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CHROMOSOMAL RELATIONSHIPS AMONG THREE SPECIES OF JACKRABBITS (*LEPUS*: LEPORIDAE) FROM MEXICO

Consuelo Lorenzo¹, Fernando A. Cervantes², and Julieta Vargas²

ABSTRACT.—We studied differentially stained karyotypes of the leporids *Lepus californicus*, *L. callotis*, and *L. flavigularis* and described their banding patterns of euchromatin to decide whether results fit expectations of chromosomal rearrangements leading to the karyotypic evolution ancestral of the *L. californicus*–*L. callotis*–*L. flavigularis* lineage. Results confirmed previous findings on numbers of chromosomes ($2n$'s) and fundamental numbers (FNs; except for *L. californicus*). Homologous G-banding patterns allowed identification of chromosome rearrangements such as pericentric inversions and addition and deletion of euchromatin. Chromosomal rearrangements that we deduced mostly support hypotheses on karyotypic changes in the chromosomal evolution of the *Lepus* ancestral lineage that we examined. The karyotypic pattern coincides with patterns of geographic variation and distribution of the species examined.

Key words: chromosomes, karyotypic evolution, jackrabbits, *Lepus*, hares, Mexico.

Jackrabbits belong to the genus *Lepus* of the family Leporidae. The genus has approximately 29 species, is widespread in both the Old and New World, and is adapted to different habitats (Flux and Angermann 1990).

In Mexico there are 15 species of leporids, represented by 10 species of rabbits (*Romerolagus* and *Sylvilagus*) and 5 species of jackrabbits (*Lepus*). Two species of jackrabbits are endemic: the black jackrabbit, *Lepus insularis*, restricted to the Espíritu Santo Island in the southern portion of the Baja California Peninsula (Thomas and Best 1994), and the Isthmus jackrabbit, *Lepus flavigularis*, occurring solely in the Isthmus of Tehuantepec in the southeastern portion of the State of Oaxaca. The Isthmus jackrabbit is considered the most endangered *Lepus* species at present (Chapman et al. 1990, Flux and Angermann 1990, SEDESOL 1994, Baillie and Groombridge 1996) because of poaching and encroachment of agriculture into its habitat (Flux and Angermann 1990). The white-sided jackrabbit, *Lepus callotis*, is found from central Oaxaca, along the Sierra Madre to Chihuahua, and East Sonora; in the United States it is restricted to 2 valleys in Hidalgo County, New Mexico (Hall 1981, Flux and Angermann 1990). The black-tailed jackrabbit, *Lepus californicus*, has a wide distribution in northern Mexico and Baja Califor-

nia (Hall 1981). The antelope jackrabbit, *Lepus alleni*, has a broad distribution in Mexico and is the largest Mexican jackrabbit. *Lepus flavigularis*, *L. callotis*, and *L. alleni* comprise the *callotis* or white-sided jackrabbit group (Flux and Angermann 1990, Cervantes 1993).

The species of jackrabbits in Mexico are distinguishable by morphological characters (Hall 1981, Flux and Angermann 1990). *Lepus flavigularis* has a black stripe in the nape, extending back from the base of each ear, and the upper parts and flanks are white. *Lepus callotis* has black on the upper part of the tail, and the dorsal parts and flanks are white. *Lepus californicus*, which lacks much white on the sides, has black on the upper surface of the tail and black-tipped ears. *Lepus alleni* is one of the largest North American jackrabbits; it lacks black ear-tips, and white extends from the undersurface well up its sides. There are observable differences in some skull measurements between *L. flavigularis*, *L. callotis*, and subspecies of *L. californicus* from the Mexican Plateau. Particularly, the tympanic bullae of *L. flavigularis* are smaller than in any other *Lepus* species of Mexico, and the lengths of nasals and palatal bridge are larger than those of *L. californicus* and *L. callotis* (Dixon et al. 1983, Cervantes and Lorenzo 1997).

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On the basis of morphological and distributional criteria, species of the *callotis* group are more closely related to *L. californicus* than to any other species of *Lepus*. Probably, a population of *L. californicus* became isolated in Mexico and diverged into *L. callotis*. Later, a population of this divergent stock became isolated on the western coastal plain, differentiating further into *L. alleni*. In a small area in southeastern Oaxaca, a 2nd isolated population evolved into *L. flavigularis* (Anderson and Gaunt 1962), which is morphologically distinctive (Cervantes and Lorenzo 1997).

A morphometric study of jackrabbit species of North America concluded that *L. flavigularis* is more similar to *L. callotis* than to *L. alleni*. A further cluster analysis showed only partial separation of *L. californicus* and *L. callotis*, but nearly complete separation between the clusters of these 2 species and *L. flavigularis*. This tends to confirm the specific taxonomic rank of *L. flavigularis* but leaves uncertain the relationships between *L. callotis* and the Mexican subspecies of *L. californicus* (Dixon et al. 1983, Cervantes and Lorenzo 1997).

Species of *Lepus* have the same diploid chromosome number ($2n = 48$); in addition, their autosomal arms numbers or fundamental numbers (FN) are very similar, as are their G-banded patterns. This means that the genus *Lepus* has been chromosomally conserved through its karyotypic evolution (Robinson 1981). At present, the karyotype and chromosomal classification of the jackrabbit species examined in this study are known (Lorenzo 1996), but there are no comparisons of their chromosome bands of euchromatin (G-bands).

The objectives of this paper therefore are: (1) to compare the non-stained karyotype and the G-banded pattern in 2 species of the *callotis* group (*L. callotis* and *L. flavigularis*) and *L. californicus* of Mexico; (2) to identify the chromosome rearrangements that took place in these species during their karyotypic evolution; and (3) to determine if the patterns of geographic variation and distribution of these species coincide with the karyotypic changes that led to the chromosomal evolution of the ancestral lineage *L. californicus*–*L. callotis*–*L. flavigularis*.

MATERIALS AND METHODS

We studied taxa collected from several localities in Mexico: *Lepus flavigularis*: Santa Maria

del Mar, Municipio Juchitan, Oaxaca (4 males, 3 females); *Lepus callotis*: Mazamitla, Municipio Mazamitla, Jalisco (2 males, 1 female); *Lepus californicus*: 20 km ENE de Apizaco, Municipio Capula, Tlaxcala (4 males, 3 females). Voucher specimens were deposited as museum specimens (skin, skeleton, and frozen-tissue samples) in the mammal collection (Coleccion Nacional de Mamiferos) of Instituto de Biología, Universidad Nacional Autónoma de México, in Mexico City.

Slides with mitotic cells were prepared from bone marrow following conventional colchicine-hypotonic treatment (Baker et al. 1982). We determined diploid counts ($2n$) by scoring 25 selected metaphase spreads from each specimen examined and established fundamental numbers based on number of autosomal arms (excluding the sex pair) as defined by Patton (1967). Computation of the centromeric index and the nomenclature for centromeric position on chromosomes follow Levan et al. (1964).

G-bands were produced using trypsin and Giemsa stain according to the method of DeGrouchy and Turleau (1977). Karyotypes of the mitotic chromosomes were prepared from photomicrographs. Individual chromosomal elements were cut from prints and paired with their presumed homologue.

RESULTS

The chromosomal complements of *Lepus flavigularis*, *L. callotis*, and *L. californicus* all share the same $2n = 48$ (Table 1). *Lepus flavigularis* has an FN of 88; its autosomes are 21 pairs of biarmed chromosomes, with 2 pairs of uniarmed chromosomes. The X and Y chromosomes are both median and submetacentric (Fig. 1). *Lepus callotis* has an FN of 90; its autosomes are 22 pairs of biarmed chromosomes, with 1 pair of uniarmed chromosomes. The X chromosome is a median submetacentric, the Y chromosome small subtelocentric (Fig. 2). *Lepus californicus* has an FN of 82; its autosomes are 18 pairs of biarmed chromosomes, with 5 pairs of uniarmed chromosomes. The X and Y chromosomes are both median and submetacentric (Fig. 3).

Sizes of chromosomes are variable, ranging from small to large. No secondary constrictions were observed in any chromosome. Sex chromosomes are biarmed, and compared with their autosomal counterparts, X chromosomes are

TABLE 1. Diploid chromosome number ($2n$), fundamental number (FN), and chromosomal classification in 3 species of jackrabbits of Mexico; m = metacentric chromosomes; sm = submetacentric chromosomes; st = subtelocentric chromosomes; t = telocentric chromosomes.

Species	$2n$	FN	Autosomes				Sexual chromosomes		Source	
			m	sm	st	t	X	Y		
<i>L. californicus</i>	48	88	-----21-----				2	sm	t	Worthington and Sutton 1966
<i>L. californicus</i>	48	82	7	4	7	5	sm median	sm median	Present study	
<i>L. callotis</i>	48	90	5	6	11	1	m large	t small	González and Cervantes 1996	
<i>L. callotis</i>	48	90	5	6	11	1	sm median	st small	Present study	
<i>L. flavigularis</i>	48	88	5	4	12	2	sm large	sm median	Uribe-Alcocer et al. 1989	
<i>L. flavigularis</i>	48	88	5	4	12	2	sm median	sm median	Present study	

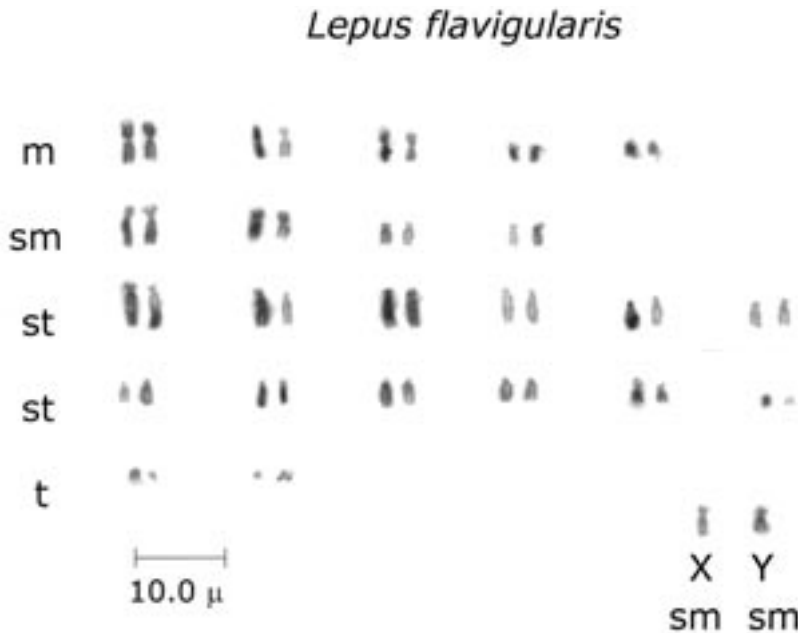


Fig. 1. Non-differentially stained karyotypes of *Lepus flavigularis* (m = metacentric chromosomes; sm = submetacentric chromosomes; st = subtelocentric chromosomes; t = telocentric chromosomes; X, Y = sexual chromosomes).

median to large, whereas Y chromosomes are median to small. Sex chromosomes are the typical XX/XY mammalian system.

Comparisons between *L. californicus* and *L. callotis* indicate noticeable differences in autosomal classification that account for the difference in their FNs (Fig. 4). Differences in euchromatin among these taxa are explained by occurrences of 6 pericentric inversions: (1)

chromosome pair 6 is metacentric in *L. californicus* but submetacentric (pair 10) in *L. callotis*; (2) chromosome pair 7 is metacentric in *L. californicus*, submetacentric (pair 11) in *L. callotis*; distribution of euchromatin also indicates that an addition of euchromatin took place in chromosome pair 11 of *L. callotis*; (3) pair 19 is telocentric in *L. californicus* but subtelocentric (pair 19) in *L. callotis*; (4) pair 20 is

Lepus callotis



Fig. 2. Non-differentially stained karyotypes of *Lepus callotis* (m = metacentric chromosomes; sm = submetacentric chromosomes; st = subtelo-centric chromosomes; t = telocentric chromosomes; X,Y = sexual chromosomes).

Lepus californicus

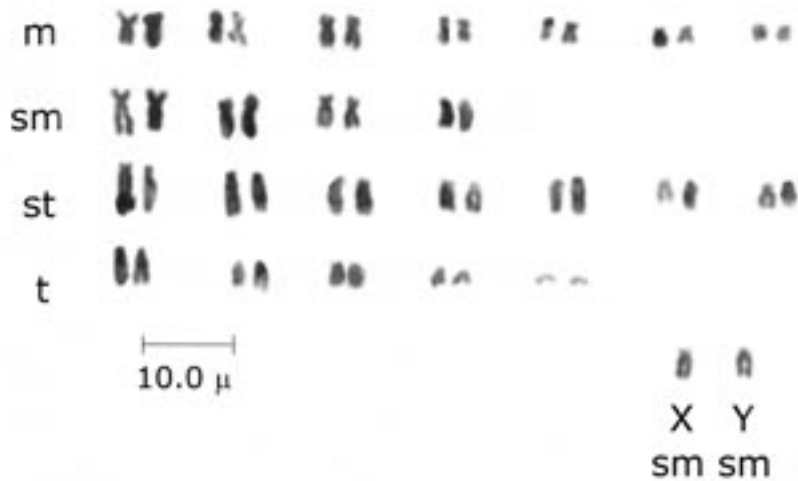


Fig. 3. Non-differentially stained karyotypes of *Lepus californicus* (m = metacentric chromosomes; sm = submetacentric chromosomes; st = subtelo-centric chromosomes; t = telocentric chromosomes; X,Y = sexual chromosomes).

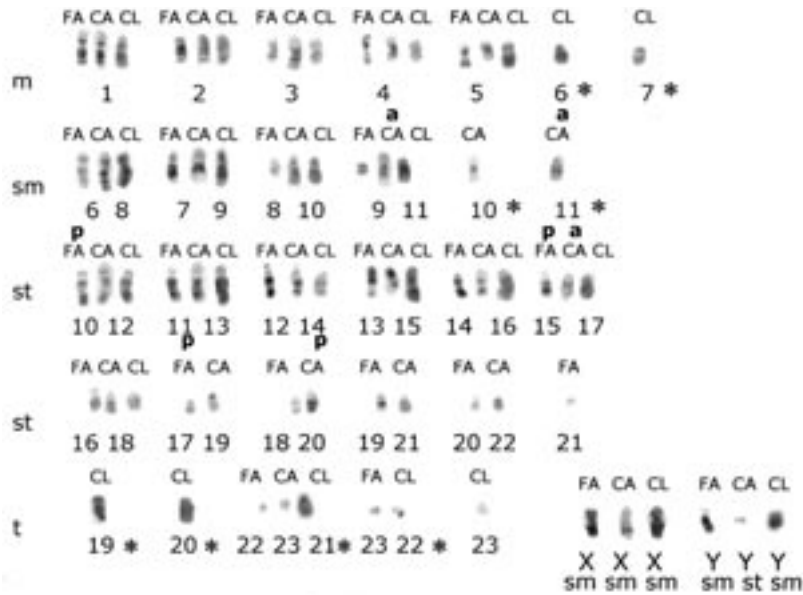


Fig. 4. Comparison of G-banding patterns. From left to right, each group of chromosomes (large numbers) contains a chromosome from *Lepus flavigularis* (FA), *L. callotis* (CA), and *L. californicus* (CL). The chromosomal pairs involved in pericentric inversion are identified with asterisk (*). Letter p denotes chromosomal pairs involved in deletions of euchromatin segments, and letter a denotes chromosomal pairs involved in additions of euchromatin segments.

telocentric in *L. californicus*, but in *L. callotis* it is subtelocentric (pair 20); (5) chromosome pair 21 is telocentric in *L. californicus*, subtelocentric (pair 21) in *L. callotis*; and (6) chromosome pair 22 is telocentric in *L. californicus* but subtelocentric (pair 22) in *L. callotis* (Fig. 5). Moreover, distribution of euchromatin also indicates that additions of euchromatin took place in chromosome pairs 9 and 17 of *L. callotis*, and loss of euchromatin took place in chromosome pair 20 of *L. callotis* (Fig. 4).

Lepus callotis and *L. flavigularis* have similar FNs. The differences in euchromatin among these taxa are explained by occurrences of 2 pericentric inversions (Fig. 4). Chromosome pair 10 is submetacentric in *L. callotis* but telocentric (pair 23) in *L. flavigularis*. Distribution of euchromatin also indicates that a loss of euchromatin took place in chromosome pair 10 of *L. flavigularis*. Chromosome pair 11 is submetacentric in *L. callotis* but subtelocentric (pair 21) in *L. flavigularis*. Distribution of euchromatin also indicates that a loss of euchromatin took place in chromosome pairs 15 and 17 of *L. flavigularis* (Figs. 4, 6).

Comparisons of *Lepus californicus* and *L. flavigularis* indicate the FN of *L. californicus* is low. Differences in euchromatin between

these taxa are explained by the occurrence of 5 pericentric inversions (Fig. 4): chromosome pair 6 is metacentric in *L. californicus* but subtelocentric (pair 20) in *L. flavigularis*; pair 7 is metacentric in *L. californicus*, subtelocentric (pair 21) in *L. flavigularis*; chromosome pair 19 is telocentric in *L. californicus* but subtelocentric (pair 17) in *L. flavigularis*; likewise, chromosome pair 20 is telocentric in *L. californicus* but subtelocentric (pair 18) in *L. flavigularis*; and pair 21 is telocentric in *L. californicus*, subtelocentric (pair 19) in *L. flavigularis* (Fig. 7).

We constructed a dendrogram on the basis of $2n$, FN, G-bands, and chromosomal rearrangements observed in the evolutionary lineage of all taxa studied, where the ancestor of *Lepus* had $2n = 48$ (Fig. 8). In summary, 5 pericentric inversions are considered in the basal point of the dendrogram, and they all involved the same chromosome pairs in the lineage that led to *L. callotis* and *L. flavigularis* from the ancestor of *L. californicus*. Just 3 of these pericentric inversions altered the FN.

Another pericentric inversion is considered in the ancestral lineage of *L. callotis*, where the resulting chromosomal pair involved is unique in this lineage; this pericentric inversion

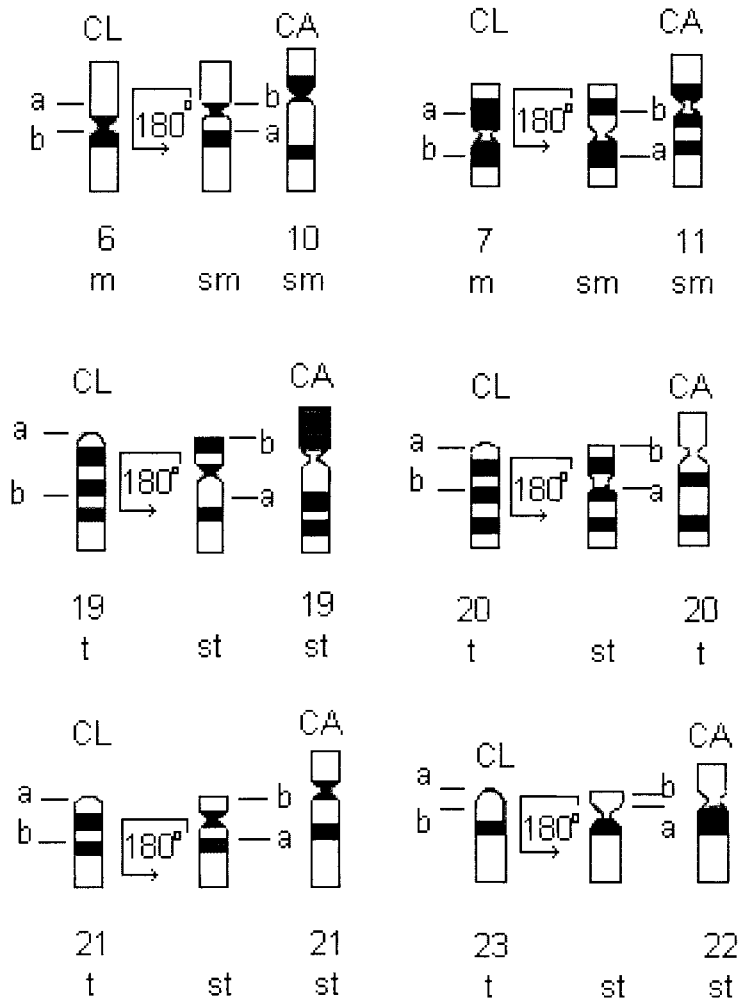


Fig. 5. Differences between G-banded karyotypes of *Lepus californicus* and *L. callotis* are explained by 6 pericentric inversions. *L. californicus* (CL); *L. callotis* (CA). Letters a and b represent points where breaks occurs. The symbol $\boxed{180^\circ}$ represents a 180° rotation of a chromosome fragment corresponding to a pericentric inversion.

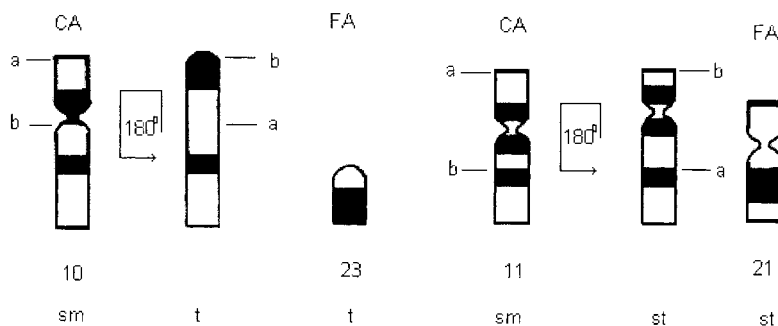


Fig. 6. Differences between G-banded karyotypes of *Lepus callotis* and *L. flavigularis* are explained by 2 pericentric inversions. *L. callotis* (CA); *L. flavigularis* (FA). Letters a and b represent points where breaks occurs. The symbol $\boxed{180^\circ}$ represents a 180° rotation of a chromosome fragment corresponding to a pericentric inversion.

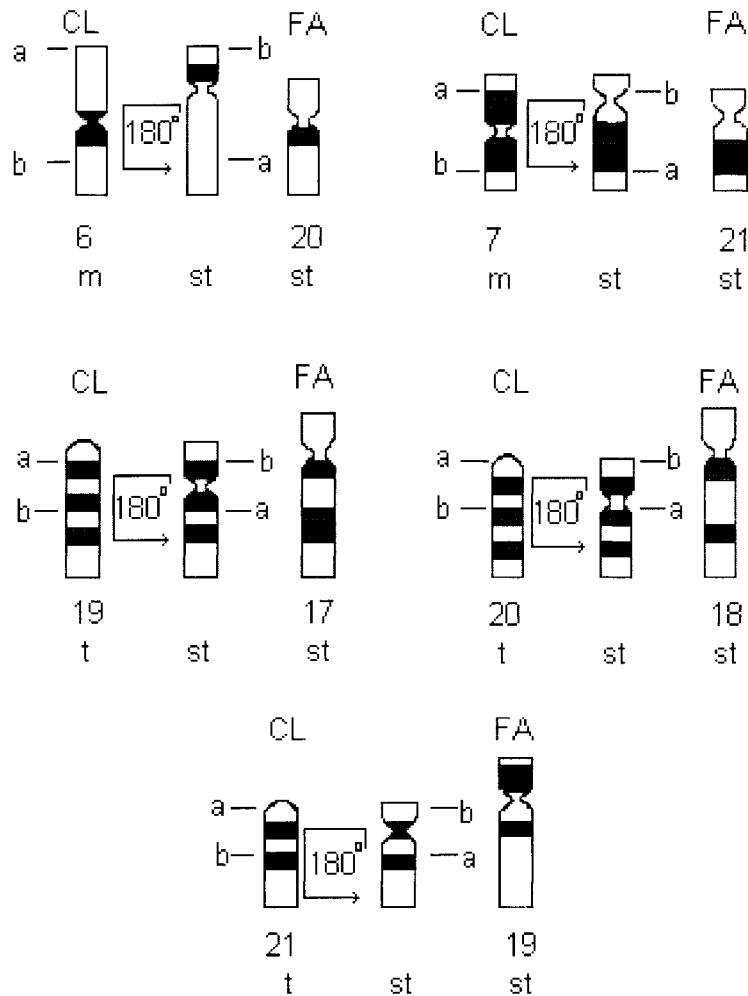


Fig. 7. Differences between G-banded karyotypes of *Lepus californicus* (CL) and *Lepus flavigularis* (FA) are explained by 5 pericentric inversions. Letters a and b represent points where breaks occur. The symbol \curvearrowright represents a 180° rotation of a chromosome fragment corresponding to a pericentric inversion.

altered the FN. Two pericentric inversions in the ancestral lineage of *L. flavigularis* after diverging from *L. callotis* are unique in *L. flavigularis* (Fig. 8). One of these altered the FN and the other did not. There are 2 more pericentric inversions in the ancestral lineage of *L. flavigularis* that did not alter the FN.

Distribution of euchromatin indicates 3 additions and 1 deletion of euchromatin in chromosomal pairs of *L. callotis* in the ancestral lineage of *L. californicus*–*L. callotis*, and 3 deletions of euchromatin in chromosomal pairs of *L. flavigularis* in the ancestral lineage of *L. callotis*–*L. flavigularis* (Fig. 8).

DISCUSSION

Our findings on the $2n$ and FN of *L. flavigularis*, *L. callotis*, and *L. californicus* are similar to karyotypes reported in previous studies (except the FN of *L. californicus*).

Lepus californicus has the lowest FN (82) compared with *L. flavigularis* (88) and *L. callotis* (90). The most similar FNs were those of *L. callotis* and *L. flavigularis*. This is supported by the difference of only 1 pair of uniarmed chromosomes between them. Morphology of the X chromosome in the species of jackrabbits studied is in accord with the general

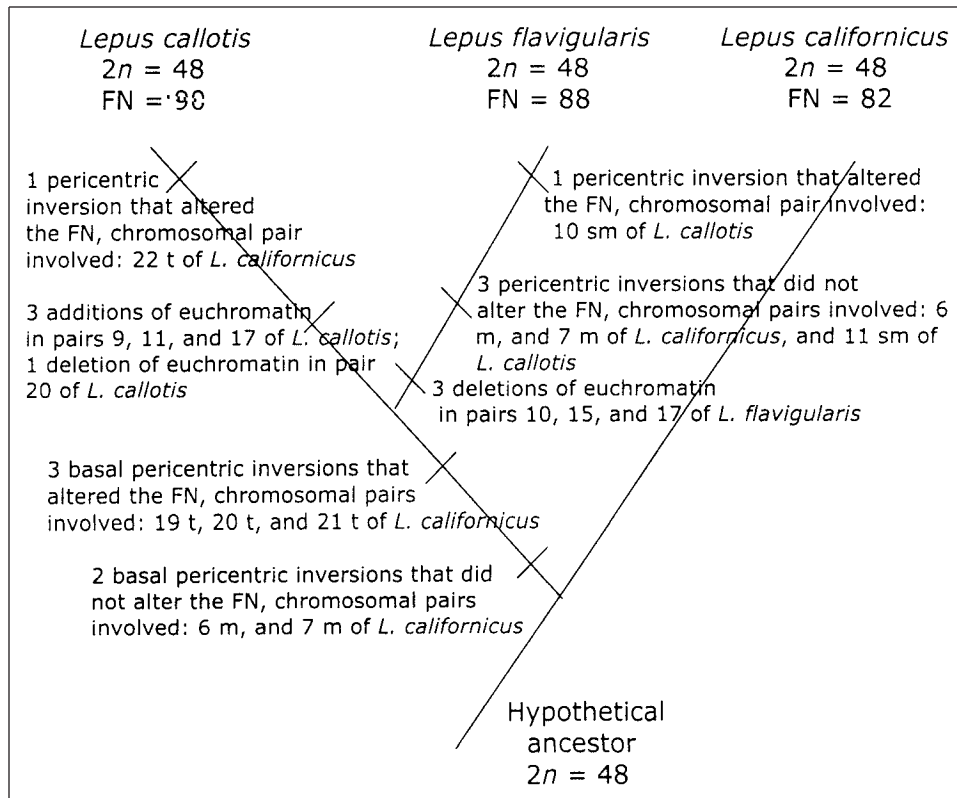


Fig. 8. Dendrogram showing chromosomal relationships among Mexican jackrabbits. Points where hypothetical chromosomal rearrangements occurred are illustrated. $2n$ = diploid chromosome number; FN = fundamental number.

patterns of the genus *Lepus* because all species share a median submetacentric X chromosome (with exception of *L. callotis* in González and Cervantes 1996). In contrast, the morphology of the Y chromosome is more variable. Previous reports indicate this chromosome is small telocentric, but our study found it submetacentric to telocentric in the species examined herein. *Lepus flavigularis* and *L. californicus* each present a medium Y chromosome.

Our results on morphology of autosomes and sexual chromosomes differed from previous reports. This turns out to be remarkable in *L. californicus* regarding differences in banded and unbanded chromosomes (Worthington and Sutton 1966) and in morphology of the Y chromosome. *Lepus californicus* has a broad distribution in Mexico and the United States, and within-species comparisons of chromosomal morphology have included different subspecies from distant, isolated localities. There are differences in chromosomal structure of sexual

chromosomes in *L. californicus* (González and Cervantes 1996), and the size of the X chromosome is different in *L. flavigularis* (Uribe-Alcocer et al. 1989). These differences could depend on the classification system used by each author and on the inter-individual variation in how chromosomal measurements were made.

In general, the G-banding patterns of the jackrabbit species were clear and consistent. Our results are consistent with previous findings on the karyotypic characteristics of these species and support predictions on the types of chromosomal rearrangements. Similar patterns of chromosomal changes have taken place in other lagomorph lineages. Particularly, pericentric inversions are the mechanisms of change in *Lepus* and additions of heterochromatin in lagomorphs (Stock 1976).

The extant species of jackrabbits, of course, inherited their chromosomal complements from their ancestors. However, this does not mean

that their present complements are the same as those of their ancestors. The chromosomal rearrangements documented in this study illustrate changes fixed through the chromosomal evolution of the genus *Lepus*.

Between *L. californicus* and *L. callotis* exists a difference in 4 pairs of uniarmed chromosomes, due to 4 pericentric inversions that changed uniarmed into biarmed chromosomes in the ancestor of *L. callotis*. *Lepus callotis* also exhibits 2 fewer pairs of metacentric chromosomes due to 2 pericentric inversions.

Lepus callotis and *L. flavigularis* differ in only 1 pair of biarmed chromosomes, due to 1 pericentric inversion that changed 1 pair of biarmed into uniarmed chromosomes in the ancestor of *L. flavigularis*. *Lepus flavigularis* also has 1 more pair of submetacentric chromosomes due to another pericentric inversion.

Lepus californicus differs from *L. flavigularis* in having 3 more pairs of uniarmed chromosomes. Three pericentric inversions of uniarmed chromosomes changed them to biarmed in the ancestor of *L. flavigularis*. Two further pericentric inversions resulted in 2 fewer pairs of metacentric chromosomes in the ancestor of *L. flavigularis*.

This is the first study of differentially stained karyotypes that addresses the karyotypic evolution of *Lepus* from Mexico. Our data indicate that the species of jackrabbits studied are closely related, particularly *L. callotis* and *L. flavigularis*. They have a similar FN and a lower number of chromosomal rearrangements. This indicates closer evolutionary development between these 2 species with a common origin derived from 1 ancestral karyotype. Our results confirm the hypothesis on karyotypic changes that led to the chromosomal evolution ancestral of the *Lepus* lineage examined; they also coincide with reported patterns of morphological differentiation and species distribution of the sequence: *L. californicus*–*L. callotis*–*L. flavigularis* (Fig. 8).

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