

Chromosomes of the Asian Chipmunk *Eutamias sibiricus* Laxmann (Rodentia: Sciuridae)

Taxonomic relationships of chipmunks belonging to the genera *Tamias* and *Eutamias* have been evaluated using cranial, skeletal and pelage characters¹⁻⁵, and more recently, chromosomal data⁶⁻⁸. Some investigators classify *Eutamias* and *Tamias* as subgenera of the genus *Tamias*^{1,2,5} while others regard them as distinct genera^{3,4}. Differing opinions also exist concerning the relationship of Asian chipmunks to *Tamias* and *Eutamias* of North America. WHITE⁴ reviewed the various classifications, evaluated a series of 10 characters, and concluded that Asian chipmunks resembled North American *Eutamias* most closely. Thus, Asian and western North American chipmunks are now placed in 2 subgenera of the genus *Eutamias* while chipmunks from eastern North America are referable to a separate genus, *Tamias*^{4,9}.

Chromosome studies of the monotypic genus *Tamias*^{6,7}, 15 of the 16 species of North American *Eutamias*⁶⁻⁸ and Asian *Eutamias sibiricus*¹⁰ demonstrate a diploid number ($2n$) of 38 in all species. 2 different karyotypes were observed among North American *Eutamias*; *Eutamias* karyotype A characterized most subspecies of *E. minimus* and *E. cinereicollis*, whereas *Eutamias* karyotype B was found in all other species and a few subspecies of *E. minimus*⁶⁻⁸. A third karyotype was found in *Tamias striatus*⁶. The karyotype of *E. sibiricus* from Asia has not been described. A single pericentric inversion or translocation can account for the differences between the 3 American karyotypes. Evolution of the 3 North American karyotypes may have resulted from one or more separate ancestral Palearctic chipmunk stocks which spread eastward into the Nearctic^{7,8,11}. Alternatively, *E. sibiricus* may have evolved from a westward range extension of one of the North American stocks¹².

The present report describes the chromosomes of *Eutamias sibiricus*, correlates these data with karyotypes from North American chipmunks, and reconsiders the different concepts of chipmunk taxonomy and evolution.

Materials and methods. 4 female and 4 male *Eutamias sibiricus* Laxmann were obtained from an unknown locality, probably Korea. The chromosomes of these specimens were analyzed from bone marrow cell suspensions using a colcemide, hypotonic citrate, flame dry technique⁸. Karyotypes were constructed using a system devised for North American chipmunks⁶: Group (Gr.) I chromosomes include large metacentrics; Gr. II includes large submetacentrics; Gr. III is composed of large acrocentrics; Gr. IV contains the smallest pair of metacentrics; and Gr. V contains small acrocentric and submetacentric

chromosomes. The X and Y of North American chipmunks belong to Groups II and V respectively.

Results. *E. sibiricus* has a $2n$ of 38 and karyotype containing 3 pairs of chromosomes in Gr. I, 4 pairs in Gr. II, 6 pairs in Gr. III, 1 pair in Gr. IV and 4 pairs in Gr. V (Figures 1 and 2). Males have a submetacentric X resembling the smaller pairs of Gr. II and a small metacentric Y that is slightly larger than the Gr. IV chromosomes (Figure 1). 2 submetacentric X chromosomes are found in cells from the females (Figure 2).

Discussion. The Table compares the karyotypes of *E. sibiricus* and North American *Eutamias* and *Tamias*. Interconversion between the *E. sibiricus* karyotype and each of the 3 American karyotypes requires 3 autosomal rearrangements and a fourth involving remodeling of the Y chromosome from the metacentric Y of *E. sibiricus* to the smaller dot-like or submetacentric Y of American species. 2 autosomal rearrangements differentiating Asian from American karyotypes apparently involved the same chromosome pairs. Thus, 2 pericentric inversions best explain the conversion of the larger 2 pairs of Gr. III in *E. sibiricus* to the larger 2 pairs of Gr. II chromosomes that characterize all American patterns. The third rearrangement, however, differs with each karyotype interconversion. Evolution from *E. sibiricus* to *Tamias* karyotypes is best explained by an additional pericentric inversion within a pair of Gr. III acrocentrics in the former with consequent production of the extra pair of Gr. I metacentrics found in the latter. A translocation or deletion might account for the smaller size of Gr. IV chromosomes in *E. sibiricus* as compared with the same pair in *Eutamias*

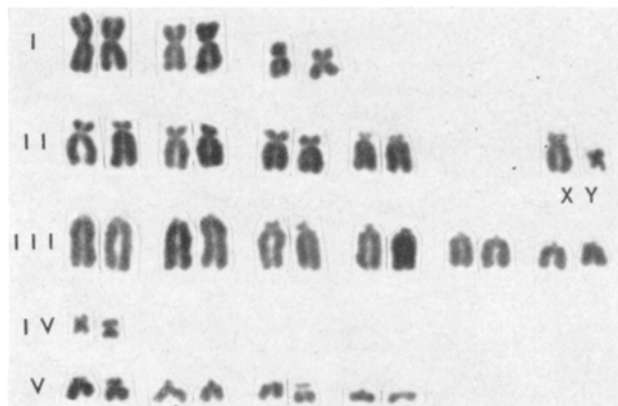


Fig. 1. A karyotype of a male *Eutamias sibiricus*. $\times 2700$.

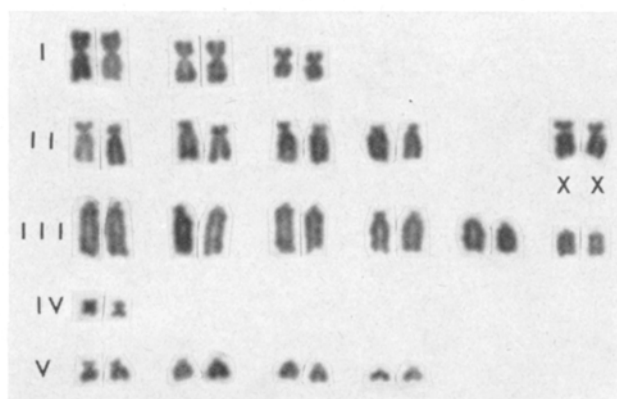


Fig. 2. A karyotype of a female *Eutamias sibiricus*. $\times 2700$.

¹ J. R. ELLERMAN, *The Families and Genera of Living Rodents* (British Museum, Natural History, London 1940), vol. 1.

² M. D. BRYANT, *Am. Midl. Nat.* 33, 257 (1945).

³ A. H. HOWELL, *N. Am. Fauna* 52, 1 (1929).

⁴ J. A. WHITE, *Univ. Kans. Publ. Mus. nat. Hist.* 5, 543 (1953).

⁵ I. M. GROMOV, D. I. BIBIKOV, N. I. KALABUKHOV and M. N. MEIER, *Fauna SSSR, Mlekopitayushchie* 3, 2 (1965).

⁶ C. F. NADLER and M. H. BLOCK, *Chromosoma* 13, 1 (1962).

⁷ C. F. NADLER, *Am. Midl. Nat.* 72, 298 (1964).

⁸ D. A. SUTTON and C. F. NADLER, *J. Mammalogy*, in press (1969).

⁹ E. R. HALL and K. R. KELSON, *The Mammals of North America* (Ronald Press, New York 1959), vol. 1.

¹⁰ T. NAKAMURA, *Kromosomo* 16, 602 (1953).

¹¹ J. C. MOORE, *Am. Mus. Novit.* 2044, 1 (1961).

¹² C. C. BLACK, *Bull. Mus. comp. Zool., Harvard Univ.* 130, 109 (1963).

karyotype A. Lastly, a pericentric inversion converting a pair of acrocentrics in Gr. V of *E. sibiricus* to the extra pair of Gr. I metacentrics seen in *Eutamias* karyotype B best explains the third autosomal rearrangement in this interconversion. These hypothetical explanations assume that North American karyotypes are derived from the *E. sibiricus* karyotype. It is possible, although less likely, that the reverse of any of the above conversions may have occurred with evolution of the *E. sibiricus* karyotype from a North American pattern. Also, both Asian and North American forms might have diverged from an extinct ancestor with karyotype different from any of the recent patterns.

The close karyological similarity between North American *Tamias* and *Eutamias* and their equal degree of cytological divergence from Asian *Eutamias* supports the views^{1,2,6} that ranked these taxa as subgenera of a single genus *Tamias*. Thus, chipmunks from Asia, western North America, and eastern North America are referable to the subgenera *Eutamias*, *Neotamias*, and *Tamias* respectively. Reconciliation of the chromosomal findings with the morphological data of WHITE⁴, which recognized *Tamias* and *Eutamias* as distinct genera, can only be achieved if differing rates of evolution between chromosomes and morphological features are postulated.

The origin and the dispersal pattern of chipmunks across the Bering land bridge have been interpreted differently. According to MOORE¹¹ ancestral *E. sibiricus*, with attributes of a dominant species, originated in the Palearctic and spread eastward repeatedly across the Bering land bridge to occupy the Nearctic Region. The opposite interpretation was later proposed by BLACK¹² and the Nearctic Region was regarded a major area of squirrel radiation with migration occurring subsequently westward into the Palearctic.

Fossil evidence is somewhat ambiguous on this point. Isolated teeth, tentatively identified as *Tamias* (*sensu lato*), are known from early to late Miocene deposits in North America^{12,13}, and from late Miocene of Siberia⁵. BLACK¹² comments that 'the material has been placed in *Tamias* as a purely arbitrary assignment'. The first more complete chipmunk fossils are *Eutamias orlovi*, probably of mid-Pliocene age, from Poland¹⁴, and *Tamias* (*Eutamias?*) *wimani* from the mid-Pleistocene and possibly late Pliocene of China¹⁵. These forms probably represent the subgenus *Eutamias*. In North America, fossils assignable to modern *Tamias* and *Eutamias* do not appear until the late Pleistocene¹⁶⁻¹⁸.

This suggests that even if primitive forms of the chipmunk tribe Tamiini were present in both Old and New World as early as the Miocene, modern chipmunks are probably descendent from a Eurasian *Eutamias* stock which dispersed eastward across the Bering land bridge in the Pliocene or early Pleistocene. *Eutamias sibiricus*, a morphologically variable and ecologically plastic species, may be a descendant of that Pliocene form. The chromosome patterns also suggest that *E. sibiricus* spread eastward into the Nearctic. Thus, if *E. sibiricus* comprised the ancestral stock it underwent 2 pericentric inversions and loss of Y chromosome material to produce a primitive North American chipmunk stock. A point in favor of the eastward spread of chipmunks may be derived from the Y chromosome changes; it seems more likely that losses of Y chromosome material occurred rather than additions to the functionally efficient minute Y of North American chipmunks which would need to occur if a westward spread were correct.

Later, during divergence of ancestral Asian stock within the Nearctic a fourth rearrangement may have arisen in each of 3 populations to account for the 3 different karyo-

types now observed in North American chipmunks. Alternatively, one ancestral stock may have diverged to form chipmunks with *Eutamias* karyotype B and the *Tamias* karyotype. *Eutamias* karyotype A may have evolved from a second mid-to-late-Pleistocene (Mindel-Kansan?) spread of *E. sibiricus* eastward across the Bering land bridge. Support for this alternative is provided by the ecological and zoogeographic affinities between *E. sibiricus* and the boreal and montane populations of *E. minimus* having karyotype A.

Chromosomal, paleontological, and morphological evidence together support the following conclusions: (1) all chipmunks may be placed in a single genus; (2) ancestors of modern chipmunks arose in the Palearctic and spread into the Nearctic across the Bering land bridge once and possibly twice; (3) Pleistocene speciation, including the development of several karyotypes and many species within North America, was aided by the many available ecological niches and barriers such as the grassland barrier of the Great Plains^{7,19}.

Comparison of chipmunk karyotypes

	Number of autosome pairs				
	Gr. I	Gr. II	Gr. III	Gr. IV	Gr. V
Asia					
<i>E. sibiricus</i> (2n=38)	3	4 ^a	6	1 ^b	4
North America ⁶⁻⁸					
<i>Eutamias</i> Karyotype A (2n=38)	3	6 ^a	4	1	4 ^b
<i>Eutamias</i> Karyotype B (2n=38)	4	6 ^a	4	1	3 ^b
<i>Tamias</i> Karyotype (2n=38)	4	6 ^a	3	1	4 ^b

^a The X chromosome, not included in the table, belongs to Gr. II.

^b The Y of North American species is a minute chromosome that is classified in Gr. V; the Y of *E. sibiricus* is slightly larger than the chromosomes of Gr. IV.

Zusammenfassung. Der Karyotyp von *Eutamias sibiricus* Laxmann (2n = 38) ist ein neuer Typus, der von den früher beschriebenen Karyotypen von *Eutamias*- und *Tamias*-Arten abweicht. Der Karyotyp von *E. sibiricus* weicht von den Karyotypen anderer Tamiini durch das Vorkommen von 4 «Rearrangements» ab, während die Karyotypen der Tamiini aus Nordamerika nur in einem «Rearrangement» voneinander differieren.

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Chicago (Illinois, USA), 24 March 1969.

¹³ E. R. HALL, Univ. Calif. Publs. Bull. geol. Sci. 19, 313 (1930).

¹⁴ A. SULIMSKI, Acta paleont. pol. 9, 149 (1964).

¹⁵ C. C. YOUNG, Palaeont. sin. 8, 3, 1 (1934).

¹⁶ E. D. COPE, Proc. Am. phil. Soc. 11, 171 (1869).

¹⁷ B. BROWN, Am. Mus. nat. Hist. Mem. 9, 155 (1908).

¹⁸ W. J. SINCLAIR, Univ. Calif. Publs. Amer. Archeol. Ethnol. 2, 1 (1904).

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