i>	1) TWB	1	34	34.0	<i>LDHB*1</i>	0.99
		1-3	1	1.0	<i>LDHB*3</i>	0.01
	2) TEB	1	16	16.0	<i>LDHB*1</i>	0.94
		1-3	2	1.9	<i>LDHB*3</i>	0.06
	3) Mixed	1	971	971.1	<i>LDHB*1</i>	0.99
		1-3	18	17.8	<i>LDHB*3</i>	0.01
<i>Saimiri sciureus sciureus</i>	1	7	7.0	<i>LDHB*1</i>	0.94	
	1-4	1	1.0	<i>LDHB*4</i>	0.06	
<i>Pithecia irrorata</i>	1	142	142.0	<i>LDHB*1</i>	> 0.99	
	1-5	1	1.0	<i>LDHB*5</i>	< 0.01	

TWB: west bank of Tocantins River; TEB: east bank of Tocantins River; Mixed: individuals from both the west bank of Tocantins River and Tocantins Island.

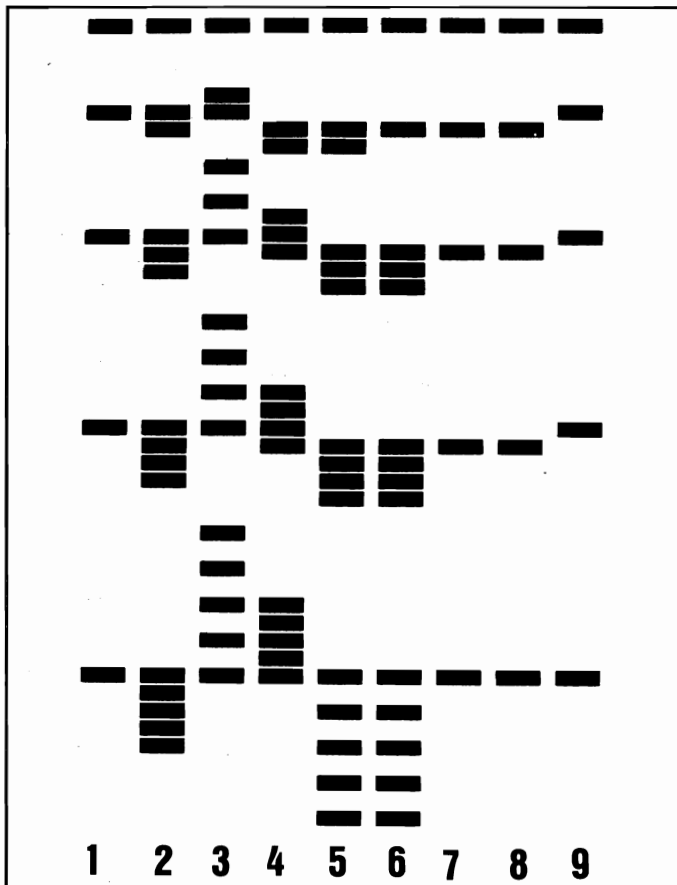


Figure 2 - Diagrammatic LDHA electrophoretic patterns in the following species: (1) *Saimiri sciureus ustus* LDHA 1; (2) *S. sciureus ustus* LDHA 1-2; (3) *Pithecia pithecia* LDHA 1-3; (4) *Alouatta belzebul* LDHA 1-4; (5) *Callithrix kuhli* LDHA 1-5; (6) *C. jacchus penicillata* LDHA 1-5; (7) *C. kuhli* LDHA 1; (8) *A. belzebul* LDHA 1; (9) *Pithecia irrorata* LDHA 1. Origin at the bottom, anode in the upper part of the diagram.

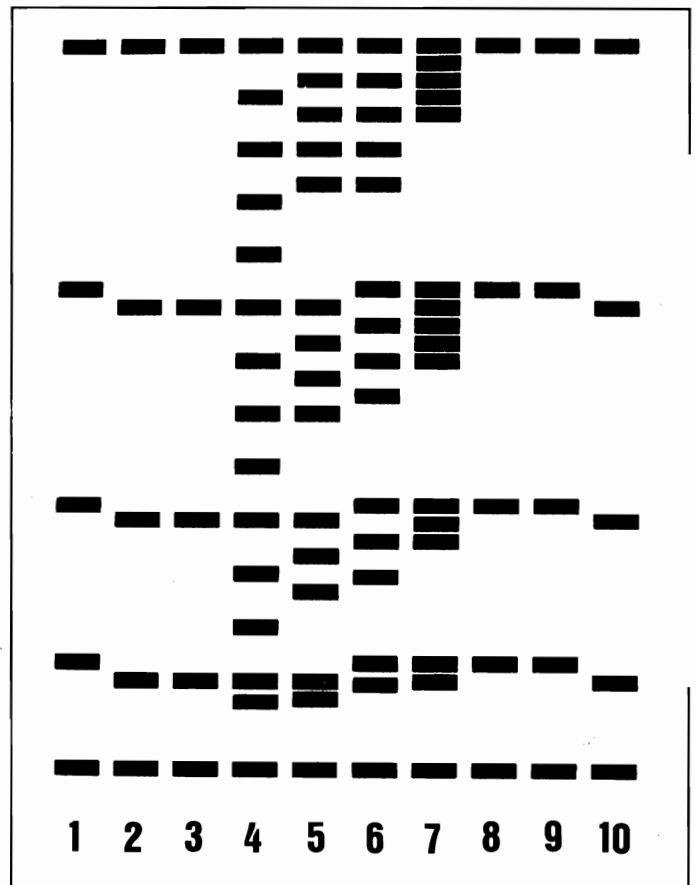


Figure 3 - Diagrammatic LDHB electrophoretic patterns in the following species: (1 and 8) *Pithecia irrorata* LDHB 1; (2 and 10) *Alouatta belzebul* LDHB 1; (3) *Callithrix humeralifer humeralifer* LDHB 1; (4) *C. humeralifer humeralifer* LDHB 1-2; (5) *A. belzebul* LDHB 1-3; (6) *Saimiri sciureus macrodon* LDHB 1-4; (7) *P. irrorata* LDHB 1-5; (9) *S. sciureus macrodon* LDHB 1. Origin at the bottom, anode in the upper part of the diagram.

*LDHB\*3* from 1% to 6%. No variation was found in the Tocantins Island population (N=27) for either locus and on the east bank (N=28) for *LDHA*, which may be due to the small sample sizes. Previous studies in two other species of the genus, *Alouatta palliata* (Malmgren, 1979) and *A. seniculus* (Pope, 1989), did not show variation for either LDH locus.

In *C. humeralifer humeralifer* we detected just one heterozygote (*LDHB* 1-2). *C. jacchus penicillata* and *C. kuhli* also showed polymorphic variation, but only at the *LDHA* locus. The same allele (*LDHA\*5*) is shared by both species with frequencies of 60% in *C. jacchus penicillata* and 47% in *C. kuhli*. This is not surprising since they belong to the same taxonomic group, and according to Hershkovitz (1977) and Coimbra-Filho (1984), *C. kuhli* could be a hybrid form between *C. jacchus penicillata* and *C. jacchus geoffroyi*. But conflicting with this view, the two samples of *C. jacchus geoffroyi* studied in the present paper did not share the same patterns of *LDHA* with the other two species. Another Callitrichidae species did not show variation (*Leontopithecus rosalia*, Forman et al., 1986).

In *Pithecia irrorata*, one heterozygote was found for the *LDHB* locus (*LDHB* 1-5), while among the four individuals of *P. pithecia* studied one presented the *LDHA* 1-3 phenotype.

In the genus *Saimiri*, variants were found at both loci. Five heterozygotes for *LDHA* (*LDHA* 1-2) were found in *S. sciureus ustus* while one out of eight showed the *LDHB* 1-4 phenotype in *S. sciureus sciureus*. Previous studies in *Saimiri sciureus* and *Saimiri boliviensis* (VandeBerg et al., 1990) did not show variation for the LDH isozymes.

No intrapopulational variation was detected in *Cebus*, but the "tufted" and "untufted" groups of species can be clearly characterized by *LDHB* patterns. The "tufted" *Cebus apella* (*C. apella paraguayanus* and *C. apella apella*) showed monomorphism in relation to the pattern shared with 14 other New World monkey genera, while the two "untufted" species, *C. nigrivittatus* and *C. albifrons*, were monomorphic for a distinct pattern (Figure 4, lanes 1, 6 and 7). This suggests that the allele shared by *C. apella* with other genera is the ancestral pattern (Figure 5).

With the exception of *Cebus albifrons* and *C. nigrivittatus*, which differ from the other species in relation to *LDHB*, all New World monkey populations listed in Table I present the same pattern of mobility for A4 (*LDH5*) and B4 (*LDH1*) bands (Figure 5). Given this, a similar pattern would be expected for the internal bands (B3A1, B2A2, B1A3), but in *Callicebus*, *Saimiri*, *Chiropotes*, *Cacajao*, and *Pithecia* they are slightly faster than in the other genera (lanes 11-15, Figure 5). Dilution of the hemolysates (1:10) did not alter the patterns observed. The differences in mobility could be explained by some kind of

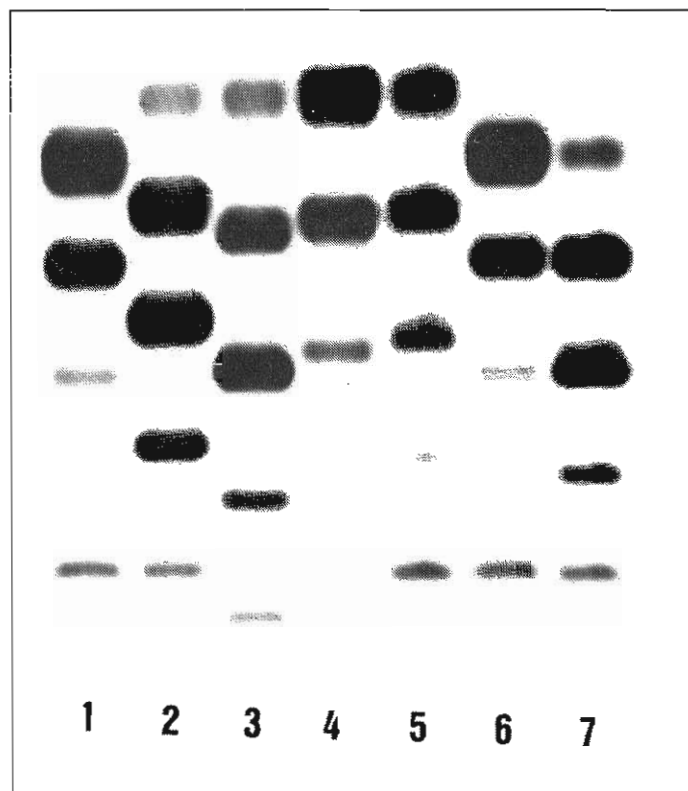


Figure 4 - LDH patterns observed in *Cebus nigrivittatus* (1 and 6), *Callicebus cupreus* (2), *Cercopithecus aethiops* (3), *Homo sapiens* (4), *Cebus apella paraguayanus* (5) and *Cebus albifrons* (7). Origin at the bottom, anode in the upper part of the photograph.

regulatory mechanism controlling the generation of hybrid isozymes, but we cannot exclude the possibility that the A4 or B4 bands are actually different in these diverse genera, the variability being undetectable with the buffers and supports used. Similar findings were observed in *Cercopithecus aethiops* and man, which share the A4 and B4 bands, but differ in relation to the internal bands (Figure 4, lanes 3 and 4).

The pattern of LDH variation in Platyrrhines is similar to those reported for other primates. The variants in most populations occur at low frequencies (less than 1%). The only remarkable exceptions are the results found for *Callithrix jacchus penicillata* and *C. kuhli*, where the *LDHA\*5* variant occurs at high frequencies (60% and 47%, respectively). Sample sizes, however, are small (11 and 32 animals, respectively). New studies in these taxa are necessary to confirm these results.

The 22 *Cercopithecus aethiops* analyzed here showed a monomorphic pattern similar to the common human LDH phenotypes, but *LDHA* was different from all New World monkeys (see the less anodic band, lane 3, Figure 4). In other Old World monkeys only *Macaca* presented variants for both loci (Table IV). No variation has been detected in *Cercopithecus aethiops*, *Macaca cyclops*, *M. mulatta* from China, Pakistan and India, *M.*

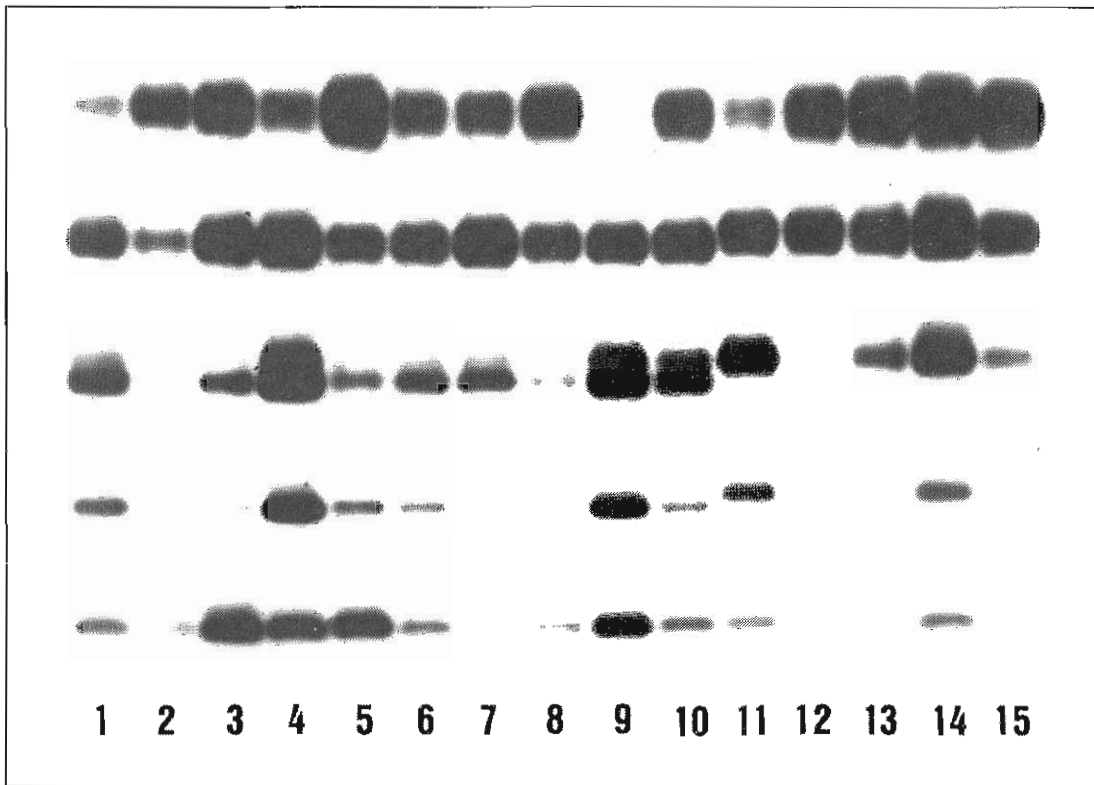


Figure 5 - LDH patterns among 15 genera of Cebidae and Callitrichidae, *Leontopithecus* (1), *Cebuella* (2), *Saguinus* (3), *Callithrix* (4), *Aotus* (5), *Cebus* (6), *Brachyteles* (7), *Lagothrix* (8), *Alouatta* (9), *Ateles* (10), *Callicebus* (11), *Saimiri* (12), *Chiropotes* (13), *Cacajao* (14), *Pithecia* (15). Origin at the bottom, anode in the upper part of the photograph.

Table IV - LDH variation in *Macaca*.

Species	No.	Allele frequencies <sup>1</sup>	References
<i>M. assamensis</i>	28	<i>LDHB*U</i> 0.91 <i>LDHB*V</i> 0.09	Shotake (1979)
<i>M. fascicularis</i> (Malaya)	33	<i>LDHA*U</i> 0.98 <i>LDHA*V</i> 0.02	Kawamoto <i>et al.</i> (1982)
<i>M. fuscata</i> (Japan)	1394	<i>LDHA*U</i> 0.98 <i>LDHA*V1</i> 0.01 <i>LDHA*V2</i> 0.01 <i>LDHB*U</i> > 0.99 <i>LDHB*V</i> < 0.01	Kawamoto <i>et al.</i> (1982)
<i>M. mulatta</i> (Thailand)	31	<i>LDHA*U</i> 0.98 <i>LDHA*V</i> 0.02	Kawamoto <i>et al.</i> (1982)

<sup>1</sup>U = usual; V = variant.

*fascicularis* from the Philippines and Indonesia, or from *M. radiata*, *M. sinica*, *M. speciosa*, *Papio anubis*, *P. hamadryas* and *Theropithecus gelada* (McDermid and Ananthkrishnan, 1972; Shotake, 1974, 1981; Nozawa *et al.*, 1977, 1982; Shotake *et al.*, 1977; Turner, 1981; Kawamoto *et al.*, 1982; Shotake and Santiapillai, 1982; Shotake and Nozawa, 1984).

Among hominoids, LDH variants have been reported only in humans. However, most of the studies have shown frequencies of less than 1% (Roychoudhury and Nei, 1988). The absence of variation in chimpanzees, gorillas, orangutans and gibbons (Khan and Balner, 1972; Bruce and Ayala, 1979; Lucotte, 1980; Nozawa *et al.*, 1982) may be a consequence of the small sample sizes used

in these studies, or may be due to the fact that they are endangered groups whose populational sizes are decreasing drastically as a consequence of hunting and environmental damage.

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## RESUMO

A variação eletroforética da LDH foi investigada em 3.200 animais de 28 espécies e 15 gêneros de macacos do Novo Mundo. Também foi testada, para comparação, uma pequena amostra de *Cercopithecus aethiops*. Foi observada variação em sete espécies, sendo detectados 5 alelos em ambos os locos, LDHA e LDHB. A frequência dos alelos variantes foi baixa em quase todas as espécies, as exceções sendo *Callithrix kuhli* e *Callithrix jacchus penicillata*, onde o alelo LDHA\*5 apresentou frequências de 47% e 60%, respectivamente. Nos padrões monomórficos as bandas B4 e A4 foram as mesmas em todos os 15 gêneros, mas foram observadas diferenças nas bandas híbridas B3A1, B3A2 e B3A3. Além disso, apenas a banda B4 é compartilhada entre humanos e macacos do Velho e Novo Mundo. Um marcador importante foi encontrado no gênero *Cebus*, que distingue claramente os grupos "com tufos" e "sem tufos".

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