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KARYOTYPIC EVOLUTION IN BATS: EVIDENCE OF EXTENSIVE AND CONSERVATIVE CHROMOSOMAL EVOLUTION IN CLOSELY RELATED TAXA

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Abstract

Baker, R. J., and J. W. Bickham (The Museum and Department of Biological Sciences, Texas Tech University, Lubbock, Texas 79409 and Department of Wildlife and Fisheries Sciences, Texas A and M University, College Station, Texas 77843) 1980. Karyotypic evolution in bats: evidence of extensive and conservative chromosomal evolution in closely related taxa. Syst. Zool., 29:239–253.—G- and C-band data for seventy-eight species of bats from four families were subjected to a cladistic analysis to determine the number of chromosomal rearrangements required to convert the karyotype proposed as primitive for a family into the karyotype of extant species in that family. The number of rearrangements ranged from 0 to 36, and if the age of families is 60 million years, average rate of incorporation of rearrangements per million years ranged from 0 to 0.6. When chromosomal variation in congeneric species were subjected to a similar cladistic analysis, most (34 of 54) species had undergone no chromosomal rearrangements; however, some species had undergone from 14 to 20 rearrangements and the types of rearrangements that were incorporated in species having the largest amount of change were generally rearrangements that should produce considerable reduction in gamete fertility in individuals heterozygous for such rearrangements. Radically reorganized karyotypes appear not only in bats but in a wide variety of vertebrates. Factors related to demography, breeding structure, and speciation do not appear adequate to explain the occurrence of such radically reorganized genomes. Factors less related to demographic and vagility characteristics, such as mutation rate and mechanisms which reduce the meiotic constraints on the heterozygote, are phenomena which may be involved in evolving a radically reorganized karyotype. [Chromosomal evolution; G-bands; rates of evolution; cladistic analysis; bats.]

In order to understand the meaning of chromosomal evolution, it is necessary to have accurate estimates of magnitude of chromosomal change and documentation of the degree to which the evolution of species with differing biological characteristics has been associated with karyotypic change. Knowledge of rates are important in the development and testing of models of chromosomal evolution (Bush et al., 1977; Bickham and Baker, 1979; Lande, 1979; Bengtsson, 1980). This report is concerned with results of G-band studies of the bat families Phyllostomatidae (37 species), Vespertilionidae (29 species), Mormoopidae (6 species), and Noctilionidae (2 species). Approximately nine percent of known bat species are included in this report. We give estimates of magnitude of change in lineages extending back to the hypothesized primitive karyotype for each family and shorter term estimates from congeneric species. Also, we describe and discuss a phenomenon which we call "karyotypic megaevolution" which appears to occur not only in bats but in a wide variety of living forms.

METHODS AND MATERIALS

All species of bats included in this report have been studied from G- and C-band preparations. Most of these karyotypes have been described elsewhere (Bickham and Baker, 1977, table 1; Bickham and Hafner, 1978; Bickham, 1979a and 1979b; Bass, 1978; Baker, 1979; Baker et al., 1979a; Johnson, 1979; Patton and Baker, 1978).

Within each family, chromosomal data were arranged such as to require the minimum number of events to derive karyotypes of living species. From such arrangements, it was possible to hypothesize a primitive karyotype for each family (and in the case of the Phyllostomat-

idae for subfamilies). The proposed primitive karyotype for the Phyllostomatidae used herein is described with the assumptions made in deriving it in Patton and Baker (1978) and Baker (1979). Additional data and discussion of the primitive karyotype for the subfamily Stenoderminae is described by Johnson (1979). The proposed primitive karyotype for the Vespertilionidae and the assumptions made in deriving it were described by Bickham (1979a). There is no karyotypic variation within the Noctilionidae and the karyotype proposed as primitive is like that characteristic of extant species. Karyotypic variation in the Mormoopidae is restricted to a paracentric inversion and the presence or absence of a heterochromatic short arm (Table 1). The condition in the five *Pteronotus* species examined is like that found in the Noctilionidae and the Phyllostomatidae, therefore we conclude that the condition characteristic of *Pteronotus* is primitive for the family Mormoopidae. Results from such methods are shown in Figure 1 and in Bickham (1979a).

To determine the amount of evolution over the long-term in the phylogeny of a species, we calculated the number of rearrangements required to derive the karyotype of a species from that hypothesized as primitive for its family. As most recent bat families are thought to have originated in the Eocene or earlier (Smith, 1976), we utilized the beginning of the Eocene (roughly 60 million years ago) as the age of families. Therefore, the minimum number of rearrangements required to convert the karyotype proposed as primitive for a family into the karyotype of a species in that family, divided by 60 million years, provides a rough estimate of rate of chromosomal rearrangement incorporation per million years.

An exception to the above procedure was in the case of the Stenoderminae, where we converted the karyotype of each species from this subfamily into the karyotype hypothesized as primitive for this subfamily (Johnson, 1979) and added the number of rearrangements required to convert the subfamilial primitive karyotype to that proposed as primitive for the family. This route (extant species to primitive karyotype for the Stenoderminae to primitive karyotype for the family) was not as parsimonious as extant species to primitive karyotype for the family in species marked by asterisk in Table 1.

To determine the pattern of chromosomal evolution since generic characters were established, a cladistic analysis was performed on each genus where more than one species (Table 1) had been studied by G-band analysis. For each genus a proposed primitive karyotype was derived by modifying the "hypothesized primitive karyotype" for the family until it included all rearrangements common to members of the genus. Then we calculated the number of rearrangements required to derive the karyotype of each species in the genus from that hypothesized as primitive for that genus. We have used the estimate of Bush et al. (1977) of 9 million years as the average age of bat genera.

Attempting to put an age on families and genera is most difficult and fraught with pitfalls as different genera (or families) may have originated in different ages. However, such calculations do provide a handle for comparing estimates from different techniques (such as those of Bush et al., 1977). However, the reader should be aware that there is considerable variation in age of genera and we have used an estimate of 9 million years because it was the age used in previous estimates.

Some comment is merited on the reliability of the above methods of determining the amount of rearrangements in the phylogeny of a species. We are sure that within the families Phyllostomatidae and Vespertilionidae there are some errors in identifying homologous G-band segments of chromosomes between divergent taxa; however, we think that the error level is below 10 percent. It should

TABLE 1. LIST OF SPECIES FROM FOUR BAT FAMILIES THAT HAVE BEEN G-BANDED, SHOWING THE NUMBER AND TYPES OF REARRANGEMENTS REQUIRED TO DERIVE THE KARYOTYPES OF THE SPECIES FROM THE KARYOTYPE PROPOSED AS PRIMITIVE FOR ITS FAMILY. 2N = DIPLOID NUMBER; FN = NUMBER OF ARMS OF THE AUTOSOMAL COMPLEMENT; FU = FUSION; FI = FISSION; PI = PERICENTRIC INVERSION; PA = PARACENTRIC INVERSION; TO = OTHER TYPE OF TRANSLOCATION, IN MOST CASES A TELOMERE-CENTROMERE TRANSLOCATION; H+ = HETEROCHROMATIC ADDITION OF A SHORT ARM; UN = CHANGES NOT IDENTIFIABLE FROM G-BANDS BUT A MINIMUM ESTIMATE IS GIVEN. * = KARYOTYPE CHANGED TO PRIMITIVE FOR SUBFAMILY THEN TO SPECIES.

Taxon	2N	FN	FU	FI	PI	PA	TO	H+	UN	Source
	Number and Types of Rearrangements									
Family Phyllostomatidae										
Macrotus waterhousii	46	60	0	0	0	0	0	0	0	Patton & Baker, 1978
Macrotus californicus	40	60	3	0	0	0	0	0	0	Bass, pers. comm.
Micronycteris nicefori	28	52	4	0	0	0	4	0	1	Patton & Baker, 1978
Micronycteris brachyotis	32	60	6	0	0	0	2	0	2	Patton & Baker, 1978
Micronycteris minuta	28	50	2	—	—	—	1	0	15	Patton & Baker, 1978
Micronycteris megalotis	40	68	—	—	—	—	—	0	16	Patton & Baker, 1978
Phyllostomus hastatus	32	58	7	0	2	0	0	0	0	Patton & Baker, 1978
Phyllostomus elongatus	32	58	7	0	2	0	0	0	0	Johnson, pers. comm.
Phyllostomus discolor	32	60	7	0	1	0	0	0	0	Patton & Baker, 1978
Mimon crenulatum	32	60	7	0	1	0	0	0	0	Patton & Baker, 1978
Tonatia minuta	30	56	5	0	1	0	1	0	1	Patton & Baker, 1978
Tonatia bidens	16	20	—	—	—	—	—	0	20	Patton & Baker, 1978
Carollia perspicillata	20/21	36	—	—	—	—	—	—	15+	Stock, 1975
Rhinophylla pumilio	34	56	5	0	1	0	2	0	0	Baker & Haiduk, pers. comm.
Choeroniscus intermedius	20	36	—	—	—	—	—	—	15+	Stock, 1975
Glossophaga soricina	32	60	7	1	4	0	0	0	0	Baker & Bass, 1979
Monophyllus redmani	32	60	7	1	4	0	0	0	0	Baker & Bass, 1979
Erophylla sezekorni	32	60	7	1	4	0	0	0	0	Baker & Bass, 1979
Phyllonycteris aphylla	32	60	7	1	4	0	0	0	0	Baker & Bass, 1979
Brachyphylla nana	32	60	7	1	4	0	0	0	0	Baker & Bass, 1979
Desmodus rotundus	28	52	5	1	7	0	3	0	0	Bass, 1978
Diaemus youngii	32	60	5	1	8	0	0	0	0	Bass, 1978
Diphylla ecaudata	32	60	6	1	8	0	1	0	0	Bass, 1978
*Enchisthenes hartii**	30	56	10	2	3	0	1	0	1	Baker et al., 1979
Artibeus cinereus	30	56	10	2	3	0	0	0	1	Johnson, 1979
Artibeus jamaicensis	30	56	10	2	3	0	0	0	1	Johnson, 1979
Artibeus lituratus	30	56	10	2	3	0	0	0	1	Johnson, 1979
Artibeus phaeotis	30	56	10	2	3	0	0	0	1	Johnson, 1979
Artibeus watsoni	30	56	10	2	3	0	0	0	1	Johnson, 1979
Phyllops haitiensis	30	56	10	2	3	0	0	0	1	Johnson, 1979
Sturnira erythromos	30	56	10	2	3	0	0	0	1	Johnson, 1979
*Sturnira lilium**	30	56	10	2	4	0	0	0	1	Baker et al., 1979
Vampyrops vittatus	30	56	10	2	3	0	0	0	1	Johnson, 1979

TABLE 1. CONTINUED.

Taxon	Number and Types of Rearrangements									Source
	2N	FN	FU	FI	PI	PA	TO	H+	UN	
*Centurio senex**	28	52	11	2	6	0	0	0	1	Johnson, 1979
*Chiroderma villosum**	26	48	13	2	5	0	0	0	1	Johnson, 1979
*Vampyressa nymphaea**	26	48	12	2	5	0	0	0	1	Johnson, 1979
*Vampyressa pusilla**	18	20	10	2	5	0	0	0	19	Johnson, 1979
*Uroderma bilobatum**	44	48	10	10	5	0	0	0	1	Baker et al., 1979
Family Noctilionidae										
Noctilio albiventris	34	62	0	0	0	0	0	0	0	Patton & Baker, 1978
Noctilio leporinus	34	62	0	0	0	0	0	0	0	Baker, unpublished
Family Mormoopidae										
Pteronotus parnellii	38	60	0	0	0	0	0	0	0	Patton & Baker, 1978
Pteronotus personatus	38	60	0	0	0	0	0	0	0	Sites & Haiduk, pers. comm.
Pteronotus gymnonotus	38	60	0	0	0	0	0	0	0	Sites & Haiduk, pers. comm.
Pteronotus fuliginosus	38	60	0	0	0	0	0	0	0	Sites & Haiduk, pers. comm.
Pteronotus macleayii	38	60	0	0	0	0	0	0	0	Sites & Haiduk, pers. comm.
Mormoops blainvillii	38	60	0	0	0	1	0	1	0	Sites & Haiduk, pers. comm.
Family Vespertilionidae										
Myotis nigricans	44	50	0	0	0	0	0	0	0	Bickham, 1979b
Myotis carteri	44	50	0	0	0	0	0	0	0	Bickham, 1979b
Myotis keenii	44	50	0	0	0	0	0	0	0	Bickham, 1979b
Myotis grisescens	44	50	0	0	0	0	0	0	0	Bickham, 1979b
Myotis keaysi	44	50	0	0	0	0	0	0	0	Bickham, 1979b
Myotis velifer	44	50	0	0	0	0	0	0	0	Bickham, 1979b
Myotis yumanensis	44	50	0	0	0	0	0	0	0	Bickham, 1979b
Myotis austroriparius	44	50	0	0	0	0	0	0	0	Bickham, 1979b
Myotis sodalis	44	50	0	0	0	0	0	0	0	Bickham, 1979b
Myotis albescens	44	50	0	0	0	0	0	0	0	Bickham, 1979b
Myotis nattereri	44	50	0	0	0	0	0	0	0	Harada & Yosida, 1978
Myotis hosonoi	44	50	0	0	0	0	0	0	0	Harada & Yosida, 1978
Myotis frater	44	52	0	0	0	0	0	1	0	Harada & Yosida, 1978
Myotis macrodactylus	44	52	0	0	0	0	0	1	0	Harada & Yosida, 1978
Myotis evotis	44	52	0	0	0	0	0	1	0	Bickham, 1979b
Myotis thysanodes	44	52	0	0	0	0	0	1	0	Bickham, 1979b
Myotis auriculus	44	52	0	0	0	0	0	1	0	Bickham, 1979b
Pipistrellus subflavus	30	50	7	0	0	0	0	0	0	Bickham, 1979a
Plecotus townsendii	32	50	6	0	1	0	0	0	0	Bickham, 1979a
Idionycteris phyllotis	30	50	7	0	0	0	0	0	0	Bickham, 1979a

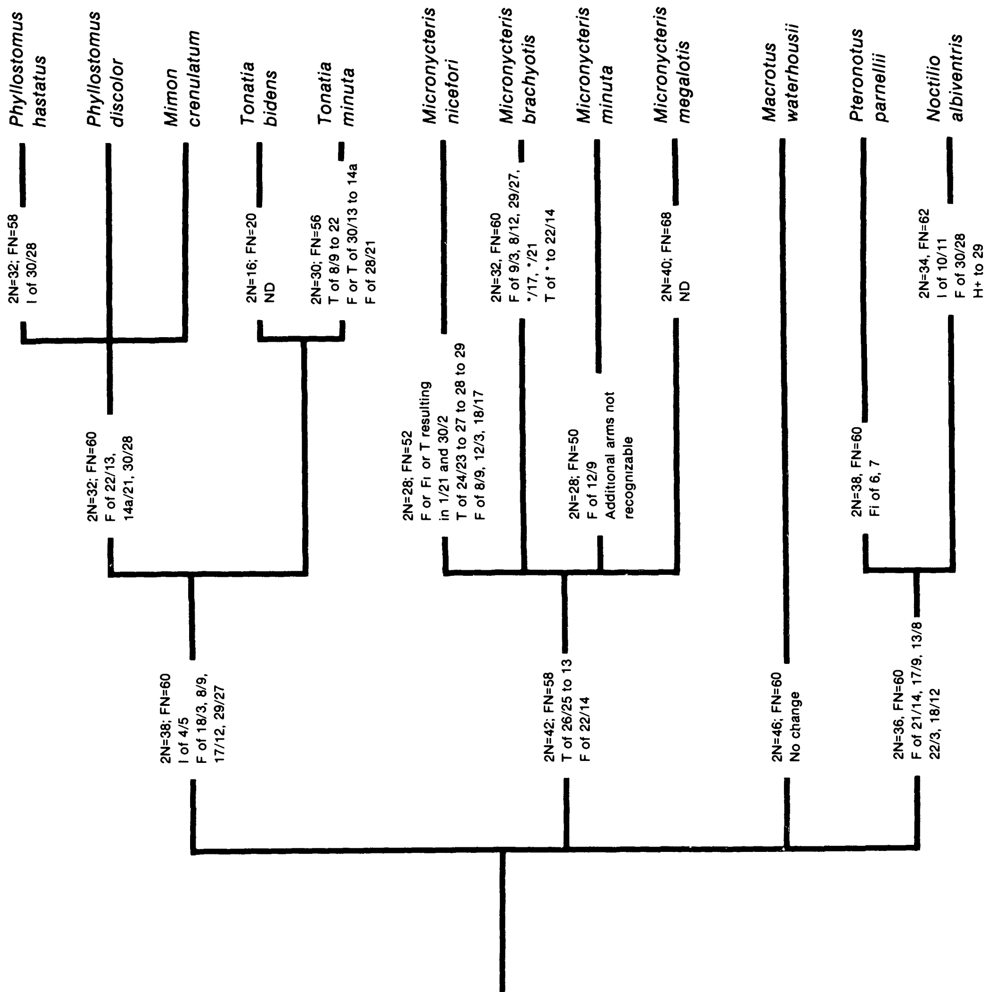
TABLE 1. CONTINUED.

Taxon	Number and Types of Rearrangements									Source
	2N	FN	FU	FI	PI	PA	TO	H+	UN	
Lasiurus borealis	28	48	8	0	1	0	0	0	0	Bickham, 1979a
Lasiurus seminolus	28	48	8	0	1	0	0	0	0	Bickham, 1979a
Lasiurus cinereus	28	48	8	0	1	0	0	0	0	Bickham, 1979a
Lasiurus ega	28	48	8	0	1	0	0	0	0	Bickham, 1979a
Lasionycteris noctivagans	20	28	2	0	1	1	10	0	0	Bickham, 1979a
Miniopterus schreibersii	46	50	0	1	2	0	0	0	0	Bickham, 1979a
Eptesicus fuscus	50	48	0	3	1	0	0	0	0	Bickham, 1979a
Eptesicus lynni	50	48	0	3	1	0	0	0	0	Bickham, 1979a
Antrozous pallidus	46	50	2	3	1	0	0	0	1	Bickham, 1979a
Nycticeius humeralis	46	48	2	3	3	1	0	0	0	Bickham, 1979a
Rhogeessa tumida	30	50	10	3	0	0	0	0	0	Bickham & Baker, 1977
Rhogeessa tumida	34	50	8	3	0	0	0	0	0	Bickham & Baker, 1977

further be noted that even if homologs are misidentified, the specific type of rearrangements (for instance, a fusion, a terminal translocation, or an inversion) will still be required to derive the karyotype of a living species from that proposed as primitive for the family, even if the exact homologous segment that underwent this change is not correctly identified. This report is concerned only that such a rearrangement must have occurred, and is not dependent on which chromosomes were fused, inverted, etc. Clearly, the methods used in this report are much more accurate than those used in any previous estimates for vertebrates. Accurate identification of homologous elements is important in determining the proposed primitive karyotype. However, minor changes in the proposed primitive will not significantly alter conclusions concerning the number of rearrangements required to derive the karyotypes of extant species. It should also be noted that our estimates are minimal and better techniques, reversals, convergences, etc. will always raise the minimal number of events that have occurred.

The range of rates is far more important than the average of rates because the method employed counts events that may have occurred in a single lineage (for instance, that leading to the basal stock of the fruit-eating Stenoderminae), which subsequently radiated into many species without additional chromosomal evolution (8 such stenodermine species are included in Table 1 that underwent no additional chromosomal evolution from the primitive for the subfamily). If the average rate for the Phyllostomatidae was computed using many such stenodermines with the 2n = 30 karyotype, the rate would be inflated because even though there had been no chromosomal evolution during the subsequent speciation, all eight species are credited with sixteen rearrangements that gave rise to the primitive for the stenodermines.

Finally, our calculations of rates have not specified which types of rearrange-



Proposed Primitive Karyotype for Phyllostomatoidea
2N=46; FN=60
Biarmed Chromosomes 1/2, 4/5, 6/7, 10/11, 15/16, 19/20, 23/24, 25/26
Acrocentric Chromosomes 3, 8, 9, 12, 13, 14, 17, 18, 21, 22, 27, 28, 29, 30

FIG. 1.—Example of the type of results that are produced by cladistic analysis of G- and C-band chromosomal data. Numbers refer to standard karyotype for the Phyllostomatidae (Baker, 1979). Values in Table 1 were derived by totaling changes in a lineage from a species to primitive karyotype (figure after Patton and Baker, 1978).

ments have been incorporated in each lineage. It is well documented that different types of rearrangements are incorporated at different rates (White, 1978a); however, we have provided, in Table 1, the types of rearrangements demonstrated by our G- and C-bands. Of note, however, is the fact that the type of rearrangement (heterochromatic addition) which probably causes the lowest degree of meiotic constraint on the heterozygote occurs very infrequently in the bats ex-

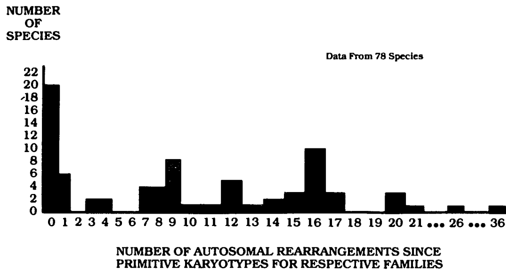


FIG. 2.—Histogram of the frequency of species with various amounts (expressed as number of rearrangements) of chromosomal change required to derive the karyotype of extant species from the karyotype proposed as primitive for its family. Data from 78 species, including 38 phyllostomatids, 2 noctilionids, 6 mormoopids, and 32 vespertilionids.

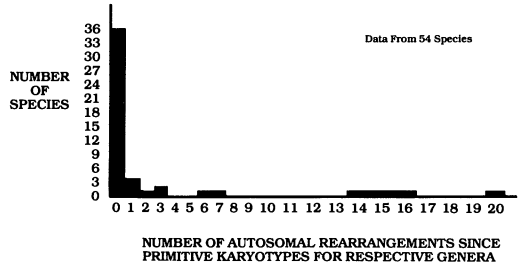


FIG. 3.—Histogram of the frequency of species with various amounts (expressed as number of rearrangements) of chromosomal change required to derive the karyotype of a species from the karyotype proposed as primitive for its genus. All genera that have more than one species listed in Table 1 were used in calculating values for this histogram.

amined. Further, it might be noted that species which have evolved the largest number of rearrangements have not been the species which have necessarily undergone the largest number of rearrangements which have little or no negative heterotic effect due to malassortment in meiosis. We are preparing another manuscript on the types of rearrangements which have been incorporated in bats as opposed to frequency of such types in other species.

RESULTS

Species examined, and number and type of events, are given in Table 1. Estimates of rates of long-term chromosomal evolution in bats ranged from 0 to 0.60 changes per million years (Table 1, Fig. 2). Average rates for all bats was 0.144 changes per million years. Values within the Noctilionidae were 0, within the Mormoopidae were 0–.03, within the Vespertilionidae rates ranged from 0 to .23 and within the Phyllostomatidae values ranged from 0 to .60. Average for the Vespertilionidae was .07 and for the Phyllostomatidae was .24. Rates of short-term chromosomal evolution within genera ranged from 0 to 2.2 changes per million years (average .197), with most species (34 of 54, or 65%) experiencing no detectable chromosomal evolution (Fig. 3). Table 2 gives estimates of rates from other studies.

DISCUSSION

Long-term Evolution

Several features of long-term chromosomal evolution are worthy of note. First, there is considerable variation in estimates of rates. Twenty of 78 species (23%) have undergone no chromosomal evolution from that proposed as primitive for their respective families and species which have undergone no karyotypic evolution are found in all four families examined. Although most bats may have a conservative rate of chromosomal evolution, it is obvious that some species of bats have undergone extensive chromosomal evolution, and bats cannot be classified unequivocally as having a conservative rate of evolution. The species which have undergone the greatest number of changes are *Vampyressa pusilla* (with a minimum of 36 rearrangements) and *Uroderma bilobatum* (with 26 rearrangements). The types of rearrangements required of *V. pusilla* involve a number of rearrangements that are considered to cause severe meiotic problems in producing balanced gametes. Second, rates are highest in the Phyllostomatidae, although there is considerable overlap

TABLE 2. ESTIMATES OF RATES OF KARYOTYPIC EVOLUTION IN MAMMALS. SOURCE OF TAXA EXAMINED IN ESTIMATES LISTED AS THIS PAPER ARE IN TABLE 1. * = IN MILLIONS OF YEARS.

Taxonomic Group	Method	Time*	Number of Genera in Sample	Changes per Million Years per Species		Source
				Average	Range	
Bats (from Table 1)	G-band homology	60	39	0.144	0–0.6	This paper
1. Noctilionidae	G-band homology	60	1	0	—	This paper
2. Mormoopidae	G-band homology	60	2	0	—	This paper
3. Vespertilionidae	G-band homology	60	11	0.07	0–0.23	This paper
4. Phyllostomatidae	G-band homology	60	25	0.24	0–0.60	This paper
Congeneric Species						
1. All families	G-band homology	9	13	0.197	0–2.2	This paper
2. Noctilionidae	G-band homology	9	1	0	—	This paper
3. Mormoopidae	G-band homology	9	1	0	—	This paper
4. Vespertilionidae	G-band homology	9	4	.05	0–0.56	This paper
5. Phyllostomatidae	G-band homology	9	7	0.48	0–2.2	This paper
Bats	Diploid and Fundamental Numbers	9	15	.059	—	White, 1978a, p. 82
Horses	same	3.5	1	1.395	—	White, 1978a, p. 82
Primates	same	3.8	13	.746	—	White, 1978a, p. 82
Lagomorphs	same	5.0	3	.633	—	White, 1978a, p. 82
Rodents	same	6.0	50	.431	—	White, 1978a, p. 82
Artiodactyles	same	4.2	15	.561	—	White, 1978a, p. 82
Insectivores	same	8.1	7	.187	—	White, 1978a, p. 82
Marsupials	same	5.6	15	.176	—	White, 1978a, p. 82
Carnivores	same	12.9	10	.078	—	White, 1978a, p. 82
Whales	same	6.5	2	.025	—	White, 1978a, p. 82

with values from the Vespertilionidae. The hypothesized primitive karyotypes for both the Phyllostomatidae and the Vespertilionidae were composed primarily of acrocentric chromosomes. A trend within the Phyllostomatidae has been to reduce the number of linkage groups with the majority of species having evolved a karyotype consisting mostly of biarmed elements. In the Vespertilionidae, the trend toward a reduction in number of acrocentrics is evident, but not carried to the extreme found in the Phyllostomatidae.

Short-term Evolution

Within genera where two or more species have been examined, there is even greater variation in estimates of rates of karyotypic evolution (0 to 2.2, see Table 2, Fig. 3). Estimates for four species from the Phyllostomatidae are greater than the highest average estimates by Bush et al. (1977) for any animal group. Estimates by Bush et al. (1977) are highly conservative as they consider only changes in diploid number and fundamental number, whereas we have identified many rearrangements that would not have been observable from diploid and fundamental numbers. When other groups are analyzed by the methods employed here, estimates of amounts of chromosomal evolution will undoubtedly be higher for higher taxa. If the conclusions from this study are applicable to other genera then it will not be possible to simply classify a genus as having a high or low rate of chromosomal evolution. For instance, some genera (such as *Equus*, *Tonatia*, *Vampyressa*, and *Pipistrellus*) which Bush et al. (1977) and/or Bengtsson (1980) classified as having a high rate of karyotypic evolution, un-

doubtedly contain some species which have undergone little or no chromosomal evolution since the primitive karyotype for each genus. The importance of this observation is that any valid analysis of the features which accompany the highest rates of chromosomal evolution must be more sophisticated than simply an overview of the features that characterize the genus.

A histogram showing the frequency of the number of rearrangements in the 54 species for which two or more congeners were studied is shown in Figure 3. There was one unexpected result in the estimates on short-term rates of chromosomal evolution of species within a genus. Although most species (34 of 54 species) have undergone no chromosomal evolution since the establishment of the morphological features which distinguished each genus, four species have undergone a disproportionate amount of change which has totally altered the G-banding pattern of each until its karyotype is essentially not relatable by our G-banded karyotypes to those of its closest relative examined in this study.

Data from these bats suggest that rates of karyotypic evolution do not behave in clock-like fashion and there are periods of relatively rapid and extensive change in some lineages. Patterns of karyotypic evolution in bats generally seem to fit into three categories, conservatism, karyotypic orthoselection (White, 1975), and karyotypic megaevolution (described below). Taxa that are conservative have slow rates of karyotypic evolution and related species differ by few or no chromosomal rearrangements (examples are species of *Myotis, Eptesicus, Pteronotus, Artibeus*). Taxa that evolve by karyotypic orthoselection often have a few or even numerous karyotypic rearrangements when closely related species are compared, but only one or a few kinds of rearrangements are involved. Linkage groups and G-band sequences are conserved and rates of chromosomal evolution vary from low to moderately fast. (Examples are *Rhogeessa*, Bickham and Baker, 1977; *Uroderma bilobatum*, Baker et al., 1979a; as well as most evolution above the generic level in the Phyllostomatidae.) Taxa that have evolved through karyotypic megaevolution have linkage groups and G-band patterns that are remarkably altered through the incorporation of a large number of rearrangements of several different types. Thus, these taxa have undergone extreme chromosomal evolution and the karyotypes of closely related species can be so different that banding homologies cannot be determined with the quality of G-bands currently being produced for systematic study of bats. At this time, we cannot put a time limit on the process, but we suggest that the process is limited to a few million years, and indeed may occur over a much shorter time period, as proposed for karyotypic saltation (Lewis, 1966) and the Breakage-Fusion-Bridge Cycle (McClintock, 1978).

A brief description of the specific situation associated with the four species of bats that have undergone karyotypic megaevolution is as follows:

Tonatia bidens: The genus *Tonatia* consists of six living species in which diploid numbers that characterize species are 2n = 34, 30, 26, and 16. No chromosomal races have been described in any of the species. G-band patterns for *Tonatia bidens* (2n = 16; FN = 20) and *T. minuta* (2n = 30; FN = 56) were described by Patton and Baker (1978). It was possible to relate the karyotype of *T. minuta* to that proposed as primitive for the family (2n = 46; FN = 60, as seen in *Macrotus waterhousii*). The karyotype of *T. bidens*, however, was found to be so divergent that homologies could not be determined between it and its congener *T. minuta*. We estimate that no fewer than 20 rearrangements can account for the karyotypic differences between these two species with most or all of these rearrangements occurring in the *T. bidens* lineage.

Micronycteris minuta and *M. megalotis:* There are 10 living species in the genus *Micronycteris* in which reported diploid numbers are 2n = 40, 38, 32, 30, 28.

Chromosomal races have been described in *M. hirsuta* (2n = 30, 28, Baker, 1979). G-band patterns for *M. minuta* 2n = 28, *M. megalotis* 2n = 40, *M. nicefori* 2n = 28 and *M. brachyotis* 2n = 32 were described by Patton and Baker (1978). The G-banded segments of karyotypes of *M. nicefori* and *M. brachyotis* were relatable to the proposed primitive karyotype for the family. The karyotype of *M. minuta* has been sufficiently rearranged that only six of the autosomal arms of *Macrotus* were identified to homologous segments in the karyotype of *M. minuta.* The karyotype of *M. megalotis* has been rearranged to such an extent that none of the autosomal elements of *Macrotus* could be identified. Additionally, none of the derived chromosomes of *M. megalotis* and *M. minuta* are shared by these two species. We estimate that a minimum of 14 and 15 independent rearrangements are required to account for the respective karyotypic differences that distinguish *M. minuta* and *M. megalotis* from the proposed primitive karyotype for the genus (Patton and Baker, 1978).

Vampyressa pusilla: The genus *Vampyressa* consists of five living species in which the diploid numbers range from 2n = 26, 24, 24 ♀♀ 23 ♂♂, 23 ♀♀ 22 ♂♂, 20, 18, 14. Four chromosomal races have been described (Johnson, 1979) in *Vampyressa pusilla.* G-band patterns for *V. nymphae* (2n = 26; FN = 48) and *V. pusilla* (2n = 18, 20, 23–24; FN = 20) were reported by Johnson (1979). All but two chromosome pairs in the karyotype of *V. nymphae* were identical to chromosomes found in *Artibeus* (proposed as possessing a karyotype like that primitive for the subfamily Stenoderminae). However, none of the chromosomes of the three cytotypes of *V. pusilla* could be related to *Artibeus* or *V. nymphae,* but all of the chromosomal segments could be related among the three cytotypes examined of *V. pusilla.* We estimate that, minimally, 16 rearrangements are required to derive the karyotype of *V. pusilla* from that proposed as primitive for *Vampyressa.*

In addition to the four species of phyllostomatid bats that exhibit karyotypic megaevolution there are several other examples in the literature that may be examples of the process. If these are examples of karyotypic megaevolution, then most of the differences that distinguish the specific karyotypes occurred in the phylogeny of one of the two.

Muntiacus muntjak: The barking (muntjac) deer genus *Muntiacus* consists of five species (Ellerman and Morrison-Scott, 1951). *Muntiacus reevesi* has 2n = 46, while *M. muntjak* has 2n = 6 ♀♀, 7 ♂♂ (Fredga, 1977).

We estimate that no fewer than 20 rearrangements can account for the karyotypic differences between these 2 congeneric species (2n = 46 and 2n = 6) and that most if not all of these changes occurred on the *M. muntjak* lineage.

Callicebus torquatus: Two species of the New World monkey genus *Callicebus* have remarkably different karyotypes (Egozcue, 1969). *C. moloch* has 2n = 46, a diploid number identical to, or not far removed from, the other cebid genera while *C. torquatus* has 2n = 20. We estimate a minimum of 13 rearrangements can account for the differences between these two species.

Gonostoma bathyphilum: Karyotypes of three species of fish of the family Gonostomatidae (Stomiatiformes) were reported by Post (1974). *Gonostoma elongatum* and *Bonapartia pedaliota* have 2n = 48, while *G. bathyphilum* has 2n = 12. We estimate a minimum of 16 rearrangements are required to account for the differences between the 2n = 48 and 2n = 12 karyotypes.

Lasionycteris noctivagans: Two closely related genera of vespertilionid bats are characterized by remarkably divergent karyotypes. *Myotis* (2n = 44; FN = 50) is extremely conservative (Bickham, 1979a). *Lasionycteris,* a monotypic genus, has a karyotype of 2n = 20, FN = 28. G-band patterns (Bickham, 1979a) indicate the 2n = 20 karyotype was derived from the 2n = 44 karyotype by at least 14 rearrangements (Table 1). There is no known

form with an intermediate karyotype between these two genera. *L. noctivagans* is considered to be the most closely related genus to *Myotis* (Koopman and Jones, 1970) and occupies a geographical range that includes most of the United States, southern Canada, and into northern Mexico.

Some features concerning the examples of karyotypic megaevolution described above are the following: 1) The diploid number may or may not (as in *Micronycteris minuta*) be strongly altered, and it may be raised or lowered. 2) The types of rearrangements involved include many which should cause severe meiotic problems (pericentric inversions, telomere-centromere translocations, etc.). 3) Based on a cladistical analysis, closely related species have a karyotype similar to that primitive for the genus. 4) In bats, the geographic distribution of these species is as large or larger than that of most bats which have a conservative rate of chromosomal rearrangement. *Tonatia bidens* is distributed from Guatemala south through Central America and most of northern South America. *Micronycteris megalotis* is distributed from eastern and western Mexico throughout Central America and most of northern and central South America. *Micronycteris minuta* ranges from Nicaragua to Brazil and eastern Peru. *Vampyressa pusilla* is distributed from southern Mexico throughout Central America and northern and central South America. Although these rearrangements may have arisen in a bottleneck phenomenon in peripheral isolates, as described in karyotypic saltation by Lewis (1966), available data from these same examples do not lead to such a conclusion. 5) The degree to which these species are distinguished on an exomorphological and cranial basis from other congeners is not greater than that which distinguishes other species in the same genus which have not undergone such a radical reorganization of the karyotype. 6) In two of the four cases (*Tonatia bidens* and *Micronycteris minuta*), no speciation or chromosomal variation is known. Chances are that in most cases congeners will not be found that have intermediate karyotypes to document step-wise evolution (Baker, 1979). 7) The degree to which these four taxa are karyotypically distinguished from their respective congeners is far greater than that which distinguished the respective proposed primitive karyotype for the families Mormoopidae, Noctilionidae and Phyllostomatidae from each other and of the same order of magnitude as the karyotypic distinctness which separates most other families of bats (Bickham and Baker, 1979). The significance of this observation is that all of the stage I karyotypic evolution in the canalization process (Bickham and Baker, 1979) for bats may require no greater time than that involved in the divergence of these congeneric species.

Is karyotypic megaevolution simply the extreme of the pattern observed in other species, or have these species encountered a different biological phenomenon? Several papers explain why rates of karyotypic evolution vary between taxa. In the following paragraphs we attempt to relate these theories as a possible explanation of karyotypic megaevolution.

Low Deme Size, Local Extinctions, Bottlenecks and Colonization

Several explanations of chromosomal evolution (White, 1968; Arnason, 1972; Bush, 1975; Hall, 1973; Wilson et al., 1975; Bush et al., 1977; Lewis, 1966; Lande, 1979) in animals account for variation in rates of chromosomal evolution by fixation of new arrangements in small inbred demes with the process of local bottlenecks, extinction and colonization accounting for the spread of rearrangements. In a summary of organisms with "great variation in karyotypic patterns," Arnason (1972) concluded that 1) high reproduction, 2) restricted mobility, and 3) environment with delimited niches, characterized the species that underwent extensive chromosomal evolution. Clearly, *Tonatia bidens, Micronycteris mega-*

lotis, M. minuta, and *Vampyressa pusilla* do not fit Arnason's first two criteria. The reproductive biology of phyllostomatid bats has been reviewed by Wilson (1979) and he concludes that most species have seasonal polyestry, producing no more than two young per year. Data for all four of the species of bats (Wilson, 1979) which have experienced karyotypic megaevolution are compatible with the conclusion of a reproductive pattern of seasonal polyestry (one young per reproductive period and two reproductive cycles per year). On mobility, these bats may not be as vagile as might be predicted for a flying mammal but it is certainly doubtful that these species have a vagility level as low as most rodents or insectivores. Data from another species of phyllostomatid bat, *Uroderma bilobatum* (which has undergone extensive evolution from the proposed primitive karyotype for the subfamily Stenoderminae as well as karyotypic raciation resulting from three chromosomal rearrangements), do not suggest low vagility (Baker, 1979).

We do not know of any data which suggest that the four species with a rapid rate of chromosomal rearrangement incorporation are different in deme size and population biology from their congeners or from most other species in the Phyllostomatidae which have a conservative rate. It would seem to us that these four examples would be excellent choices for studies on population biology to test the validity of the deme size model as an explanation for the process of karyotypic megaevolution.

Canalization Model

Another explanation of why species undergo a series of radical changes in the karyotype is that when a lineage invades a new adaptive zone, a greater number of new rearrangements are at a selective advantage (Bickham and Baker, 1979) as a result of a species being under a new set of selective pressures. We cannot at this time find any data to suggest that these four bat species have invaded a new adaptive zone and the canalization process does not appear to explain examples of karyotypic megaevolution.

Speciation Models

Several papers (Lewis, 1966; Fredga, 1977; Bush et al., 1977; White, 1978b) explain chromosomal evolution as part of the speciation process, with new arrangements being selected as isolating mechanisms. The effectiveness of chromosomes as isolating mechanisms has been questioned (Key, 1968; Bickham and Baker, 1980). We do not see any reason to suppose that these radical changes are selected as part of a speciation process. In some groups, such as bats and whales, chromosomal change is phyletic (a new karyotype becomes characteristic of a species without production of a sister species), and chromosomal change does not play a major role as an isolation mechanism. Several factors were involved in our reaching the above conclusions. 1) In bats, there is no correlation between how speciose a genus is and the amount of chromosomal rearrangements found within the genus. This is exemplified by examining the data from the three most speciose genera of bats (*Myotis* with 68 species, *Pipistrellus* with 50 and *Eptesicus* with 31). *Pipistrellus* has several different species with distinct karyotypes as well as several species which have undergone no chromosomal change; however, of all the mammals studied to date, *Myotis* and *Eptesicus* (Bickham, 1979a and 1979b) seem to be among the most conservative. This is in contrast to the conclusions that there is a strong correlation between degree of speciation and a high rate of chromosomal evolution in animals (Bush et al., 1977; Bengtsson, 1980). 2) For chromosomal rearrangements to play an important role in isolation, they act as a post-mating mechanism which is inefficient, especially in organisms which mate in a synchronized pattern. For example, consider the species of bat which mates once a year and produces a single young. If the female mates with an individual which has a karyotype

sufficiently different from her own, to be an effective post-mating isolating mechanism she would still become pregnant and either lose the embryo to developmental problems or more likely produce a viable young which has reduced fertility but which could still compete for food and space resources. Each time a female makes such a mating error, the results are a 5–10% or greater loss in lifetime reproduction potential (estimate 20 young maximum per lifetime). How much more efficient is a behavioral premating isolating mechanism where a female makes the correct choice in mates and produces the maximum number of normal, fertile young during her lifetime? Behavioral premating isolating mechanisms appear common in bats where several closely related species may be sympatric (live in the same cave and even be found in the same cluster). Morphological differences that distinguish some of these forms are so slight (in *Myotis,* for instance) that professional mammalogists often have trouble with field identification, yet these forms seldom, if ever, hybridize. In many cases such sympatric forms have undergone no chromosomal divergence. 3) For a postmating isolating mechanism to be most effective, a narrow zone between cytotypes is required (White, 1978a) to reduce the production of F_1s and backcross individuals. In bats where one zone has been studied in detail (Baker, 1979) the zone was 200 km wide and reflected the high level of vagility of bats. 4) For chromosomes to be effective postmating isolating mechanisms, rearrangements must reduce fertility of heterozygotes to a point where the heterozygote will play a reduced role in the production of the next generation. Data from Peters' tent-making bat do not support the conclusion that such negative heterosis for three rearrangements is adequate to keep F_1s from playing a significant role in production of the next generation. 5) In some cases where two species have evolved radically different karyotypes, viable offspring can sometimes still be produced (for instance, the apes, Myers and Shafer, 1979), showing that many such rearrangements still are a poor post-mating isolating mechanism. If chromosomal divergence were of primary importance in the production of these species pairs, such multiple rearrangements should have produced a greater degree of isolation than is found in apes and *Uroderma* (Myers and Shafer, 1979; Baker, 1979).

Factors Independent of Demographic and Vagility Characteristics

One area that may be the most promising in explaining cases of rapid reorganization of the genome may be genetic and environmental factors which increase rates of chromosomal mutation. Examples of such factors are discussed by McClintock (1978). However, such an increased rate of chromosomal mutation still does not explain how many such rearrangements with large negative heterosis in meiosis become characteristic of a species (as in examples of karyotypic megaevolution). Other factors could be involved, such as decreased crossing over. Unfortunately, our study does not provide data on such factors; however, chromosomal mutation rates are an important factor in explaining differential rates of chromosomal incorporation (Lande, 1979).

In summary, factors which appear the most attractive in explaining karyotypic megaevolution are an increased mutation rate and a reduction of meiotic constraints on chromosomal heterozygotes. It appears less likely that karyotypic megaevolution will be adequately explained by theories based on vagility, reproductive patterns, speciation rates and inbreeding. Clearly, cladistic studies of comparable G- and C-band data are needed from other major vertebrate taxa before the exact extent of karyotypic megaevolution can be determined. It does appear that some taxa such as bats, which have been labeled "conservative" in their rate of chromosomal rearrangement incorporation, cannot be unequivocally placed in this category. It should be an

interesting task determining the factors which result in one species having a totally reorganized genome while a closely related species undergoes no change.

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