KARYOTYPES OF SOME HARVEST MICE, GENUS *REITHRODONTOMYS*

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ABSTRACT.—Karyotypes of six species of harvest mice, representing both the subgenus *Reithrodontomys (humulis, sumichrasti,* and *fulvescens)* and the subgenus *Aporodon (gracilis, mexicanus,* and *creper)*, are described. The karyotype of *R. sumichrasti* (2n = 40) resembles those previously reported for *R. megalotis* and *R. raviventris,* which possess mainly metacentric chromosomes. ***Reithrodontomys humulis*** (2n = 51), ***R. fulvescens*** (2n = 50), ***R. gracilis*** (2n = 52), ***R. mexicanus*** (2n = 52), and *R. creper* (2n = 52) exhibit a large proportion of acrocentric chromosomes. Karyotypic evidence suggests that intrageneric relationships of *Reithrodontomys* may not be accurately reflected by use of the subgenera *Aporodon* and *Reithrodontomys.*

The rodent genus *Reithrodontomys,* containing approximately 18 species divided among two subgenera (*Reithrodontomys* and *Aporodon*), occurs in southern North America, throughout Central America, and in Colombia and Ecuador. Present knowledge of chromosomal numbers of harvest mice is confined to the North American species *fulvescens* (Hsu and Benirschke, 1968), *megalotis* (Matthey, 1961; Shellhammer, 1967; Hsu and Benirschke, 1970), and *raviventris* (Shellhammer, 1967), all members of the subgenus *Reithrodontomys.* Information on karyotypes of Central American forms, particularly ones belonging to the more morphologically specialized subgenus *Aporodon* (*sensu* Hooper, 1952) is lacking. In this report we describe karyotypes of six species of *Reithrodontomys,* representing both the subgenus *Reithrodontomys* (*humulis, sumichrasti,* and *fulvescens*) and the subgenus *Aporodon* (*gracilis, mexicanus,* and *creper*), and discuss their taxonomic implications.

MATERIALS AND METHODS

All animals were live-trapped and returned to the Museum of Zoology, University of Michigan, where breeding colonies were maintained. Thus, karyotypes reported herein represent both wild-caught individuals and their laboratory-reared offspring; no karyotypic differences were noted between individuals raised in captivity and their field-caught progenitors. Preparation of somatic chromosomes followed Patton (1967). We used the standard four-class system (metacentric, submetacentric, subtelocentric, and acrocentric) for describing chromosomal morphology. The total number of autosomal arms is designated by FN. Voucher specimens are deposited in the University of Michigan Museum of Zoology (UMMZ). The number, sex, and dates of collection of *Reithrodontomys* karyotyped (or source of parental stock) are listed alphabetically by species.

R. creper—COSTA RICA: Cartago; Cerro de la Muerte, 2,800 m (3 ♂♂, 1 ♀). February 1975.

R. fulvescens tropicalis—MEXICO: Tamaulipas; El Nopal, near Jaumave, 1,065 m (1 ♀). August 1971.

R. gracilis gracilis—MEXICO: Campeche; 6 km S Champoton (5 ♂♂, 2 ♀♀). May 1971.

R. humulis humulis—South Carolina; Savannah River Plant, Aiken Co., (2 ♀♀). March 1978.

R. mexicanus howelli—GUATEMALA: Huehuetenango; Barillas (1 ♀). May 1971.

R. mexicanus soderstromi—ECUADOR: Pichincha; eastern foot of Mt. Casitagua (5 ♂♂, 1 ♀). July 1970.

R. sumichrasti australis—COSTA RICA: Cartago; Volcan Irazu, 2,850 m (1 ♂, 3 ♀♀). February 1975.

RESULTS

The diploid number ranged from 40 to 52 among the six species examined (Table 1). No intraspecific variation in the diploid count was noted, but relatively few indi-

TABLE 1.—*Chromosomal data for some species of* Reithrodontomys.

Subgenus and species	2N	Autosomes		Sex chromosomes		FN	Source
		Bi-armed	Acro-centric	X	Y		
Reithrodontomys							
humulis	51	10?	40?	?	?	60?	Present study
raviventris	38	36	0	SM	ST	72	Shellhammer (1967)
megalotis	42	40	0	SM	ST	80	Blanks and Shellhammer (1968) Hsu and Benirschke (1970)
sumichrasti	40	38	0	M	SM	76	Present study
fulvescens	50	0	48	SM	A	48	Hsu and Benirschke (1968); Present study
Aporodon							
gracilis	52	0	50	A	A	50	Present study
mexicanus	52	2	48	A	A	52	Present study
creper	52	0	50	A	A	50	Present study

viduals of each species were examined. Basically, four karyotypic patterns were evident.

Reithrodontomys gracilis, mexicanus, and *creper* all had a 2n of 52. The chromosomal complement of *gracilis* and *creper* consisted of an evenly graded series of acrocentrics in both the male and female (Fig. 1A). Consequently, we could not identify the sex chromosomes, which apparently were isomorphic in these two species. *R. mexicanus* had a pair of very small submetacentrics. The small size of these chromosomes made recognition difficult and they were not positively identified in the other two species. Otherwise, the imperceptibly graded acrocentrics of *mexicanus* closely resembled those of *gracilis* and *creper*.

We observed a diploid count of 50 in *R. fulvescens tropicalis*. The karyotype was similar to that previously described for *R. f. aurantius* from Texas and Louisiana (Hsu and Benirschke, 1968). The chromosomal complement consisted of 24 pairs of small to large acrocentrics and a single pair of large submetacentrics, which we assumed to represent the sex chromosomes (Hsu and Benirschke, 1968).

The karyotype of *R. sumichrasti* (2n = 40) contained seven pairs of subtelocentrics and 13 pairs of small to medium metacentrics and submetacentrics (Fig. 1B). The sex chromosomes were represented by a large metacentric X and a slightly smaller submetacentric Y.

The two female *R. humulis* had a fourth chromosomal type; the diploid number was odd (2n = 51), and the karyogram consisted mainly of small to medium acrocentrics plus five pairs of small to larger-sized biarmed chromosomes (Fig. 1C). The unpaired element in both females was a small metacentric. The identify of the sex chromosomes and nature of sex determination in this species cannot be ascertained until a male is karyotyped.

DISCUSSION

Howell (1914) recognized two subgenera of *Reithrodontomys*, and based his division primarily on the absence (subgenus *Reithrodontomys*) or presence (subgenus *Aporodon*) of accessory lophs and styles on the molar teeth. In his classic revision, Hooper (1952) retained Howell's subgenera, but demonstrated that the characters distinguishing them intergrade when all species are considered, and provided a more detailed estimate of their phyletic relationships. Hooper (1952) further hypothesized

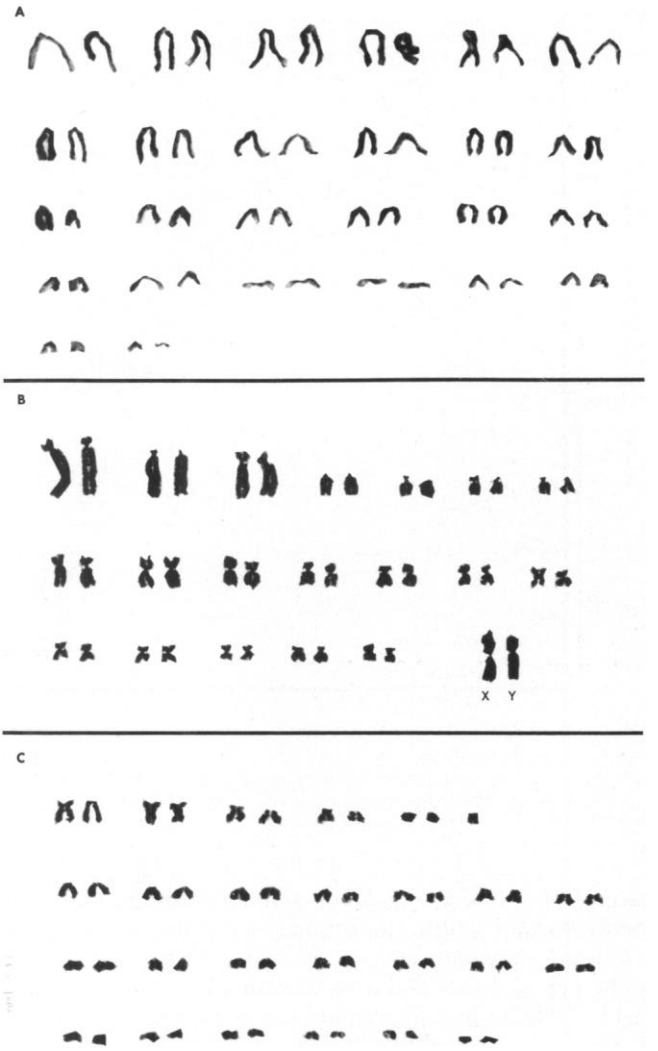

FIG. 1.—Karyograms of three species of *Reithrodontomys*: (A) female *R.* (*Aporodon*) *creper* (UMMZ 125638), sex chromosomes not identified; (B) male *R.* (*Reithrodontomys*) *sumichrasti* (UMMZ 125637); (C) female *R.* (*Reithrodontomys*) *humulis* (UMMZ 125635), sex chromosomes not identified.

that the ancestral morphotype of *Reithrodontomys* inhabited grasslands, was small-bodied and short-tailed, possessed a short, broad skull with simple molars, and was terrestrial in habits; he viewed large size and long tail, a skull with large brain case and long rostrum, complex molar teeth, and scansorial or arboreal habits as derived traits. Thus, certain mice of the subgenus *Reithrodontomys*, (e.g., *humulis* or *montanus*) most closely approximate this ancestral form, whereas those of *Aporodon* (e.g., *mexicanus* and *creper*) exhibit many derived characters. Hershkovitz (1962) disputed Hooper's (1952) interpretation of the direction of character evolution, especially dental modifications, and underscored his disagreement by maintaining *Aporodon* and *Reithrodontomys* as separate genera (Hershkovitz, 1966). Carleton (1973) found that

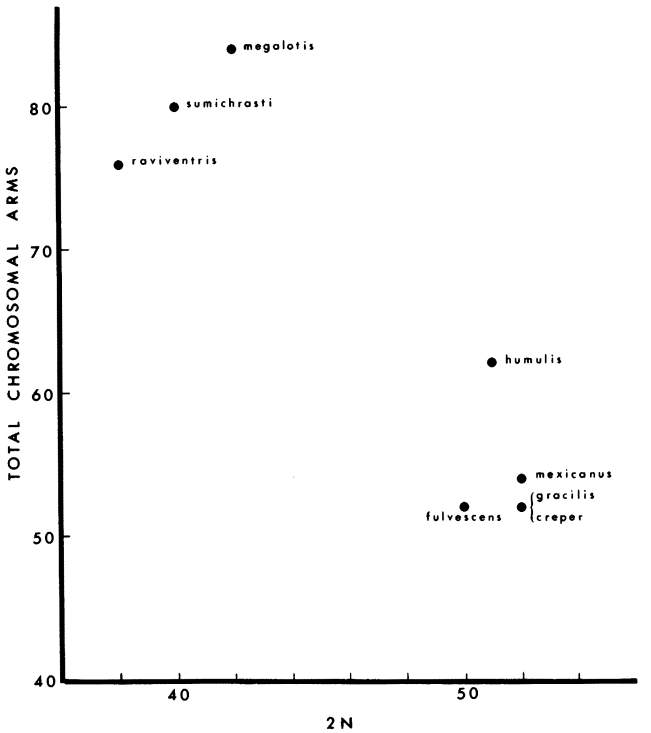

FIG. 2.—Bivariate plot of total number of chromosomal arms (including autosomes and sex chromosomes) versus diploid number (2n) for species of *Reithrodontomys* (see Table 1).

information derived from gastric anatomy generally agreed with Hooper's (1952) estimation of specializations within the genus, but disclosed no hiatus corresponding to the currently defined subgenera.

A body of data now suggests that a chromosomal complement consisting mainly of acrocentrics and a relatively high diploid count represents the ancestral karyotype within a particular lineage, and that the general trend in karyotypic modification is reduction in 2n or increase in the FN/2n ratio. This generalization emerged from studies of a variety of murid rodents, including *Microtus* (Matthey, 1957), *Neotoma* (Baker and Mascarello, 1969; Mascarello et al., 1974*b*), *Peromyscus* (Bowers et al., 1973; Lee and Elder, 1977; but see Lawlor, 1974), *Sigmodon* (Zimmerman, 1970), *Phyllotis* (Pearson and Patton, 1976), *Oryzomys* (Gardner and Patton, 1976), and even the entire South American cricetine complex (Gardner and Patton, 1976). Therefore, the ancestral karyotype in *Reithrodontomys* may resemble that exhibited by members of the subgenus *Aporodon*; a 2n of 52, mostly acrocentrics. A karyotype comprised of a lower diploid number of mostly biarmed chromosomes, such as those possessed by *megalotis, raviventris,* and *sumichrasti,* would be considered highly derived.

Viewed in this perspective, some of Hooper's (1952) hypotheses concerning patterns of evolution within *Reithrodontomys* are corroborated, while others are contradicted by the karyotypic data as enumerated below.

1.—Among those species possessing more primitive karyotypes (i.e., largely acrocentric) are *R. mexicanus* and *R. creper,* species which Hooper considered structurally highly specialized. This apparent discrepancy may reflect a lack of correspondence

between rates of karyotypic change and morphological evolution within the genus. Thus, body form and dental characters may have evolved rapidly in *Aporodon* while these mice retained a primitive karyotype. Alternatively, the common ancestor of *Reithrodontomys* may have resembled a medium-sized, scansorial species similar to *fulvescens* or *gracilis*, instead of a small, short-tailed, grassland form as suggested by Hooper.

2.—The intermediate nature of *R. fulvescens* is supported (Fig. 2; Table 1). Although he placed it in the subgenus *Reithrodontomys*, Hooper thought *fulvescens* (and *hirsutus*) approached species within *Aporodon* in many characteristics.

3.—The large number of biarmed chromosomes and reduced diploid count (2n = 40) of *R. sumichrasti* suggest phyletic proximity to *megalotis* and *raviventris* (Fig. 2), in agreement with Hooper's proposed phylogeny.

4.—*Reithrodontomys humulis* is distinctive. Its karyotype, consisting of a relatively high 2n, many acrocentrics, and few biarmed elements, suggests affinity to species of *Aporodon*. As argued by Hooper (1952), *humulis* (along with *montanus* and *burti*) probably represents an early offshoot of the stock ancestral to the *megalotis* and *sumichrasti* species groups. The progenitor of *humulis* was isolated in the southeastern United States and differentiated there. The present-day occurrence of other relictual forms, e.g., *Ochrotomys nuttalli* and *Peromyscus floridanus*, in this region of North America lends zoogeographic credence to this argument. Consequently, the karyotypic resemblance of *humulis* to members of the subgenus *Aporodon* simply may indicate a shared, primitive condition.

5.—The arrangement of species of *Reithrodontomys* into two subgenera is not wholly consistent with the karyotypic information. In particular, the placement of the species *fulvescens* illustrates the arbitrariness of this classification. Until the intrageneric relationships of harvest mice are better understood, it seems reasonable to emphasize the separate species groups identified by Hooper (1952)—that is, the *humulis*, *megalotis*, *sumichrasti*, *fulvescens*, *mexicanus*, and *tenuirostris* groups—rather than to retain the two subgenera and the notion of a fundamental dichotomy that they impart.

We recommend further karyotypic study of the genus *Reithrodontomys*. The chromosomal numbers of *burti* and *montanus* may prove informative, because Hooper considered them, along with *humulis*, to be morphologically the most primitive species. (Pizzimenti, 1972, reported a 2n of 24 for *R. montanus*, citing Matthey, 1957. This is evidently an error, because Matthey does not report on *R. montanus*, and the morphology reported by Pizzimenti is identical to that given by Matthey for *Microtus montanus*.) In addition, species allied to *mexicanus* and *creper* must be investigated to determine if the mainly acrocentric, 2n = 52 pattern is ubiquitous for that group. The wide range in diploid numbers (2n = 38–52), coupled with the diversity in chromosomal morphology (all-acrocentric, intermediate, and all-metacentric karyotypes), exhibited by harvest mice offers a convenient system for investigating mechanisms of chromosomal change, perhaps through the use of banding techniques such as those employed in studies of *Neotoma* (Mascarello et al., 1974*a*, 1974*b*; Mascarello and Hsu, 1976).

The genus *Reithrodontomys* embraces relatively few species but great morphological and ecological diversity. As noted by Hooper (1952), the extreme forms are so different (consider the large size, long tail, complex dentition, and high elevation, cloud-forest habitat of *R. creper* versus the small size, short tail, simple dentition, and low elevation, grassland habitat of *R. montanus*) that we would hesitate to relate them in the same genus, except that their morphologies and ecologies are connected through a graded series of intermediate species. Moreover, some of the morphological dissimilarities between species of *Reithrodontomys* approach the amount of differ-

ence that often marks different genera or even generic groups of Muridae, including complex and simple dental patterns (Hooper, 1952; Hershkovitz, 1962), and hemiglandular and discoglandular stomachs (Carleton, 1973).

The results reported herein demonstrate substantial karyotypic variation within the genus *Reithrodontomys*. Understanding the selective context in which these differences between species evolved may contribute greater insight to character trends within the Muridae.

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