

Order Chiroptera

Approximately one-quarter ($n = 977$) of all mammal species are bats, so there are many species to be studied to document patterns and mechanisms associated with chromosomal change. Although bat karyotypic variation is generally described as conservative relative to other mammalian species, there are indeed many examples of extensive chromosomal rearrangement within bats. There is an unranked taxon, karyovarians (Baker et al., 2003), in the family Phyllostomidae (New World, leaf-nosed bats) that is named to recognize the extensive chromosomal evolution present in this clade, which includes 55 genera and 140 species. No member of this clade retains the proposed primitive karyotype for this complex of bats.

In addition to the extreme morphological modifications required for flight (i.e., wings, 180° rotation of the hind limbs, etc.), bats possess a unique set of characteristics for a mammal of their body size. While there is considerable variation in the features listed, from an overview the following is true. Relative to other mammals of equal size and weight, bats have a longer life expectancy and generation time and a later gestation period. Several features of reproduction are also atypical. These include delayed implantation and embryonic diapause, delayed ovulation and fertilization, and sperm storage for several months (Neuweilier, 2000). Bats have a small litter size (one to four young per litter, but for most species one or two per pregnancy) and one or two litters per year. For many vespertilionids, a female will produce a single young per year. For microchiroptera there is a sophisticated development of echolocation and in megachiroptera the development of the visual system is advanced relative to other mammals. In both megachiroptera and microchiroptera, there is advanced encephalization of the brain (Stephan, 1977). Of course bats are more mobile than most other species of mammals, and some species migrate hundreds of miles annually. Greater mobility implies greater vagility; however, there is little scientific data available to understand how vagile bat species are. Further, the relative role of female versus male dispersal is poorly documented. Within bats there is a high level of diversity in social structuring. Sexual relationships characteristic of different species range from monogamy to polygamy and harems, in extreme to complete promiscuity, and in some cases what appears to be huge deme sizes (Neuweilier, 2000).

Bats have a lower diploid number than is typical of other eutherian mammals. Diploid numbers range from 14 to 62 and the average has been reported to be 36.8 chromosomes (reviewed in Neuweilier, 2000). At the cellular level, the characteristics of the genome of bats are unique among mammals in that the total amount of DNA, the C-value, is less than is typical (50–87% of that of humans) (Burton et al., 1989). This reduction in genome size appears to be accomplished by a reduced amount of C-band positive material as well as a reduction in repetitive elements such as ribosomal genes and microsatellite clusters (Baker et al., 1979; Baker et al., 1992; Van Den Bussche et al., 1995).

The karyotypic data from bats have been used in the literature for a number of studies with theoretical implications. An example is a study by Wilson et al. (1975), who used a review of bat karyotypic data, along with those from other mammals, to advance the idea that chromosomal evolution in mammals was driven by small deme sizes and inbreeding resulting from greater development of social structuring in mammals when compared to the social structure among amphibians, especially the order Anura. Wilson et al. (1975) extended their conclusions to include a cause-and-effect relationship between more chromosomal rearrangements and greater morphological evolution in mammals. Inbreeding as a consequence of social structuring has been questioned and rejected as a possible means of driving chromosomal change to fixation (Chesser and Baker, 1986). There are many examples where the karyotype has been radically reorganized without any substantial mor-

phological evolution, distinguishing the species with the radical reorganized karyotype from closely related species that have retained the primitive karyotype for the genus in question (Ellerman and Morrison-Scott, 1951; Fredga, 1977). Also, see the discussion below on karyotypic megaevolution.

The canalization model of chromosomal evolution (Bickham and Baker, 1979) was described to explain the patterns of karyotypic change in bats and turtles. This model predicts that when an evolutionary lineage first enters a new grade of evolution (Simpson, 1948), the types of chromosomal rearrangements that will become established will be those that rearrange linkage groups. However, as morphology is canalized and becomes more adapted to this new grade, the types of chromosomal rearrangements that will become established will be those that are less disruptive to linkage groups (such as centric fusions and heterochromatic additions). The implications are that as the morphology becomes canalized, so will the karyotype, an example being when bats evolved from a terrestrial insectivore ancestor into a volant mammal. When bats first began to fly and exploit the volant grade, the karyotype was rearranged into linkage groups that more efficiently accommodated the developmental changes required to exploit this grade.

Bats were used by Baker and Bickham (1980) to describe the phenomenon of karyotypic megaevolution. In karyotypic megaevolution, one species within a genus will have a radically reorganized karyotype such that it is difficult to relate the G-band patterns to those of congeneric species. Other species in the genus might exhibit little or no change from the primitive karyotypic condition associated with that genus. The first example of karyotypic megaevolution was described for the muntjacs (Ellerman and Morrison-Scott, 1951; Fredga, 1977). In this genus of barking deer, one species, *Muntiacus reevesi* ($2n = 46$), is thought to have an essentially unrearranged karyotype while *M. muntjak* greatly reorganized the karyotypes to produce $2n = 6$ females and $2n = 7$ males. The point here is that essentially all of the rearrangements that distinguish these two muntjak species have occurred in the $2n = 6, 7$ species. Examples of this same pattern have been described for bats, including *Lasionycteris noctivagans*, *Tonatia bidens*, *Tonatia schultzei*, *Micronycteris minuta*, and *Vampyress pusilla*. Explaining how karyotypes in a one species can become so radically reorganized while closely related species experience little or no chromosomal evolution has been so difficult that these examples are a cytogenetic scandal. It has been argued that the number of chromosomal rearrangements could be used as a predictor of the number of population bottlenecks that a species had encountered during its evolution (Lande, 1979). However, there is no evidence that the species with radically reorganized karyotypes have social structuring or any other demographic factor that would disproportionately force them through numerous bottlenecks while the species with conserved karyotypes experienced none. These examples have been used to argue that the factors driving chromosomal evolution are not demographic but cellular, molecular, and meiotic (Baker et al., 1988).

Karyotypes of the little yellow bats of the genus *Rhogeessa* (Genoways and Baker, 1996) were used to develop the model of speciation by monobrachial centric fusions (Baker and Bickham, 1986). The idea of differential fitness resulting from monobrachial homology involving centric fusions was introduced by Gropp et al. (1972) and further defined by Capanna (1982) for his emblematic model of chromosomal speciation. It has always been attractive to evolutionary biologists studying speciation to employ chromosomal rearrangements as a postmating isolating mechanism (King, 1993; White, 1975) and, L. H. Rieseberg (2001). This attraction primarily has been a product of chromosomal rearrangements reducing fertility (negative heterosis) in hybrids, which would help reduce gene flow between populations distinguished by chromosomal rearrangements (King, 1993). However, the paradox is: How can a chromosomal rearrangement become established in naturally

occurring populations if the rearrangement reduces heterozygosity sufficiently to be a postmating isolating mechanism? The idea that deme size and population bottlenecks were the solution to this dilemma was introduced by Wright (1941). Some cytogeneticists have gone to great lengths to solve this dilemma. For example, King (1993) suggested that meiotic drive could play a critical role in driving a new rearrangement to fixation in the face of negative heterosis in even a large population. Bickham (1995) pointed out that meiotic drive in King's (1993) model must be transitory in nature and disappear after the fixation of the rearrangement in one population. Otherwise, the rearrangement will spread among all populations and not act as a reproductive isolating mechanism. Because this seems highly unlikely, the paradox of how to fix within a population a deleterious rearrangement that will subsequently perform well as a reproductive barrier has never been solved (Baker et al., 1988).

The model of monobrachial speciation avoids this paradox because centric fusions are often population polymorphisms (Koop et al., 1983) and become fixed more easily in natural populations because new centric fusions do not result in unbalanced gamete formation to a point that they are highly selected against. In fact, it is not uncommon for many centric fusions to occur in a single species, as described by White (1975) as an example of karyotypic orthoselection. If different populations fix different centric fusions which have one arm that is homologous but the other arm attached to a different chromosome in one population and to a nonhomologous chromosome in another population, then a complex meiotic figure will result if hybridization occurs between these two populations (Baker and Bickham, 1986). The bottom line is that it is possible to establish chromosomal rearrangements independently in separate populations without significant selection against heterozygotes during the process of becoming fixed within that population. However, when these rearrangements undergo meiosis in a hybrid, the result is a much greater disadvantage (negative heterosis) to the hybrids than was encountered during the fixation process. Monobrachial speciation appears to be a very special model (does not occur in most species) that has been described for a variety of taxa, including the little yellow bat family *Rhogeessa* (Baker and Bickham, 1986; Dobigny et al., 2002; Kingswood et al., 2000; Qumsiyeh et al., 1999; Kumamoto et al., 1999; Gimenez et al., 1997; Searle, 1993; Piálek et al., 2001).

In situ hybridization studies further document the potential for studies for Chiroptera karyotypes. Three papers (Volleth et al., 1999, 2001, 2002) clearly document the effectiveness of Zoo-FISH (fluorescence in situ hybridization) analysis in establishing syntenic groups within bats relative to humans. Further, these papers document the use of chromosomal evolution in establishing phylogenetic relationships. Parish et al. (2002), using in situ hybridization, document that these methodologies will be useful in understanding the relationship of genome organization, long interspersed nuclear elements (LINEs), and X chromosome inactivation.

There is a tremendous amount of cytogenetic research remaining to be done within the order Chiroptera. Over half of the species of bats have yet to be described karyotypically even for diploid and fundamental numbers. In a field of science that is rapidly developing new methods of interrogating the karyotype, such as chromosomal paints, in situ hybridizations, genome sequences, and heterochromatin, few scientists are studying bat cytogenetics and genome organization. Less than 1% of the species of bats have been studied by modern techniques. Ah, so many bats, so many opportunities, and so little time.

Note: Several contributors use Reference species in their numbering system. In the family Vespertilionidae the system established by J. B. Bickham uses *Myotis nigricans*. In the family Pyllostomidae the system established by Texas Tech uses *Macrotys waterhousii*.