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Rapidly evolving repetitive DNAs in a conservative genome: a test of factors that affect chromosomal evolution

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The hypothesis that tandemly repeated DNA sequences may facilitate chromosomal rearrangements was tested by comparing a conservatively evolving karyotype of a bat species (*Macrotus waterhousii*) with data published for a rapidly evolving karyotype of an equid species (*Equus zebra*). Empirical data generated from the phylogenetic screening of rapidly evolving repetitive DNAs from approximately 0.1% of the *M. waterhousii* genome showed only one sequence that was repetitive in *M. waterhousii* but low in copy number or absent from the outgroup *Artibeus jamaicensis*. This compares to 34 such clones containing sequences which were repetitive in *E. zebra* but were low in copy number or absent from the outgroup *Ceratotherium simum*. The bat sequence represents a single family of repeated sequences, whereas six families of sequences were identified in *E. zebra*. Southern blot analysis suggested that the sequence from *M. waterhousii* is interspersed rather than tandemly repeated, as are the sequences in *E. zebra*. These data support the above hypothesis and suggest that species with conservatively evolving karyotypes have fewer numbers and families of rapidly evolving DNA sequences than do species such as the equids that possess a karyotype that is considered to have undergone rapid karyotypic evolution.

Key words: bats, chromosomal evolution, genome organization, repetitive DNA

Introduction

Chromosomal evolution has been the focal point for many systematic and evolutionary investigations; however, little is known about the factors that lead to rapid chromosomal change in one taxon and long periods of stasis in another. Hypotheses which have been proposed to explain variation in the rate of chromosomal evolution range from demographic influences (Wright 1941, Wilson *et al.* 1975, Lande 1979) to genetic and molecular factors (Pathak *et al.* 1973, Hsu *et al.* 1975, Hatch *et al.* 1976, Finnegan *et al.* 1982, Shaw *et al.* 1983, Naveria & Fointdevila 1985, Miro *et al.* 1987, Wurster-Hill *et al.* 1988, Graphodatsky 1989, Baker & Wichman 1990, Meyne *et al.* 1990, Redi *et al.* 1990, Wichman *et al.* 1991). It was recently proposed that rapid chromosomal evolution may be driven by the activity of repetitive DNA sequences (Wichman *et al.* 1991), and specifically that tandemly repeated sequences may facilitate chromosomal rearrangements. Specific predictions of this model are that lineages characterized by rapid karyotypic change, which is facilitated by rearrangements within heterochromatin, will have multiple families of tandem repeats which have actively changed chromosomal fields (Lima-De-Faria, 1980), and which are in a dynamic evolutionary state (*i.e.* are rapidly evolving). Lineages characterized by extreme chromosomal conservation are predicted to have few families of tandemly repeated sequences, and these families are predicted to be restricted to a single chromosomal field. Similar predictions would apply to interspersed repeated sequences if they act to facilitate chromosomal change.

The phylogenetic screening procedure developed by Wichman *et al.* (1985, 1990) to identify rapidly evolving repetitive DNA sequences was used to test this hypothesis in equids, a group of mammals recognized for their rapid rate of chromosomal evolution (Bush *et al.* 1977). To date, five families of rapidly evolving, tandemly repeated DNA sequences have been characterized (Wichman *et al.* 1990, 1991, Hong 1992, Wang 1992). Data from *in situ* hybridization

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studies of tandemly repeated sequences in six species of *Equus* reveal intragenomic movement of these types of sequences among the non-homologous chromosomes and between chromosomal fields (Wichman *et al.* 1991). Southern blot and slot blot analyses indicate that these families have also undergone changes in copy number and sequence organization. These five families of tandemly repeated sequences isolated from *E. zebra* by virtue of their absence in the rhinoceros (*Ceratotherium simum*) appear unrelated at the sequence level (Wang 1992).

Data such as those generated by Wichman *et al.* (1990) document the need for further study on the relationship between rapidly evolving repetitive sequences and rapid karyotypic change. Two stages of study are needed to examine this relationship critically. The first stage (which is presented in this paper) involves a comparison between a taxon that exhibits extreme conservation of karyotypic change and the rapidly evolving condition present in *E. zebra*. The second stage involves a pair-wise comparison of closely related taxa in which one species exhibits extreme conservation of karyotypic change and the other has recently undergone radical reorganization of its euchromatic karyotype (karyotypic megaevolution, Baker & Bickham 1980).

The bat family Phyllostomidae, which contains 46 genera and 140 species (Koopman 1984), offers an ideal situation in which to test both stages described above. The Phyllostomidae contains species with highly conserved karyotypes as well as species that have undergone karyotypic megaevolution (Baker & Bickham 1980) resulting in karyotypes that are radically reorganized compared to other species in the family. Karyotypically, the most conserved Phyllostomidae species is *Macrotus waterhousii* (diploid number 46; fundamental number 60), which is thought to possess a karyotype identical to that proposed as primitive for the lineage that gave rise to the phyllostomid, mormoopid, and noctilionid radiation (Patton & Baker 1978, Baker & Bickham 1980). This indicates that the karyotype of *M. waterhousii* has remained unchanged for at least 30 million years and possibly as long as 60 million years. In fact many of the chromosomes found in the karyotype of *M. waterhousii* appear to share G-band sequences with those of megachiropterians (Qumsiyeh & Baker 1985). For the above reasons, *M. waterhousii* was selected as a species with a conservative genome for comparison with the more rapidly evolving genome of equids as outlined above.

Artibeus jamaicensis, also a member of the Phyllostomidae, was chosen as an outgroup taxon as it shared a common ancestor to *M. waterhousii* at least 20 million years ago (R. J. Baker, personal communication). *A. jamaicensis* has a diploid number of 30 and a fundamental number of 56, and differs from *M. waterhousii* by 16 rearrangements identified by G-bands (Baker *et al.* 1989).

Using the same methods as Wichman *et al.* (1990, 1991) used in equids we generated a comparable data set for the *M. waterhousii* genome and used this to test the hypothesis that radically reorganized genomes (such as those of equids) are associated with a high activity of rapidly evolving repetitive sequences, and that conservative genomes (such as *M. waterhousii*) are associated with a lower abundance of such elements. Although bats have smaller genomes than do other mammals such as rodents (Burton & Bickham 1989, Burton *et al.* 1989), and a direct comparison of bats to equids does not completely resolve the relationship of rapid karyotypic change to an accumulation of rapidly evolving repetitive DNA sequences, this study provides baseline data necessary for comparison of (1) a conservative genome with that of a rapidly evolving genome and (2) a relatively small genome compared to the standard size of a mammalian genome.

If the data from *Macrotus* are not different from those described by Wichman *et al.* (1991), or if there is a greater copy number and intragenomic movements of repetitive DNA classes in *Macrotus*, then the hypothesis that intragenomic movement and multiple classes of repetitive sequences are associated with rapid chromosomal evolution would not be supported. If, on the other hand, the data from *Macrotus* reveal little or no intragenomic movement (restricted to a few chromosomal fields) and fewer classes of repetitive elements than are found in *Equus*, then the hypothesis remains as a viable explanation of stasis versus rapid chromosomal evolution.

Materials and methods

Tissue samples were obtained for DNA preparations of *Macrotus waterhousii* and *Artibeus jamaicensis* from the Frozen Tissue Collection, The Museum, Texas Tech University, Lubbock, TX. Voucher specimens are housed in The Museum, Texas Tech University. Specimen identification number, sex and locality are as below. *M. waterhousii* (TK 32010, male; TK 32011, male; TK 32031, male; and TK 32178, male), Cuba; Guantanoma Province, Guantanamo Bay Naval Base. *A. jamaicensis* (TK 32042, male; TK 32048, male, TK 32075, male; and TK 32082, male), Cuba, Guantanoma Province, Gantanamo Bay Naval Base.

High molecular weight DNA was isolated from liver and muscle tissue of *A. jamaicensis* and *M. waterhousii*. A genomic library was constructed from *M. waterhousii* by generating partial digests of genomic DNA using the restriction enzyme *Sau*3A1. Digests were electrophoresed on low melting point agarose gels and DNA fragments in the 4–6 kb range were extracted from the gel and ligated into the *Bam*HI site of pUC 18 vector and transformed by electroporation into the JM103 strain of *E. coli*. Care was taken not to amplify the partial genomic library

in any way to ensure uniqueness of clones. Operationally, each clone represented a unique DNA fragment and was treated as such by assigning each an identification number.

DNA from each clone was triple digested using *Bam*HI, *Eco*RI and *Hin*dIII to remove the DNA insert from the pUC 18 vector (*Eco*RI and *Hin*dIII) and to produce smaller fragments. Digests were then electrophoresed on 0.8% agarose gels. DNA was transferred from the gels to nylon membranes following a modified technique of Southern (1975) or by placing nylon filters above and below the gel. This generates two identical filters of the clones for the phylogenetic screening procedure of Wichman *et al.* (1985). One was hybridized to a probe made from genomic DNA of the ingroup taxon (*M. waterhousii*), and the other filter was hybridized to a probe made using genomic DNA of the outgroup taxon (*A. jamaicensis*). Under the conditions used, only repetitive sequences in the genomic DNA will show detectable hybridization to the clones. Probes were made by random-primed labelling techniques using [^{32}P]dCTP. Hybridization was at 60°C in a 4 × SSCP (1 × SSCP is 120 mM NaCl, 15 mM sodium citrate and 20 mM Na_3PO_4, pH 7), 1 × Denhardt's hybridization mix, using 1.5×10^7 c.p.m. of the labelled probe. Following hybridization, filters were washed in a 2 × SSCP, 0.1% SDS solution for 2 h at 60°C with a final wash in 2 × SSCP at 60°C for 30 min and exposed to X-ray film for 24 h using two intensifying screens. The autoradiograms of the two sets of filters were overlaid for comparison of each clone. Clones from the ingroup and the outgroup were scored as either similar or identical, possessing different intensity of hybridization (which indicates copy number differences), having different numbers of bands (indicating loss or gain or divergence of an element or portion of the element), or as present/absent. Clones identified as being different between the ingroup and outgroup were verified by repeating the phylogenetic screening process and were designated as hypervariable.

Efforts were made to standardize hybridization conditions of filters and development of autoradiograms of each set of *M. waterhousii* and *A. jamaicensis* filters to ensure that comparisons reflected differences in DNA sequences and not technical artefacts. This was critical for a direct comparison of the abundance and rates of change of repetitive DNA evolution in bats to rates of evolution in equids and rodents (Wichman *et al.* 1990) and primates (Lloyd *et al.* 1987) which were screened using these same techniques.

Clones that were scored as hypervariable, either initially or after rescreening, were sorted into families by Southern blot cross-hybridization (Southern 1975). If clones possessed multiple bands, each band was numbered sequentially beginning with the largest band. Cross-hybridization experiments involved labelling the hypervariable band(s) of each clone with ^{32}P and using it to probe the other hypervariable clones. The same filters that were probed with genomic DNA of *M. waterhousii* and *A. jamaicensis* were used in these experiments. Hybridization conditions were as described above. The cross-hybridization experiments were repeated until all clones were assigned to at least one family. Additionally, clones identified as hypervariable were digested with *Bam*HI, *Eco*RI, *Hin*dIII, *Kpn*I, *Pst*I and *Pvu*II, and restriction maps were generated to determine relatedness of clones. To determine whether clones contained tandemly repeated or interspersed sequences, genomic DNAs of *M. waterhousii* and *A. jamaicensis* were digested using *Alu*I, *Bam*HI, *Cla*I, *Dde*I, *Eco*RI, *Eco*RV, *Hae*III, *Hin*CI, *Hin*dIII, *Hin*FI, *Kpn*I, *Msp*I, *Pst*I, *Pvu*II and *Xba*I and were electrophoresed on agarose gels and transferred to nylon membranes using the techniques of Southern (1975).

Results

A total of 649 clones were screened using the techniques of Wichman *et al.* (1985, 1990). Of these, 80 did not hybridize with sufficient intensity to be visualized on autoradiograms. These clones probably represent either single- or very low-copy sequences, which do not produce detectable hybridization to the radioactive probe. Using the calculations of Burton *et al.* (1989) that bats possess a genome size that is approximately 80% of a 'typical' mammalian genome (*Mus*), then the 649 clones examined represent approximately 1/1000 of the bat genome, with each clone possessing an average size of 4.3 kb. Of the 569 clones that were visualized (indicating they contain repetitive sequences), four clones (Mw102, Mw529, Mw623 and Mw629) were initially identified as hypervariable using the criteria defined above. In subsequent experiments to confirm these differences, only Mw629 was found to show a consistent and significant difference between the two species (Figure 1). Seven additional clones which hybridized more intensely to the outgroup than to the ingroup were not identified as hypervariable because the activity of these sequences would not be expected to contribute to rapid chromosomal evolution by the mechanisms proposed in the hypotheses set forth in this study.

The sequence similarity between Mw629 and the other clones originally identified as hypervariable was examined by Southern blot cross-hybridization. The hypervariable band was used to generate a probe for cross-hybridization to the hypervariable clones. In addition, similar experiments were carried out using bands from Mw102, Mw529 and Mw623. Only medium or strong signals were used as an indication of actual cross-hybridization. Mw102 cross-hybridized to the hypervariable band in Mw629, but did not cross-hybridize to Mw623; however, Mw629

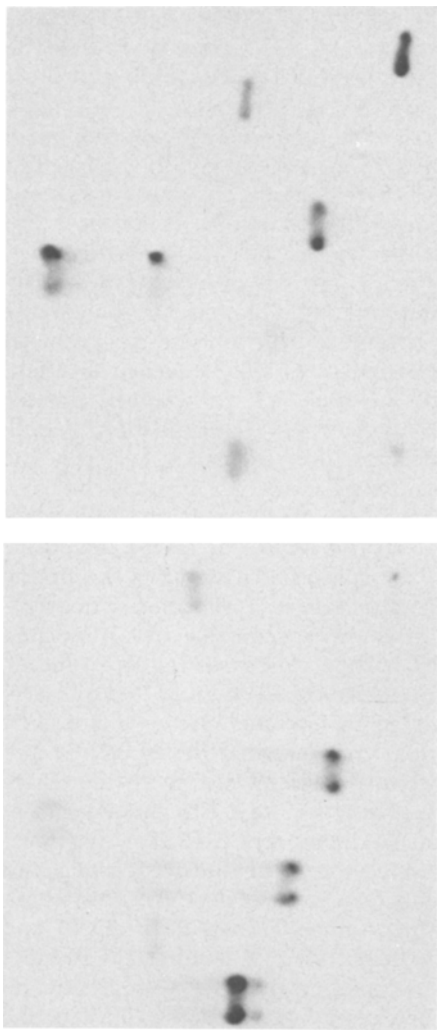

Figure 1. Autoradiogram depicting the phylogenetic screening process for *Macrotus waterhousii* clones; probed with total genomic DNA from *M. waterhousii* (left) and *Artibeus jamaicensis* (right). Only hybridization to repetitive sequences is evident under these conditions. The eight clones were chosen as representative of the clones showing the greatest variation among the 649 clones screened. Only one clone, Mw629, meets the criteria of being clearly repetitive in *M. waterhousii* but greatly reduced in copy number or absent from *A. jamaicensis*.

hybridized to Mw623 and Mw102, while Mw623 did not hybridize to either of the other two clones. None of these clones hybridized to Mw529. Note that some clones which cross-hybridized did not do so in a reciprocal manner. Although Mw102 and Mw623 were less variable between species than Mw629, it is possible that all three clones contain sequences from a single repetitive sequence family. Alternatively, cross-hybridization may be due to the presence of some repeat in one or more of the clones. Restriction maps were generated for each clone and are depicted in Figure 2. Comparisons of the restriction patterns for these four clones show no obvious pattern of similarity.

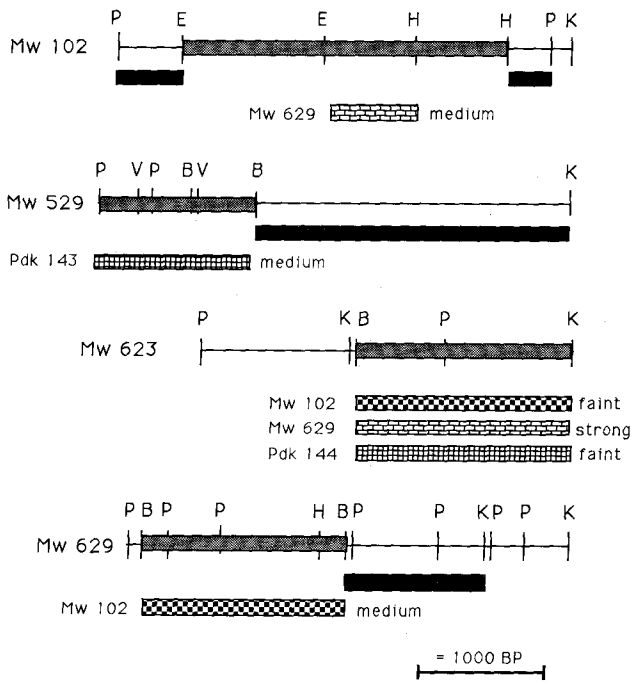

Figure 2. Restriction maps of the four original hypervariable clones examined in this study. Restriction sites are abbreviated as follows: B = *Bam*HI, E = *Eco*RI, H = *Hin*dIII, K = *Kpn*I, P = *Pst*I, V = *Pvu*II. ▒, regions that are hypervariable; ■, regions that are repetitive but are not hypervariable. Individual clones that cross-hybridize to certain regions are depicted as ▒, Mw102 and ▒, Mw629. Mw529 does not cross-hybridize to any other clone. ▦, hybridization to the LINE elements Pdk143 and Pdk144.

Southern blots of *M. waterhousii* and *A. jamaicensis* genomic DNA that had been digested with a cross-section of restriction enzymes were hybridized with each of the four hypervariable clones. The same bands used in the cross-hybridization experiments were used as probes. One clone (Mw102) produced long smears of strong hybridization to digests of both *M. waterhousii* and *A. jamaicensis*. Two clones (Mw529 and Mw623) produced faint hybridization in both *M. waterhousii* and *A. jamaicensis*. Mw629 produced dark smears in *M. waterhousii* but medium smears in *A. jamaicensis*. These results further suggest that only Mw629 contains a repetitive sequence which is consistently and significantly different between the two species. No discrete bands were seen in these genomic Southern blots for any probe with any of the enzymes tested.

Discussion

Most of the clones examined contained repetitive sequences that have not diverged rapidly since the divergence of *M. waterhousii* and *A. jamaicensis*. During this approximate 20 million year time frame, 99%

(645 of 649) of the clones examined did not possess sequences that were more highly repeated in *M. waterhousii* than in *A. jamaicensis*. Additionally, 98% (639 of 649) did not show any hypervariable characteristics in either species that were detectable by the phylogenetic screening process. These data are comparable to the phylogenetic screening study of Lloyd *et al.* (1987), who found 480 of 500 (96%) human repetitive clones to be non-hypervariable when compared to the outgroup *Galago crassicaudatus*. Additionally, a phylogenetic screening study involving *Equus zebra* and rhinoceros (*Ceratotherium simum*) as an outgroup generated 34 clones out of 452 which were repetitive in the zebra but low in copy number or absent in the rhinoceros (H. A. Wichman, unpublished data). This resulted in approximately 85% of the zebra clones remaining non-hypervariable after the divergence of the zebra and rhinoceros. In both instances, the phylogenetic screening study of *M. waterhousii* generated fewer hypervariable clones than did the primate or equid studies.

The fact that one clone (Mw629) contains a repetitive sequence that was present in the ingroup but not in the outgroup taxon suggests that this repetitive DNA belongs to a family of sequences that invaded or was amplified in *M. waterhousii* after the divergence of *M. waterhousii* and *A. jamaicensis* from a common ancestor. Alternatively, a related sequence family may have been present in the common ancestor, but may have differentiated more rapidly than other repetitive sequences in the genome after the divergence of *M. waterhousii* and *A. jamaicensis*. This could occur, for example, if the family was actively moving by reverse transcription, because of the high error rate of reverse transcriptase. Thus sequences which move by retrotransposition could be expected to accumulate many differences during bursts of retrotransposition.

Long interspersed element (LINE) probes from *Peromyscus* (Pdk143 and Pdk144; Kass *et al.* 1992) and human (CD11B, provided by T. Fanning) hybridized to two of the original hypervariable clones. Pdk143 and CD11B hybridized to clone Mw529 and Pdk144 hybridized to Mw623. These data suggest that these two sequences possess regions that have some sequence identity to the LINE element. However neither LINE probe nor the human LINE probe hybridized to clone Mw629 indicating that it has little or no sequence identity to LINE elements.

Hybridization of clone Mw629 to Southern blots of *M. waterhousii* and *A. jamaicensis* genomic DNA (digested with the 15 restriction enzymes) produced dark smears of hybridization to *M. waterhousii* and medium smears in *A. jamaicensis*. No ladder-like pattern was found with any enzyme, and strong hybridization to infrequently digested DNA near the wells was not observed. This pattern suggests an interspersed arrangement of this sequence throughout the genome of both *M. waterhousii* and *A. jamaicensis*. The intensity of hybridization varied, suggesting copy number differences between the genomes of *M. waterhousii* and *A. jamaicensis*.

The data (Table 1) generated from the phylogenetic screening study of rapidly evolving repetitive sequences in a bat species (*M. waterhousii*) fit the predictions of Wichman *et al.* (1991) for a conservatively evolving genome. Specifically, they predicted that there would be few classes of tandem repeats, that elements in these classes would possess few copies of the sequences, and that elements would be restricted to certain chromosomal fields. Only a single family of rapidly evolving repetitive sequences was identified in this study, and this sequence does not appear to be tandemly repeated.

The data generated for bats contrast strongly with those from rodents (Wichman *et al.* 1985, 1990, Hamilton *et al.* 1990), primates (Lloyd *et al.* 1987) and equids (Wichman *et al.* 1990, 1991). First, the number of hypervariable clones of all types was greatly reduced in bats. Sampling approximately 0.1% of the genome of *M. waterhousii* produced one hypervariable clone, whereas equids generated 34 hypervariable clones (Wichman *et al.* 1990, 1991). Similarly, the phylogenetic screening study of primates (Lloyd *et al.* 1987) generated 20 hypervariable clones in a sampling of 0.17% of the human genome, and Wichman *et al.* (1985, 1990) found 11 clones that were hypervariable in the rodent genome based on sampling 0.1% of the *P. leucopus* genome.

Second, the number of families of elements was reduced in the bat genome. Only one family was identified in the *M. waterhousii* library compared to

Table 1. Summary of three phylogenetic screening studies in which approximately 0.1% of the genome was sampled. The number of identified hypervariable clones and variable families are presented for each study.

Species	Outgroup taxon	Variable clones	Variable families
Equus zebra	*Ceratotherium simum*	34	6
Peromyscus leucopus	*Mus domesticus*	11	4[a]
Macrotus waterhousii	*Artibeus jamaicensis*	1	1

[a] Two clones were lost in storage, so this represents a minimum estimate of the number of families to which the 11 variable clones might be assigned.

six in equids, three in primates and four in rodents. This element is probably dispersed and may represent a family of elements moving by retrotransposition. Conversely, the families of elements in primates, rodents and equids contained several divergent types of repetitive sequences. The primate genome (Lloyd *et al.* 1987) consisted of three families of elements, including: 5′ regions of LINEs, alphoid satellite-like sequences and the transposon-like human element (THE) sequences, which are retrotransposon-like elements. The phylogenetic study of the rodent genome (Wichman *et al.* 1985, 1990) has produced at least four families of repetitive sequences including *mys*, which is a retrovirus-like element (Wichman *et al.* 1985), a family of heterochromatic repeats (Reeder 1990, Hamilton *et al.* 1992), B3 a family of interspersed repeats (Hamilton 1989) and several hypervariable bands which cross-hybridize to LINE elements from *Peromyscus* (unpublished data). Wichman *et al.* (1990, 1991) have identified six families of elements in equids, five of which have been characterized as tandemly repeated sequences and one as interspersed. Additionally, the hypervariable clones from the rodent and equid studies (Hamilton 1989, Wichman *et al.* 1991) tended to show more pronounced differences in copy number between the ingroup and the outgroup than the sequences isolated in this phylogenetic screening procedure.

The data herein are consistent with the hypothesis of Wichman *et al.* (1991) that chromosomal evolution may be associated with the activity of rapidly evolving repetitive DNA sequences such as tandem repeats. *M. waterhousii*, which has a conservatively evolving genome (Patton & Baker 1978, Baker 1979, Baker & Bickham 1980), has a lower number and fewer kinds of rapidly evolving repetitive DNA sequences compared with the rapidly evolving genome of *E. zebra* (Bush *et al.* 1977, Wichman *et al.* 1990, 1991). It is possible that bats, which possess approximately 80% of the DNA found in typical mammalian species (Burton *et al.* 1989), possess some mechanism to 'streamline' the genome and eliminate repetitive DNAs (Baker *et al.* 1992). However, C-band studies of bats have revealed several species with large amounts of heterochromatic regions. Additionally, most repetitive elements which showed differences between *M. waterhousii* and *A. jamaicensis* were actually found in greater copy number in *A. jamaicensis*, which has a more rapidly evolving genome than *M. waterhousii*. This suggests that rapid chromosomal evolution in bats may be correlated with, and perhaps driven by, a failure in genomic streamlining mechanisms. Baker *et al.* (1992) proposed that bats and rodents have mechanisms to increase the number of ribosomal DNA repeats in the genome but bats possess a stabilizing mechanism to reduce or contain such repeats. A failure of such a stabilizing mechanism in taxa undergoing karyotypic megaevolution may result in the accumulation or amplification of other repetitive DNAs (non-ribosomal DNAs). Phylogenetic screening studies of species of bats such as *Rhinophylla pumillio*, which has a radically reorganized genome, should provide data to confirm whether bats in general have reduced amounts of rapidly evolving repetitive sequences, regardless of their mode of karyotypic evolution, or whether this is a feature of only conservative karyotypes.

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