

## CHROMOSOMAL EVOLUTION IN *GEOMYS* AS REVEALED BY G- AND C-BAND ANALYSIS

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**ABSTRACT**—We examined G- and C-banded karyotypes of five species of *Geomys* (*G. tropicalis*, *G. pinetis*, *G. personatus*, *G. breviceps*, *G. bursarius*) and three cytotypes of *G. bursarius* (*G. b. lutescens*, *G. b. major*, and *G. b. knoxjonesi*). Our results indicate extensive euchromatic and heterochromatic variation in this genus, in excess of what was predicted by nondifferentially-stained karyotypes. All the taxa of *Geomys* examined had heterochromatin on numerous chromosomes, in addition to the usual pericentric heterochromatin observed in mammals. Although the quality of our G-bands did not permit elucidation of all euchromatic changes, it is clear from the data that euchromatic rearrangements in this genus were extensive and included both Robertsonian and non-Robertsonian rearrangements.

There is considerable chromosomal evolution within the genus *Geomys* with most of the subspecies and species having distinctive nondifferentially-stained karyotypes (e.g., Davis et al., 1971; Baker et al., 1973; Selander et al., 1974). The magnitude of change that distinguishes the various forms ranges from subtle to extensive. For example, the karyotype of *Geomys bursarius knoxjonesi*,  $2n = 70$ ,  $fn = 68$ , could have evolved from *G. b. major* by a single translocation (Baker and Genoways, 1975; Pembleton and Baker, 1978). Similarly, the karyotype of *Geomys breviceps*,  $2n = 74$ ,  $fn = 72$ , could evolve to the *G. b. major* karyotype by single translocation of an autosome and an inversion of its subtelo-centric X chromosome to an acrocentric X.

Conversely, the karyotype diversity of *G. b. lutescens*, *Geomys arenarius*, and *Geomys tropicalis*, would require extensive chromosomal evolution. The broad range of karyotype forms found within *Geomys* make it an ideal assemblage to analyze in more detail using G- and C-banding techniques. The higher degree of resolution offered by G- and C-banding should allow the elucidation of specific events in the evolution of the karyotype of *Geomys* at a level not possible with nondifferentially-stained chromosomes. Answers to several questions relative to direction of chromosomal evolution and stability of the karyotype can be addressed with these data. Do the nondifferentially-stained karyotypes of *Geomys pinetis* and *G. tropicalis* ( $2n = 42$  and  $38$ , respectively), which are similar to the closely related genera *Cratogeomys*, *Orthogeomys*, and *Zygogeomys* (Honeycutt and Williams, 1982), actually represent a primitive karyotype for the Geomyini? Does the high degree of variability in fundamental number ( $fn = 72$  to  $100+$ ) of *G. bursarius* (sensu lato) represent variation in constitutive heterochromatin or pericentric inversions or both? Given the high propensity for small variation (e.g., in  $fn$ ) within and among populations of *Geomys*, what is

the magnitude of chromosomal evolution in this genus? Finally, can the observed variation be used to generate a chromosome-based phylogeny for *Geomys*?

**MATERIALS AND METHODS**—The problem encountered in producing quality G- and C-band data for geomyid rodents is a lack of chromosomal spreading, compounded by high diploid numbers and, thus, many overlapping chromosomes in late prophases or early metaphases. We used two methods to increase chromosome spreading: 1) lengthening the time of the hypotonic treatment; 2) better fixation with cold Carnoy's (methanol/acetic acid) fixative (Baker and Qumsiyeh, in press). Best results were obtained at 27 min in 0.075 M KCl and at least 3 to 4 washes with cold Carnoy's fixative.

Other than these modifications, our methods for producing G- and C-banded chromosomes from bone marrow cells were as described by Lee and Elder (1980) and Baker and Qumsiyeh (in press). Primary conclusions for the G-band characteristics of an individual were made using complete diploid cells. Chromosomes were arranged by centric position and relative size. Specimens examined for this study are deposited at The Museum, Texas Tech University, and numbers listed for specimens examined are karyotype (TK) numbers.

Abbreviations and symbols used are as follows. Slash (/), in conjunction with arm numbers, indicates centric fusion; H+, heterochromatic addition; mod., modified condition of the numbered autosome by an unknown rearrangement; Tr., translocation; To, addition of heterochromatin or euchromatin to the numbered chromosome; A, an autosome found in some *Geomys* species that could not be related to the standardized numbered autosomes of *G. breviceps*.

**Specimens Examined**—*Geomys bursarius knoxjonesi*, Texas, Terry Co., 7.3 mi. W. Brownfield (20389 female, 20392 female); *G. b. major*, Texas, McLennan Co., Waco (24934 male, 24933 female); *Geomys b. lutescens*, Nebraska, Antelope Co. (27156 male, 27157 female, 27158 male, 27159 female, 27161 male); Nebraska, Wheeler Co. (27160 female); *G. breviceps*, Texas, Milam Co., 1.5 mi. W Maysfield (24931 female, 24932 male); *G. personatus*, Texas, Hidalgo Co., 11 mi. N, 5 mi. W, Hidalgo (24926 male, 24927 female, 24928 female); *G. pinetis*, Florida, Volusia Co., 5 mi. SE DeLand (24929 female, 24930 female); *G. tropicalis*, Mexico, Tamaulipas, 3.5 mi. SE Altamira (27117 female, 27118 male, 27119 male).

**RESULTS**—Diploid and fundamental numbers from our samples were identical to those previously reported in the literature (Table 1). Representative G- and C-banded chromosomal complements of some *Geomys* species from previous studies are shown in Figs. 1-6.

We have chosen the karyotype of *G. breviceps* ( $2n = 74$ ;  $fn = 72$ ; Fig. 1) for a standardized numbering system for *Geomys* chromosomes, because it consists of all acrocentric autosomes and shows the highest diploid number among the species we examined (thus allowing a maximum number of identified "linkage groups").

**C-band Variation**—The karyotypes of both *G. breviceps* and *G. personatus* ( $2n = 70$ ,  $fn = 78$ ) had large amounts of heterochromatin as revealed by C-banding relative to other mammals (Hsu and Arrighi, 1971; Fig. 2). In *G. breviceps* large blocks of heterochromatin were situated between centromeric regions and euchromatic arms. In addition, there were three pairs of autosomes that appeared to be totally heterochromatic (Fig. 2A). *Geomys personatus* had extensive heterochromatin on 11 pairs of autosomes (Fig. 2B). The C-banded chromosomes of *G. bursarius major* were similar to those of *G. breviceps* in the presence of large centromeric heterochromatic blocks. However, in *G. b. major*, these regions showed mostly G-negative staining (Fig. 3A). *Geomys b. lutescens* has many biarmed chromosomes (Hendrickson, 1972). In specimens of this form ( $2n = 72$ ,  $fn = 92$ ), all biarmed autosomes possessed at least one totally

TABLE 1—Karyotypic data for species of *Geomys* based on nondifferentially-stained chromosomes. Chromosome groups and variation in *Geomys bursarius* are more complex than listed here and are discussed by Hart (1978).

Taxon	2n	fn	No. of biarmed autosomes	Authority
<i>Geomys bursarius</i>	70,72,74	68-74	0-6	Kim, 1972 (as cited by Selander et al., 1974)
<i>G. b. knoxjonesi</i> (Race A)	70	68	0	Baker et al., 1973
<i>G. b. knoxjonesi</i> (Race B)	70	70	2	Baker and Genoways, 1975
<i>G. b. major</i> (Race C)	70-72	72	2-4	Baker et al., 1973
<i>G. b. major</i> (Race D)	70-72	70	0-2	Baker et al., 1973
<i>G. b. bursarius</i> (= <i>majusculus</i> )	70	68	0	Hendrickson, 1972 Hart, 1978 Timm et al., 1982
<i>G. b. lutescus</i>	72	86-98	16-28	Hendrickson, 1972 Hart, 1978 Timm et al., 1982
<i>G. b. jugossicularis</i>	72	72	2	Hart, 1971
<i>G. b. attwateri</i>	70	72	4	Hart, 1978 Honeycutt and Schmidly, 1979
<i>G. arenarinus</i>	70	102	34	Davis et al., 1971
<i>G. personatus</i>	68-70	68-74	2-6	Davis et al., 1971 Kim, 1972 (as cited by Selander et al., 1974)
<i>G. pinetis</i>	42	80	40	Williams and Genoways, 1975
<i>G. tropicalis</i>	38	72	36	Davis et al., 1971

heterchromatic arm (Fig. 3A), with the exception of the smallest metacentric autosome. The karyotype of *G. pinetis* ( $2n = 42$ ,  $fn = 80$ ; Fig. 3B) has extensive long-arm regions that are C-positive as well as having C-positive material associated with the centromeres.

*G-band Variation*—Homology between *G. bursarius knoxjonesi* ( $2n = 70$ ,  $fn = 68$ ) and *G. breviceps* ( $2n = 74$ ,  $fn = 72$ ) could be determined only for the largest 21 pairs of autosomes of the *G. breviceps* karyotype (Fig. 4). This comparison represented the largest number of autosomes in which homology could be ascertained between any two forms in this study. Ten autosomes are proposed as homologous between *G. bursarius major* and *G. breviceps*, and fifteen autosomes appear homologous between *G. personatus* and *G. breviceps* (Fig. 5). The G-banded karyotypes of *G. pinetis* (Fig. 6A) and *G. tropicalis* ( $2n = 38$ ,  $fn = 72$ ; Fig. 6B) show little homology to each other and to the *G. breviceps* standard. The unique chromosome arms that can be identified as homologous between *G. pinetis* and *G. tropicalis* (e.g., arms 17, 4, and 3) are present in different biarmed combinations.

Only three chromosomes were found to be shared by two or more taxa which were not also homologous to those in *G. breviceps* as follows. First, the acrocentric X shared between *G. bursarius knoxjonesi* and *G. b. major* appear to be derived from the metacentric X of *G. breviceps* by a simple inversion event. The X of *G. b. lutescus* is a biarmed element, but the

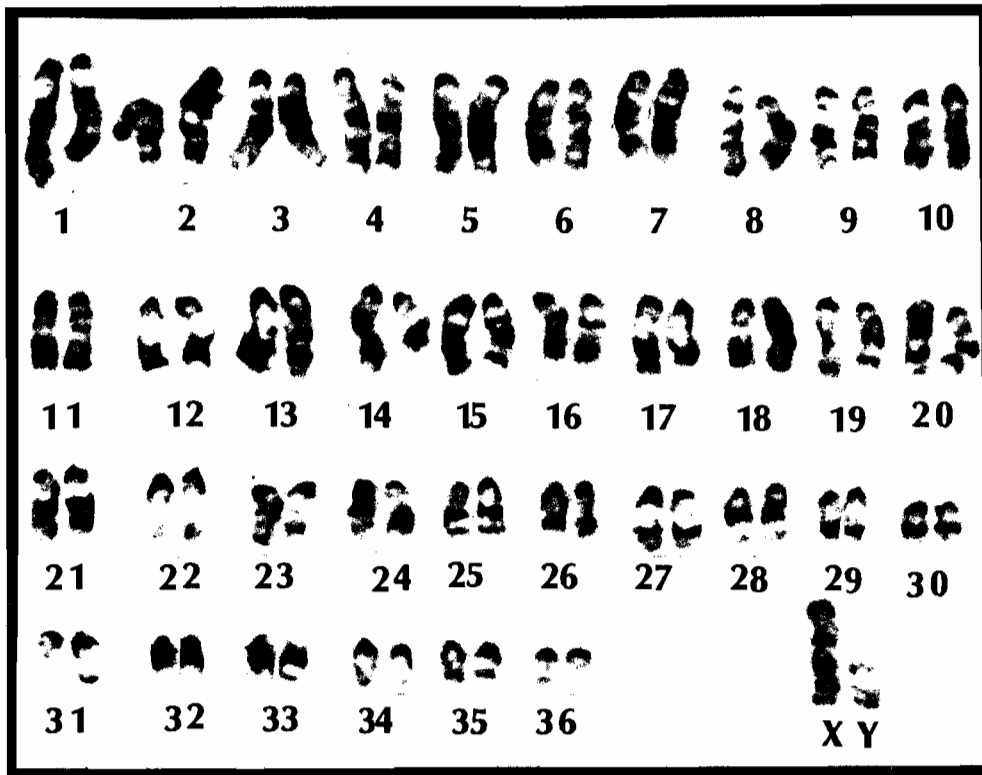


FIG. 1—G-banded karyotype of a male *Geomys breviceps* used for a standardized numbering system for *Geomys* chromosomes.

small arm appears totally heterochromatic. Therefore, the acrocentric condition of the euchromatic portion of the X appears to be shared by all examined forms of *G. bursarius*. Second, chromosome "A" (see Figs. 4 and 5) is shared by *G. personatus*, *G. b. knoxjonesi*, and *G. b. major*. To summarize the chromosomal G- and C-band data of Figs. 1-6, the following chromosomes were identified as homologous between the taxa examined and thus could be related to the numbering system in *G. breviceps*: 1) *G. bursarius knoxjonesi*; 1 to 11, H + 12, 13, modified 14, and 15 to 21; 2) *G. b. major*; 1 to 8, 10, modified 14, and 15; 3) *G. personatus*; 1 to 6, 8, 9, to 11, and 14 to 16; 4) *G. pinetis*; 2/4, H + 1, H + 12, 17/3, 21/14; 5) *G. tropicalis*; ?/2, ?/1, 17/4, ?/5, 2/3, and 4/6.

**DISCUSSION—Pattern of Chromosomal Change Not Evident in Nondifferentially-stained Karyotypes**—A goal of this study was to determine if nondifferentially-stained karyotypes were accurate indicators of the pattern of chromosomal evolution that distinguishes the various cytotypes. Our data document that, for chromosomal races of *Geomys*, nondifferentially-stained karyotypes are ineffective indicators of the magnitude of chromosomal evolution. For example, among *G. bursarius major* and *G. b. knoxjonesi*, variation in nondifferentially-stained karyotypes can be explained by a single chromosomal rearrangement. However, G- and C-band data document that as few as 11 pairs of autosomes may be homologous and that as many as 23 pairs of autosomes may be altered by

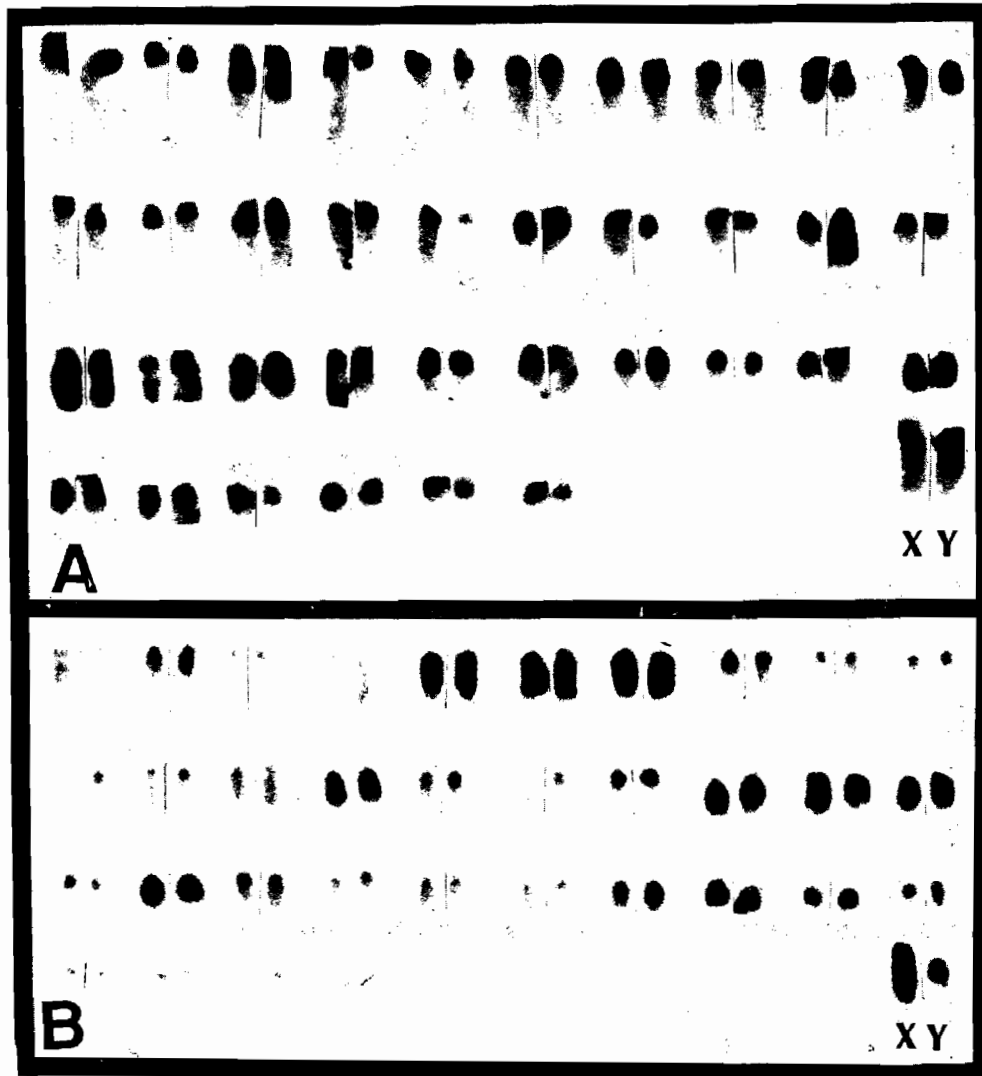


FIG. 2.—C-banded karyotypes of a male *Geomys breviceps* (A) and a male *Geomys personatus* (B). The identification of the X chromosome in this figure is tentative, and it is likely that the X shows less heterochromatin than indicated.

some type of chromosomal change (primarily but not restricted to heterochromatic additions). It is easier to propose homology between karyotypes of *G. b. knoxjonesi* and *G. breviceps* (which vary more in nondifferentially-stained chromosomes) than it is to propose homology between karyotypes of *G. b. knoxjonesi* and *G. b. major*. This should not be taken as indicating a close phylogenetic relationship between *G. b. knoxjonesi* and *G. breviceps* because many of the proposed shared homologous elements are probably primitive. Another example is the difference in arm combinations and heterochromatic variation between *G. pinetis* and *G. tropicalis* with low diploid numbers (Fig. 6). Other examples can be seen by comparing diploid and fundamental numbers in Table 1 with the magnitude of change required to explain differences demonstrated in Figs. 1-6.



FIG. 3—(A) C-banded karyotype of a male *Geomys bursarius lutescens* from the hybrid zone in Antelope Co., Nebraska. Notice G-negative material proximal to centromere representing heterochromatin. (B) C-banded karyotype of *Geomys pinetis*.



FIG. 4—Partial comparison of haploid complements from *Geomys bursarius knoxjonesi* (chromosome on left of each pair) and the largest 21 autosomes of *Geomys breviceps* (chromosome on right of each pair). The remainder of the haploid autosomal complement of *G. b. knoxjonesi* is shown on bottom row.

*Heterochromatic Variation in the Genus Geomys*—We demonstrated that species and subspecies of *Geomys* have extensive amounts of constitutive heterochromatin (C-band positive material). Regions of chromosomes which stain positively with the C-banding technique contain large amounts of highly repetitive DNA (Arrighi et al., 1970). Variation in the type and quantity of these repetitive DNA sequences remain unexplained with views ranging from considering these as “junk” DNA with no selective value to being important for chromosomal evolution and speciation (Cavalier-Smith, 1985; Deininger and Daniels, 1986; Hardman, 1986; Sessions, 1986). Whatever the forces that regulate the amount of heterochromatin in a karyotype, it is obvious that they have played a major role in karyotype variation among members of the *Geomys* complex. In different taxa of *Geomys*, constitutive heterochromatin was found 1) as the major component of a number of acrocentric chromosomes, 2) as short or long arm additions, 3) as centromeric heterochromatin, and 4) occasionally as interstitial blocks. The high fundamental number of *G. b. lutescens* seems



FIG. 5.—G-banded karyotypes of *Geomys bursarius major* (A), and *Geomys personatus* (B). Numbers refer to proposed homologous chromosomes compared with the standard karyotype shown in Fig. 1.

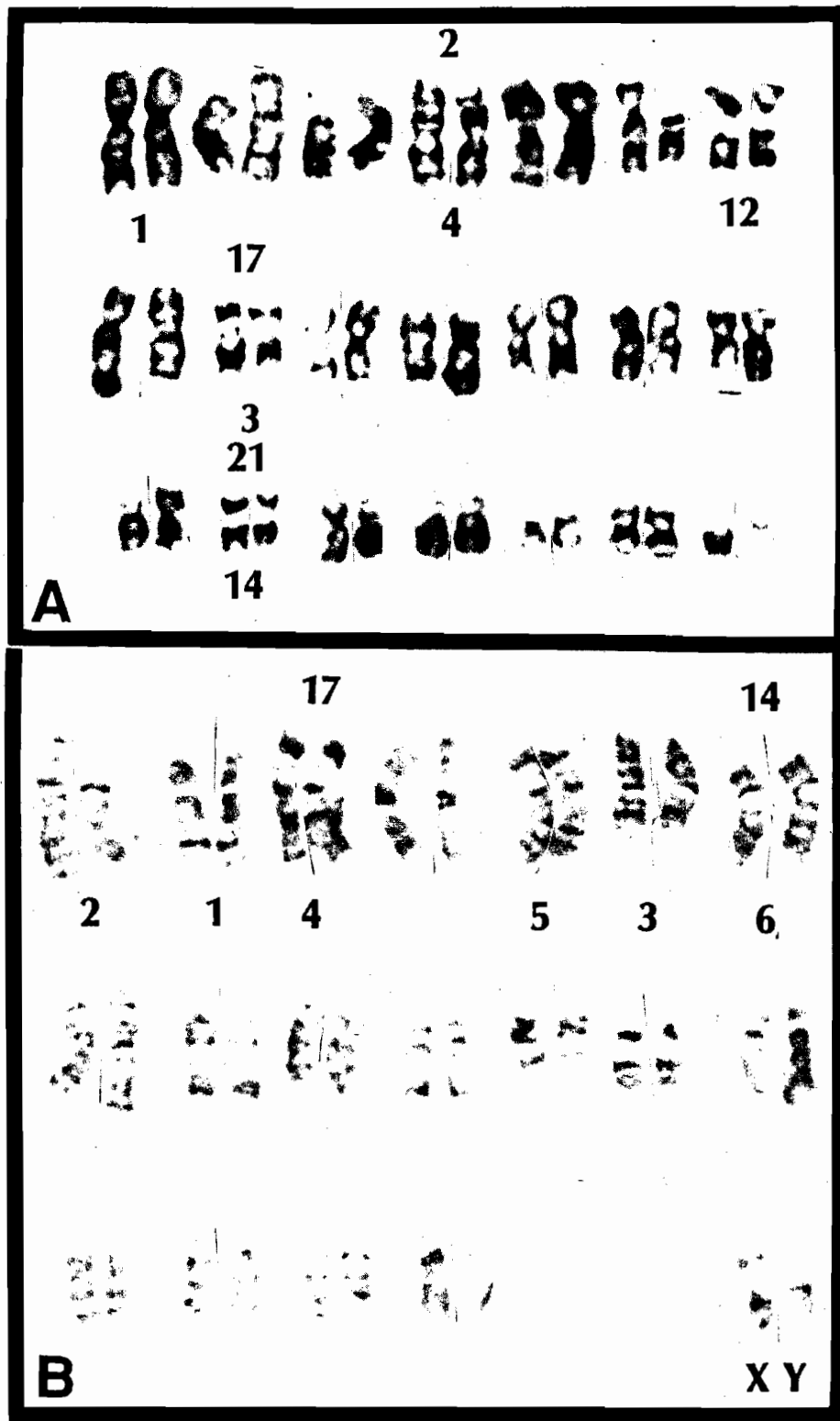


FIG. 6—(A) G-banded karyotype of female *Geomys pinetis*. Because no males were examined, the identity of the sex chromosomes cannot be ascertained. (B) G-banded karyotype of male *Geomys tropicalis*.

to be the result of numerous heterochromatic short-arm additions, with one chromosome perhaps resulting from a euchromatic inversion. Because outgroups such as *Cratogeomys* (Lee, 1985) and most other mammals (Baker et al., 1987) have less heterochromatin, we hypothesize that an increase in amount of heterochromatin is a derived condition.

*Euchromatic Variation in the Genus Geomys*—Because of the extensive amount of heterochromatin, few euchromatic rearrangements could be established in this study. Critical to phylogenetic application of chromosomal data is the establishment of a transformation series (primitive and derived rearrangements). A recent study of the G-bands of *Cratogeomys* (Lee, 1985) provided us with an outgroup, but few G-band sequences could be identified with *Geomys*. Two banded chromosomes in *G. pinetis* were identical to those found in *Cratogeomys* and, thus, are proposed as primitive chromosomal conditions (numbers 17/3 and 21/14). The karyotype of *G. tropicalis* contains the banded conditions 2/3, 17/4, and 14/6 as derived conditions. These arm combinations could have been produced by reciprocal translocations from conditions such as those found in *G. pinetis* or by independent fusions of acrocentric elements produced by fissions in the ancestor of all *Geomys* except *G. pinetis*. The acrocentric conditions of these chromosomes occur unchanged in the remaining *Geomys* examined (*G. bursarius*, *G. breviceps*, and *G. personatus*), with the exceptions of translocations to 17 in *G. personatus* and 3 in *G. b. major* (Fig. 3) representing unique derived conditions (autapomorphies). Numerous other autapomorphic conditions exist in each species of *Geomys* examined (Figs. 1-6, see results sections). These are mostly heterochromatic additions, but euchromatic rearrangements also are hypothesized to have occurred because of the differences in G-banding patterns observed. One autosome (labeled A) is found only in *G. personatus* and some members of the *G. bursarius* group and may indicate common ancestry for these two species.

*Evolutionary and Phylogenetic Considerations*—The systematic relationships of the six currently recognized species of the genus *Geomys* were addressed by Merriam (1895) who concluded that *G. bursarius* is most closely related to *G. lutescens* followed by *G. pinetis* and then the *G. breviceps* group. Russell (1968) suggested that *G. bursarius* group (including *lutescens* and *breviceps*) were related first to *arenarius* then to *personatus* and are independent of *G. pinetis*. Selander et al. (1974) indicated that *G. personatus* and *G. bursarius* are genically (based on allozyme data) closer to each other than to *G. tropicalis*.

Martin (1974a, 1974b) and Martin and Webb (1974) inferred from fossils that *G. personatus* and *G. pinetis* are more closely related and could be conspecific. Penney and Zimmerman (1970) suggested that *G. arenarius*, *G. personatus*, and *G. tropicalis* differentiated independently from *G. bursarius*. Finally, Heaney and Timm (1983) recognized *G. bursarius* as specifically distinct from *G. lutescens*, and they also concluded that *G. bursarius*, *G. lutescens*, *G. breviceps*, and *G. personatus* are more closely related to each other than to *G. pinetis*. A goal of this study was to estimate the form and polarity of chromosomal evolution in *Geomys*. Although

these data are a preliminary overview, a number of interesting points appear to be emerging. Based on parsimony and because *G. pinetis* shares two banded autosomes with outgroups, the karyotype of *G. pinetis* likely contains at least some primitive banded elements for *Geomys*. The number of primitive banded elements for *Geomys* cannot be determined, but, based on this analysis and a comparison with the condition of *Orthogeomys*, *Cratogeomys*, and *Zygozomys*, the karyotype of *G. pinetis* may not be too different from that primitive for the genus. Due to the scarcity of outgroup chromosomes for *Geomys*, the actual number of arm arrangements and fissions occurring between *G. pinetis* and the remaining *Geomys* from their common ancestor is unknown. The basal position of *G. pinetis* is concordant with the recent analyses by Heaney and Timm (1983) and restriction endonuclease gene mapping of both rDNA and mtDNA (Davis, 1986).

Although chromosomal banding data available to us were not sufficient to produce a well-documented phylogeny, these data are invaluable evolutionary tools especially when combined with other independent data sets (Baker et al., 1987; Qumsiyeh and Chesser, in press). Two facts remain clear based on our analysis of G- and C-banded chromosomes in *Geomys*. The various taxa show extreme heterogeneity in relative amount of chromosomal rearrangements, and the degree of chromosomal identity between taxa cannot even be approximated by the use of standard karyotypes. This is true even within subspecies. Our data are concordant with data on hybridization in nature of some of the taxa we examined in suggesting a more complex evolutionary history than would have been predicted by nondifferentially-stained karyotypes (Hendrickson, 1972; Pemberton and Baker, 1978; Timm et al., 1982). Further studies using high resolution chromosome banding and gene mapping are needed to fully understand chromosomal evolution in *Geomys*.

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