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CHROMOSOMAL FISSIONS AND PHYLOGENETIC HYPOTHESES: CYTOGENETIC AND ALLOZYMIC VARIATION AMONG SPECIES OF MERIONES (RODENTIA: GERBILLIDAE)

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Phylogenetic hypotheses based on morphological data for many groups of higher vertebrates have been re-examined using data derived from G-banded chromosomes. Studies of G-banded chromosomes are important because G-bands reflect genetic homology and because such data can be useful in understanding relationships among taxa as well as rates of chromosomal evolution (Baker *et al.*, 1987). The use of independent data sets generally is beneficial for several reasons. First, an inherent lack of resolution from one data set at some level of the phylogeny can be offset by using another data set that provides resolution at that level (Arnold *et al.*, 1982). Second, independent data allow for choices between equally or almost equally parsimonious explanations of a data set. Third, using independent data sets can resolve character conflicts by identifying character states that need to be reexamined. However, an independent data set can produce a phylogenetic hypothesis that is quite different from that being tested and thus additional data and re-analysis of available data may be required.

Relationships within the genus *Meriones* have been controversial. Morphological criteria based on such characters as size and shape of the bullae (Chaworth-Musters and Ellerman, 1947; Ellerman, 1941; Pavlinov, 1982) have been questioned as potentially convergent characters by authors who examined nondifferentially stained

chromosomes (Nadler and Lay, 1968; Wahrman *et al.*, 1988). Benazzou *et al.* (1982a, 1982b, 1984) presented data for R-banded chromosomes of six species of *Meriones* and produced trees of relationships of these and other genera of gerbils based on the assumption that "common equals primitive." Benazzou *et al.* (1982b) stated that either *M. tristrami* possesses an ancestral karyotype of high diploid number and those of other species of *Meriones* were derived by fusions or, alternatively, that species with high diploid numbers of chromosomes arose from ancestors having low diploid numbers by chromosomal fissions. However, the outgroup method in chromosomal analyses is preferred over "commonality" on both empirical and philosophical grounds and the two methods can yield different phylogenies (Qumsiyeh and Baker, 1988). Qumsiyeh *et al.* (1988) presented G-band data for two species of *Meriones* (*shawi* and *unguiculatus*, both with $2n = 44$), *Psammomys obesus* ($2n = 48$), *Sekeetamys calurus* ($2n = 38$), and *Desmodillus auricularis* ($2n = 52$). In that study, the outgroup method was used to analyze chromosomal data and to compare the resulting phylogeny to an electrophoretic data set from the same specimens to arrive at conclusions regarding the rates of protein and chromosomal evolution in these taxa. I herein address data on G-band and allozymic variation of *Meriones crassus* ($2n = 60$) and *M. tristrami* ($2n = 72$) and re-evaluate all previously published data on this group in light of the new information.

MATERIALS AND METHODS

Chromosomal Analyses

G-banding on two species of *Meriones* (*M. tristrami* and *M. crassus*) was performed by the method of Lee and Elder (1980) as modified by Baker and Qumsiyeh (1988). Specimens examined for these two species of *Meriones* are as follows (all voucher material deposited at Texas Tech University). *Meriones tristrami*: Jordan, Amman Gov., Al Muwaqqar, 22 km. E Amman (1 ♂, 1 ♀); Al Ghor, Ghor nimrin, near King Hussein Bridge (2 ♂♂); Northern Gov., 10 km. E Irbid (3 ♂♂, 5 ♀♀). *Meriones crassus*: Jordan, Amman Gov., Al Azraq, 5 km. W Azraq (1 ♂); Egypt, Sinai Gov., El Tor (1 ♂, 1 ♀ born in captivity).

Identification of G-band sequences from gerbils was facilitated by using a standard numbering system developed for gerbil chromosomal arms or linkage groups (Qumsiyeh, 1986). Side-by-side comparisons of all chromosomes and chromosomal arms were performed first between metaphases of the same individual, then between those of individuals of the same species, and finally between those of different species and genera. The original karyotypes from several individuals

of taxa previously examined (Qumsiyeh and Chesser, 1988) were re-analyzed in light of data presented here on *Meriones crassus* and *M. tristrami*. Additionally, the availability of the G-banded chromosomes of *Meriones tristrami* allowed comparison of numbering systems and identifying homologies to the R-band data of species studied by Benazzou *et al.* (1982a, 1982b, 1984), because these latter studies used the R-band karyotype of *M. tristrami* for a standard numbering system. Thus, postulated chromosomal rearrangements can be re-evaluated and data added for two species of *Meriones* (*libycus* and *persicus*) by using R-band homologies. Based on comparisons of karyotypes and banding patterns, only a few discrepancies were found in identifying chromosomal rearrangements between my studies and those of Benazzou *et al.* (1982a, 1982b, 1984). These are further discussed in the results section.

Abbreviations used in figures are as follows: DAU, *Desmodillus auricularis*; MCR, *Meriones crassus*; MLI, *M. libycus*; MPE, *M. persicus*; MSH, *M. shawi*; MTR, *M. tristrami*; MUN, *M. unguiculatus*; POB, *Psammodmys obesus*; SCA, *Sekeetamys calurus*; FU, centric fusion; FI, centric fission; EU +, euchromatic addition; PAI, paracentric inversion; PEI, pericentric inversion; d, distal; p, proximal. These abbreviations are used in conjunction with chromosome numbers referring to the proposed homology and standard numbering system for gerbil G-band chromosomal segments (Qumsiyeh, 1986).

Electrophoretic Analyses

Thirty-two presumed loci were assayed by starch gel electrophoresis for the same taxa and individuals used in the chromosomal analysis. Electrophoretic loci examined, abbreviations for loci, techniques, and analyses were as described by Qumsiyeh and Chesser (1988). However, a uniform nomenclature that would change names used for some enzymes has been recommended by the International Union of Biochemistry (1984) as follows: aconitase hydratase (for aconitase), dihydrolipoamide dehydrogenase (diaphorase), fumarate hydratase (fumarase), and aspartate aminotransferase (glutamine oxaloacetate transaminase). Allele frequency data were used to calculate genetic similarities and distances (Rogers, 1972). Matrices of distance values were used to construct trees by the Fitch and Margoliash (1967) algorithm. Cladistic analyses were performed by coding allelic variants as character states and the analyses were performed using a Wagner algorithm (Farris, 1970, 1978), and then subjected to multiple branch swappings using the computer program MacClade (Wayne Maddison and David Maddison). Character state changes were coded as unordered (that is, a change from any state to any other state was

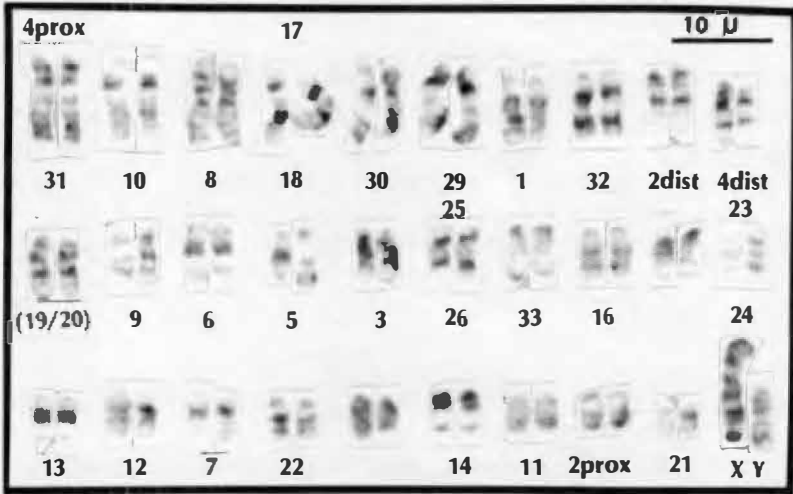


FIG. 1.—G-banded karyotype of a male *Meriones crassus*. Chromosome numbers in this and other figures and tables refer to standard gerbil linkage groups (Qumsiyeh, 1986; Qumsiyeh and Chesser, 1988).

allowed and counted as one step) because there are no *a priori* reasons to polarize transformation series for electrophoretic data.

RESULTS

Chromosomal Analyses

The karyotypes of *Meriones tristrami* ($2n = 72$, FN = 76-80) and *M. crassus* ($2n = 60$, FN = 72) show extensive homology to each other and most chromosomes can be assigned numbers referring to their homology with those of other gerbils (Qumsiyeh, 1986; Figs. 1- 2). The G-band data from these two species then were compared to G-band data for *Meriones unguiculatus*, *M. shawi* (Jordan), *Psammomys obesus*, *Sekeetamys calurus*, and *Desmodillus auricularis* (Qumsiyeh and Chesser, 1988), and with published R-band data for *Meriones crassus*, *M. tristrami*, *M. shawi* (Morocco), *M. unguiculatus*, *M. libycus*, *M. persicus*, and *Psammomys obesus* (Benazzou *et al.*, 1982a, 1982b, 1984). Results of these studies indicated that, with few exceptions, there is extensive agreement between investigations using G-bands and those using R-bands in identification of chromosomes and rearrangements (Table 1). Using the standard gerbil arm numbering system (Qumsiyeh, 1986), these exceptions are as follows. First, fusion ?/31 in *Psammomys obesus* (Qumsiyeh and Chesser, 1988) is identified as 1/31 based on correspondence with the data of Benazzou *et al.* (1982a, 1984). Second, chromosomes 21/22, 23/24, and 30 are difficult to identify in

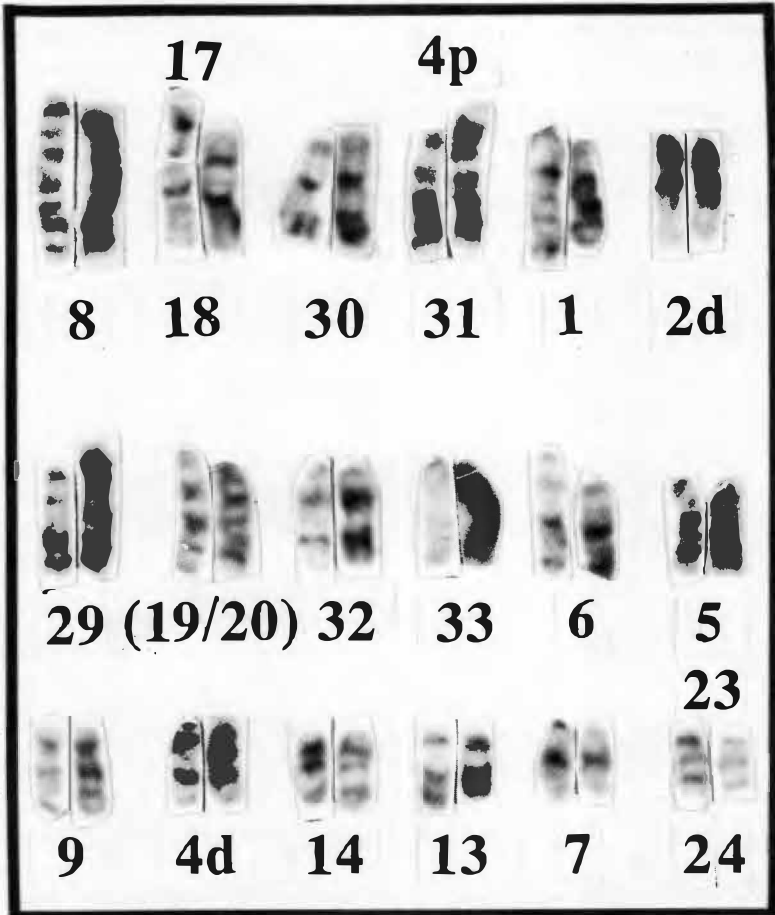


FIG. 2.—Selected chromosomal G-band comparisons between *M. tristrami* (left chromosome of each pair) and *M. crassus*.

R-banding and were either unassigned or misidentified in some taxa reported by Benazzou *et al.* (1982 *a*, 1982*b*).

However, discrepancies between the G-band data for *M. shawi* from Jordan and the R-band data for *M. shawi* from Morocco (Benazzou *et al.*, 1982*b*) clearly were not technical, but rather are due to unique rearrangement differences between the two samples. Unlike the Jordanian *M. shawi* (shown in Table 1), the Moroccan specimen differs by the presence of fused chromosomal arms 1/2d and 5/33 and the absence of fusion 9/31. Because I do not have access to the voucher specimen from Morocco, it is difficult to determine if these karyotypic differences are due to intraspecific variation or if the Moroccan specimen belongs to another species. My results (Table 1) show three

TABLE 1.—Chromosomal characteristics for six species of *Meriones*. All numbers refer to proposed homology based on standard numbering system for linkage groups in Gerbillidae proposed earlier (Qumsiyeh, 1986) except column listing the corresponding standard numbers of Benazzou et al. (1982 a, 1982 b, 1984). Two numbers separated by a comma indicate separate linkage groups; the same separated by a slash indicate the two are fused. The data for *M. shawi* is for Jordanian specimens (Qumsiyeh and Chesser, 1988) and not for the Moroccan specimen (Benazzou et al., 1982 b).

| Taxa and chromosomal character states | | | | | | | |
|---------------------------------------|-----------------|----------------|------------------|---------------------|--------------|----------------|-----------------|
| Linkage group | Benazzou number | <i>crassus</i> | <i>tristrami</i> | <i>unguiculatus</i> | <i>shawi</i> | <i>libycus</i> | <i>persicus</i> |
| 1 | 8 | 1 | 1 | 1(19/20) | 1 | 1 | 1/2d |
| 2p | 29 | 2p | 2p | 2p | 2p | 2p | 2p |
| 2d | 9 | 2d | 2d | 32/2d | 2d | 2d | 1/2d |
| 3/4p | 13/25 | 3,4p/31 | 3,4p | 3/4p | 3/4p | 3/4p | 3/4p |
| 4d | 19 | 4d | 4d | 4d/11 | 4d/11 | 4d/11 | 4d/11 |
| 5 | 11 | 5 | 5 | 5 | 5 | 5/33 | 5/33 |
| 6 | 12 | 6 | 6 | 6/8 | 6(19/20) | 6(19/20) | 6(19/20) |
| 7 | 20 | 7 | 7 | 7/12 | 7/12 | 7/12 | 7/12 |
| 8 | 5 | 8 | 8 | 6/8 | 32/8 | 32/8 | 32/8 |
| 9 | 1 | 9 | 9 | 9(27/28) | (9)/31 | 9/31 | 9 |
| 10 | 24 | EU + 10 | 10 | 10 | 10 | 10 | 16/10 |
| 11 | 26 | 11 | 11 | 4d/11 | 4d/11 | 4d/11 | 4d/11 |
| 12 | 14 | 12 | 12 | 7/12 | 7/12 | 7/12 | 7/12 |
| 13/14 | 21/18 | 13,14 | 13,14 | 13/14 | 13/14 | 13/14 | 13/14 |
| 15/16 | 28/16 | 15,16 | 15,16 | 15,16 | 15,16 | 15,16 | 15,16/10 |
| 17/18 | 27/23 | 17/18 | 17,18 | 17/18 | 17/18 | 17/18 | 17/18 |
| 19/20 | 10 | (19/20) | (19/20) | 1/(19/20) | 6/(19/20) | 6/(19/20) | 6/(19/20) |
| 21/22 | 3 or 4 | 21,22 | 21,22 | 21/22 | 21/22 | 21,22 | 21,22 |
| 23/24 | 35/31 | 23/24 | 23/24 | 23/24 | 23/24 | 23/24 | 23/24 |
| 29 | 17 + 33 | (29) | Fi(29) | (29) | (29) | (29) | (29) |
| 30 | 30 | (30) | (30) | (30) | (30) | (30) | (30) |
| 31 | 6 | 4p/31 | 31 | 31 | (9)/31 | 9/31 | 31 |
| 32 | 7 | 32 | 32 | 32/2d | 32/8 | 32/8 | 32/8 |
| 33 | 22? | 33 | 33 | ?/33 | 33 | 5/33 | 5/33 |

autosomal differences between *M. shawi* and *M. libycus* and confirm the earlier data based on hybridization and nondifferentially stained chromosomes (Lay and Nadler, 1969). Similarly, my data for *M. unguiculatus* identify an acrocentric chromosome 5, and that of Benazzou et al. (1984) shows a fusion 5/33. Although Qumsiyeh et al. (1988) did not identify the small arm fused to 33, it clearly was not 5.

The available chromosomal data for *Meriones* (Table 1) were analyzed in conjunction with data for *Desmodillus auricularis*, *Sekeetamys calurus*,

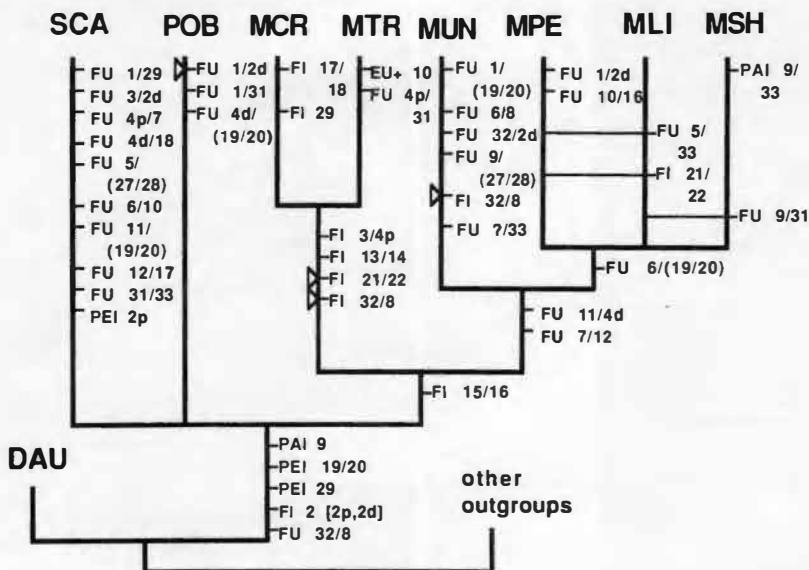


FIG. 3.—A phylogeny for *Meriones*, *Sekeetamys calurus*, *Psammomys obesus*, and *Desmodillius auricularis* based on chromosomal data from Table 1 for *Meriones* and from Qumsiyeh and Chesser (1988) for other genera. Triangles (arrow heads) indicate homoplasies (reversals and convergences). Resolving the trichotomy shown would add additional homoplasies.

Psammomys obesus, and outgroup sigmodontines (Qumsiyeh and Chesser, 1988). Figure 3 shows a resulting tree based on minimizing the number of chromosomal fusions and inversions. In this parsimony analysis, I assumed that the probability of independent fusions to yield the same biarmed condition (convergence in centric fusions) is much lower than the probability of fissions. This is because it is highly unlikely that two identical centric fusions became fixed in two independent lineages.

Electrophoretic Analyses

Of the 32 loci examined, only three (EST, GOT-1, and ICD-1) showed fixed differences among the four species of *Meriones*, whereas 20 were monomorphic for these species (Appendix). EST(100) allele is shared between *M. unguiculatus* and *Psammomys obesus*. The two other unique alleles, GOT-1(105) and ICD-1(80), occur in the two taxa for which I had small sample sizes (*M. unguiculatus* and *M. crassus*, respectively). Comparison of intrageneric (in *Meriones*) genetic distances with those among genera of gerbils suggests a close relationships within *Meriones*. For all these analyses, the data shown in the Appendix were analyzed in combination with the available data for

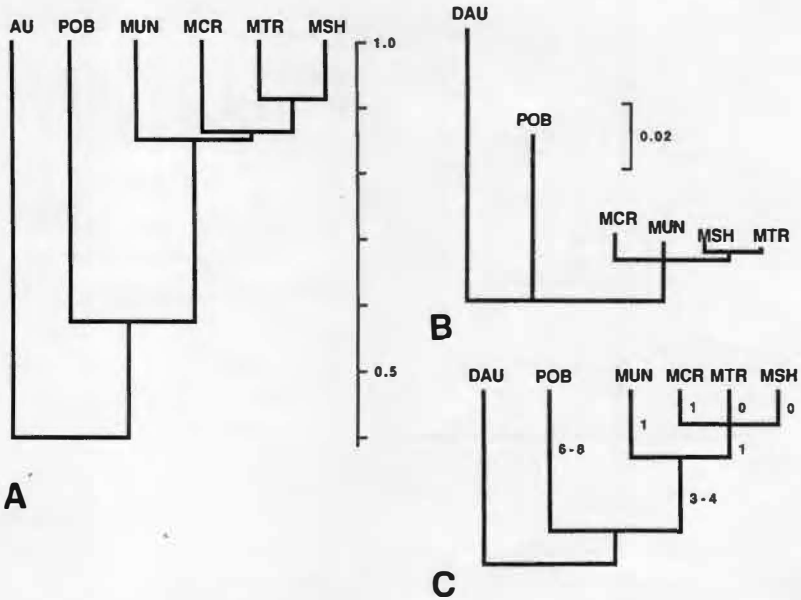


FIG. 4.—Three trees derived from the electrophoretic data: A) a UPGMA tree based on Rogers' similarity values (scale) generated from the allele frequency data; B) a tree based on the Fitch and Margoliash algorithm (1967) with the vertical axes representing branch lengths (indicative of divergence); C) a consensus tree based on cladistic analyses. Numbers indicate fixed differences. See text for discussion.

Desmodillus auricularis (Qumsiyeh and Chesser, 1988). Genetic distances (Rogers, 1972) for pair-wise comparisons of all taxa examined were used to construct a tree based on UPGMA (Fig. 4A). The lowest genetic distance value was between *M. shawi* and *M. tristrami* at 0.078, and all species of *Meriones* were closely clustered. The electrophoretic similarity among the four species of *Meriones* is corroborated by an analysis using the Fitch and Margoliash method (Fig. 4B). Cladistic analyses using a Wagner algorithm (Farris, 1970, 1978) (and optimized using MacClade) produced four tree topologies that could be distilled to a consensus tree (Fig. 4C). These latter cladistic analyses were performed using *Desmodillus* as an outgroup to *Meriones* and *Psammomys* for reasons discussed elsewhere (Qumsiyeh and Chesser, 1988).

All trees derived from the electrophoretic data show that the four species of *Meriones* shared a common ancestor after divergence of *Psammomys* (Fig. 4). Intrageneric relationships of *Meriones* are more difficult to resolve because of the high genetic similarity and the small number of specimens examined of the four species of the genus. However, none of these analyses allied *M. crassus* with *M. tristrami* as

did the chromosomal analysis. The consensus tree in Figure 4C shows that *M. unguiculatus* was the first to branch from the *Meriones* lineage, with the other three species sharing a common ancestor.

DISCUSSION

The use of electrophoretic data in systematics has been discussed at length by Avise (1974) and Buth (1984). The utility of these data in generating a rigorous phylogeny is limited by lack of knowledge about directions of change in electrophoretic mobilities and the small sample sizes used in my studies. The problem of small sample sizes in estimating genetic distances is somewhat ameliorated by increased numbers (32 in this study) of loci (Nei and Roychoudhuri, 1974). However, the problem of determining polarity in polymorphic loci is more serious (Qumsiyeh *et al.*, 1988). With these limitations in mind, the following conclusions about the electrophoretic data can be made. There was little differentiation among the four species of *Meriones*, but significant genic differences among *Desmodillus*, *Meriones*, and *Psammomys*. Within *Meriones*, a close association of *M. shawi*, *M. crassus*, and *M. tristrami* was manifested in both phenetic and cladistic analyses of the electrophoretic data (albeit no fixed differences). The electrophoretic data thus is concordant with previous hypotheses based on morphologic evidence in two aspects. First, previous authors (Chaworth-Musters and Ellerman, 1947; Corbet, 1978; Pavlinov, 1982) have agreed that the genus *Meriones* is a well-defined and monophyletic genus. Second, the divergence of *M. unguiculatus* from *M. shawi*, *M. crassus*, and *M. tristrami* also was suggested by the same studies.

Analyses of the G-band data using the outgroup method identified only a single synapomorphy for the genus *Meriones* (Fig. 3). This is in disagreement with analyses using the commonality criterion, which shows the genus *Meriones* as paraphyletic (Benazzou *et al.*, 1982b, 1984). All *Meriones* examined except *M. persicus* belong to the morphologically defined subgenus *Pallasiomys* (Chaworth-Musters and Ellerman, 1947). Clearly, *M. persicus* cannot be identified as distinct from the other five species on chromosomal grounds (Fig. 3). It would be interesting to obtain electrophoretic data for *M. persicus* to see if it can be distinguished by that method. The four species for which I had tissues are genetically similar (Fig. 4). In either case, if strict parsimony is followed, the chromosomal phylogeny would suggest that the morphologic change that defined the genus *Meriones* (Chaworth-Musters and Ellerman, 1947; Pavlinov, 1982) was accompanied by electrophoretic changes and few chromosomal changes. More importantly, a conflict exists between the chromosomal

phylogeny (Fig. 3) and electrophoretic and morphologic data relating to the interrelationships of the four species of *Meriones* for which both electrophoretic and chromosomal data are available (*M. unguiculatus*, *M. shawi*, *M. crassus*, and *M. tristrami*). Chromosomally, two groups exist representing a low as opposed to a high diploid number (Fig. 3). Neither grouping is substantiated by either morphologic (Chaworth-Musters and Ellerman, 1947; Pavlinov, 1982) or (with the reservations discussed above) electrophoretic data (Fig. 4).

The chromosomal data presented demonstrate numerous homoplasies in Robertsonian rearrangements. As suggested earlier for another group of gerbils (Qumsiyeh *et al.*, 1987), this situation can be conducive to arriving at trees that are parsimonious, but not phylogenetically compatible, with other data sets. To alter the chromosomal tree, it is possible to postulate chromosomal synapomorphies (fusions) for *Meriones* that were lost subsequently (reversal) in some taxa. For example, the centric fusion events characterizing *M. unguiculatus*, *M. persicus*, *M. libycus*, and *M. shawi* (11/4d, 7/12, 5/33) also may have been present in the ancestor of *M. crassus* and *M. tristrami*, and subsequently lost as a result of reversal events (fissions). Although this would be a less parsimonious explanation of the chromosomal data than the tree presented (Fig. 3), it is supported by several facts. First, both *M. crassus*, and *M. tristrami* underwent other independent fission events (for example in 3/4p and 13/14) and all or most of the chromosomes in these two species are acrocentric, resulting in high diploid numbers. Second, the tree in Figure 3 already shows numerous homoplasies in Robertsonian rearrangements. Thus, the arrangement of the taxa of *Meriones* can be altered with minimal additional homoplasies. Third, electrophoretic and morphological data sets generally support chromosomal phylogenies in mammals (Arnold *et al.*, 1982; Baker *et al.*, 1987; Qumsiyeh, 1988).

I postulate that the problems of determining relationships using Robertsonian rearrangements demonstrated here for *Meriones* and earlier for *Tatera* and *Gerbillurus* (Qumsiyeh *et al.*, 1987) can be explained by the nature of the rearrangements and in the limitations of the chromosomal G-band analysis. Each species has a limited number of chromosomal arms that could associate (fusions) or dissociate (fissions). This number of arms cannot change unless the species acquires other rearrangements than centric fusions and fissions (for example, pericentric inversions). A taxon with numerous acrocentric elements can produce descendants with differing metacentric chromosomes by centric fusions, a situation that results in monobrachial homology (Baker and Bickham, 1986; Capanna, 1982;

Moritz, 1986; Porter and Sites, 1986). These latter studies addressed the importance of monobrachial homology in establishing reproductive isolation (and potentially speciation) but did not address the possibility of centric fissions occurring subsequent to this differentiation. Robertsonian rearrangements are the most common types of chromosomal rearrangements observed in animals (White, 1978). Additionally, taxa developing monobrachial homology by fusions usually have few other chromosomal changes and little, if any, genic and morphologic change (see Baker and Bickham, 1986, for a review). The reverse process of fissions also would be expected to occur with little additional effect on the taxa involved.

Centric fissions are *a priori* less amenable to documentation by standard comparative cytogenetic methods than are centric fusions. This can be illustrated with a simplified hypothetical situation of Robertsonian fusions in a lineage with four unique autosomes (1-4). The ancestor could produce several descendents with unique chromosomal conditions (for example (1/2, 3/4), (1/3, 2/4), (1/3, 2, 4), and so on). However, if further evolution occurs by fissions in taxa with monobrachial homology, the resulting descendent taxa would have the same chromosomal condition (1, 2, 3, 4) even though the events were different fissions (for example, fission in 1/2 as compared to 1/3 above). Because a fission or a fusion event occurring in a natural population cannot be observed, we are limited to observing the chromosomal conditions in extant taxa that either have fissions (with little or no phylogenetic information) or fusions. Thus, fusions are retained as the informative data points for a chromosomal phylogeny because they can be traced to ancestral conditions. It is not surprising, therefore, that the simplest chromosomal explanations always involve grouping fissioned taxa (those with high diploid numbers) in more primitive branches.

Investigators, of course, are limited by the availability of additional data sets and, in the absence of such data sets, intermediate ancestors with monobrachial homology for taxa with high diploid numbers cannot be proposed. Combination of electrophoretic, morphologic, and chromosomal data thus has allowed illustration of two examples where homoplasy is underestimated when studying genera in which both high and low diploid numbers occur: 1) the relationships of *Gerbillurus* and *Tatera* (Qumsiyeh *et al.*, 1987), and 2) the relationships of species of *Meriones* discussed above.

Recently, a study of chromosome evolution in the family Canidae (Wayne *et al.*, 1987a, 1987b) also produced a dichotomy between high and low diploid number species. Wayne and O'Brien (1987) performed an electrophoretic analysis on the same group of mammals.

Although these authors did not discuss the conflict in the two data sets, this study provides another excellent example of a case of chromosomal fissions obscuring the phylogeny. This can be seen best by the phylogenetic position of the fennec (*Fennecus zerda*), which has a $2n = 64$. In the chromosomal phylogeny, this species is associated with the "high numbered acrocentric species" as opposed to the "low numbered metacentric species," which include other foxes (Wayne *et al.*, 1987b). The chromosomal placement of the fennec could have been obscured in a similar fashion to that of gerbils with high diploid numbers because: 1) the fennec is morphologically nearer to other foxes (Van Gelder, 1978); 2) in an electrophoretic analysis, the fennec clearly can be associated with other foxes and is quite distant from canids with high diploid numbers (Wayne and O'Brien, 1987); and 3) the numerous fissions acquired in canid species (Todd, 1970; Wayne *et al.*, 1987a, 1987b). In light of the above discussion, similar re-analyses of published chromosomal phylogenies in combination with independent data sets on other groups of mammals with high and low diploid numbers would be prudent.

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APPENDIX.—*Allele frequencies for Meriones and Psammomys. Bold face indicates plesiomorphic conditions determined by comparison with data for Desmodillus (Qumsiyeh and Chesser, 1988). All other conditions are derived for Meriones and Psammomys or both, except for loci indicated by an asterisk for which derived conditions could not be determined. Sample sizes in parentheses.*

| Allele | | <i>Meriones tristrami</i> (12) | <i>Meriones crassus</i> (3) | <i>Meriones unguiculatus</i> (2) | <i>Meriones shawii</i> (7) | <i>Psammomys</i> (9) |
|---------------|------|---------------------------------------|------------------------------------|---|-----------------------------------|-------------------------|
| CON | 100 | 1 | 1 | 1 | 1 | .395 |
| | 95 | | | | | .605 |
| AK-1 | 100 | .917 | .833 | 1 | .955 | .947 |
| | 70 | .083 | .167 | | .045 | .053 |
| AK-2 | -100 | 1 | 1 | 1 | 1 | |
| | -150 | | | | | 1 |
| ALB | -100 | 1 | 1 | 1 | .455 | |
| | -110 | | | | .545 | 1 |
| CAT1B | 200 | | | | | 1 |
| | 110 | .056 | .667 | 1 | .818 | |
| | 100 | .944 | .333 | | .182 | |
| CAT2W | 100 | .889 | 1 | 1 | 1 | |
| | 95 | .111 | | | | |
| | 60 | | | | | 1 |
| CK-1 | 100 | 1 | 1 | 1 | 1 | 1 |
| CK-2 | 100 | 1 | 1 | 1 | 1 | 1 |
| CK-3 | 100 | 1 | 1 | 1 | 1 | |
| DIA | 110 | .056 | 1 | 1 | .955 | |
| | 100 | .916 | | | | 1 |
| | 95 | .028 | | | .045 | |
| EST | 120 | | | 1 | | 1 |
| | 100 | .778 | .667 | | .273 | |
| | 105 | | .333 | | | |
| | 95 | .222 | | | .727 | |
| *FUM | 100 | 1 | 1 | 1 | .364 | |
| | -50 | | | | .636 | 1 |
| *GOT-1 | 105 | | | 1 | | |
| | 100 | 1 | 1 | | 1 | |
| | 70 | | | | | 1 |
| GOT-2 | -100 | 1 | 1 | 1 | 1 | |
| | -105 | | | | | 1 |
| GLUD | 100 | .945 | .333 | | .727 | 1 |
| | 95 | .055 | .667 | 1 | .273 | |
| α -GPD | 100 | 1 | 1 | 1 | 1 | 1 |

APPENDIX. — *Continued.*

| Allele | | <i>Meriones tristrami</i> (12) | <i>Meriones crassus</i> (3) | <i>Meriones unguiculatus</i> (2) | <i>Meriones shawii</i> (7) | <i>Psammomys</i> (9) |
|---------|------|---------------------------------------|------------------------------------|---|-----------------------------------|-------------------------|
| ICD-1 | 100 | 1 | | 1 | 1 | 1 |
| | 80 | | 1 | | | |
| ICD-2 | 100 | 1 | 1 | 1 | 1 | 1 |
| LDH-1 | 100 | 1 | 1 | 1 | 1 | 1 |
| LDH-2 | 100 | 1 | 1 | 1 | 1 | 1 |
| MDH-1 | 100 | 1 | 1 | 1 | 1 | 1 |
| MDH-2 | 100 | 1 | 1 | 1 | 1 | 1 |
| MPI-1 | 100 | 1 | 1 | 1 | 1 | 1 |
| MPI-2 | -100 | 1 | 1 | 1 | 1 | |
| | -90 | | | | | 1 |
| PEP-A | 100 | 1 | 1 | 1 | 1 | |
| | 95 | | | | | 1 |
| PEP-B | 100 | 1 | 1 | 1 | 1 | |
| | 90 | | | | | 1 |
| *PEP-C | 100 | 1 | 1 | 1 | 1 | |
| | 80 | | | | | 1 |
| *6PGD-1 | 100 | 1 | 1 | 1 | 1 | 1 |
| 6PGD-2 | 100 | 1 | 1 | 1 | 1 | .921 |
| | 90 | | | | | .079 |
| *PGM | 200 | | | | | 1 |
| | 100 | 1 | 1 | 1 | 1 | |
| SOD | 140 | | | | | 1 |
| | 100 | .945 | 1 | 1 | 1 | |
| | 50 | .055 | | | | |
| TRF | 100 | .111 | 1 | 1 | 1 | 1 |
| | 98 | .889 | | | | |