

LITERATURE REVIEW

CYTOTAXONOMY AND CHROMOSOMAL EVOLUTION
OF THE BATS
(*MAMMALIA-CHIROPTERA*)

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SUMMARY

An extensive literature search has compiled diploid chromosome numbers for 110 species of bats. Karyotypes for 87 of these have been reported and are used as the basis for defining tentative cytological relationships within the families *Pteropodidae*, *Rhinopomatidae*, *Phyllostomatidae*, *Desmodontidae*, *Rhinolophidae*, and *Vespertilionidae*. Before more definitive intra-familial relationships can be established, karyotypes from more species of the order *Chiroptera* must be reported.

The earliest fossil remains from Eocene deposits in Wyoming and Germany reveal almost modern bats with well-developed webbed wings (1, 21, 32). By the end of the Eocene and the first part of the Oligocene many of the modern families of bats had appeared and are represented in fossils from these periods (50).

The ancient line from which the bats developed is believed to be an extinct small arboreal insectivore. There is no fossil evidence for phylogeny and any theories on the origin of the *Chiroptera* must rest on speculation (8).

Both regional gene duplication and polyploidization have played important roles in progressively increasing the amount of nuclear D.N.A. in lower vertebrates (5, 33, 35, 40, 49). Establishment of the chromosomal sex-determining mechanism in higher vertebrates has tended to stabilize each genome with its own particular amount of D.N.A. and hence number of gene loci. Diploid cells of eutherians, monotremes, marsupials, and certain birds and reptiles all have about the same amount of nuclear D.N.A.: 7.0×10^{-9} mg (39).

The karyotypic evolution of the higher vertebrates from their ancestors has not been due to polyploidization, but to mutations at existing gene loci with accompanying rearrangements

of the chromosomes. The purpose of this paper is to review the literature on bat chromosomes and present some preliminary conclusions as to chiropteran phylogeny based on chromosomal evidence.

The first studies of bat chromosomes were performed using gonadal material (7, 24, 31). Most recent reports of bat karyotypes have been based on chromosomes isolated from bone marrow using techniques modified from that of TJO and WHANG (52). Other workers prefer to use lung, spleen, liver, gonad, or fibroblast cultures as the tissue source for the chromosomes (*eg.*, 16).

According to classical taxonomic methodology there are seventeen families in Chiroptera. Diploid numbers from at least one species in twelve families have been reported (Table 1). Of these families, karyotypes from enough species from the families *Pteropodidae*, *Rhinopomatidae*, *Desmodontidae*, *Phyllostomatidae*, *Rhinolophidae*, and *Vespertilionidae* have been published to warrant the attempt to begin to define intra-ordinal relationships on the basis of chromosome number and morphology.

FAMILIES PTEROPODIDAE AND RHINOPOMATIDAE

The suborder *Megachiroptera* is composed of the family *Pteropodidae* which has about 39 recognized genera. One of the most ancient families of *Microchiroptera* is believed to be *Rhinopomatidae* (23). The karyotype of *Rousettus leschenaulti* (*Pteropodidae*), *Rhinopoma hardwickii* (*Rhinopomatidae*), and several species of *Pteropus* (*Pteropodidae*) are quite similar in both diploid number and F.N. (The fundamental number (F.N.) is here defined to be the number of chromosomal arms among the autosomes of the diploid karyotype. Acrocentrics and telocentrics have one arm: subtelocentrics, metacentrics, and submetacentrics have two arms. Minute chromosomes whose morphology cannot be accurately determined are counted as acrocentrics). In both families the X chromosomes are the same relative size and differ only in centromere position. The acrocentric Y is present in both. The major differences between the karyotypes can be explained by pericentric inversions (47).

All *Microchiroptera* echolocate, but only *Rousettus* in *Megachiroptera* does so (23). On the basis of these and other similarities in skeleton and fetal membranes, *Rhinopomatidae* may be more closely related to *Pteropodidae* and especially to *Rousettus* than to other *Microchiroptera*. The rhinopomatid bats may represent species which early diverged from the ancestral line to form the larger, more modern suborder *Microchiroptera* (47).

FAMILY PHYLLOSTOMATIDAE

Considerable study has been devoted to *Macrotus waterhousii*. Specimens collected in Mexico (subspecies *mexicanus*) have the same F.N. but different diploid number and karyotype when compared to specimens from Arizona and California in the United States (subspecies *californicus*). The direction of this intraspecific change cannot be determined, but centric fusion of six telocentric pairs in species with fourteen such pairs would not alter the F.N. and would increase the number of non-telocentric chromosomes by three pairs and reduce the diploid number from 46 to 40. The change may have been from lower to higher number of banded chromosomes (36, 37).

Subfamilies *Glossophaginae*, *Carollinae*, and *Stenoderminae* are significant because they contain genera which possess the so-called XX/XY₁Y₂ system of sex chromosomes. Robertsonian fusion of the original X with an autosome could have reduced the F.N. by two in both sexes, and the diploid number by two in the female but by only one in the male. The result of this translocation process would be a new X composed of the original X and fused autosome, a new « Y » which is homologous with the fused autosomal portion of the new X, and the original Y (20, 39).

Carollia (*Carollinae*) is a classic example of this X-autosome translocation. Fusion with an autosome by one of the arms of the original metacentric X yielded the present subtelocentric X

and the XY_1Y_2 mechanism. The development of *Choeroniscus* is more difficult to explain. It is the only genus in the subfamily *Glossophaginae* to have this mechanism of sex chromosomes. The relationship of this karyotype to that of *Carollia* is not clear. The two genera may not be closely related and could represent parallel developments. *Artibeus jamaicensis*, *lituratus*, and *toltecus* of the subfamily *Stenoderminae* all have essentially the same karyotype and the XY_1Y_2 mechanism. *A. turpis* differs only by having a metacentric Y. This morphology suggests the fusion of Y_1 and Y_2 . Thus *turpis* may be more advanced chromosomally than the other members of the genus (20).

BAKER (2) has made extensive studies on the chromosomes of phyllostomid bats and has arranged their karyotypes into seven related groups.

a) *Pteronotus* (*Chilonycterinae*)

This genus is in a subfamily which is distinctly primitive (23). Its karyotype is somewhat similar to species in *Phyllostomatinae*, but there are enough differences to place it in a distinct chromosomal group.

b) *Cnecronycteris* and *Choeroniscus* (*Glossophaginae*), and *Carollia* (*Carollinae*)

This group is characterized by low diploid numbers (16-21) and FN (?24-36), the $XX/X_1Y_1Y_2$ mechanism, and about twice as many metacentric and subtelocentric as acrocentric chromosomes.

c) *Leptonycteris* and *Glossophaga* (*Glossophaginae*), *Phyllostomus*, *Trachops*, and *Macrotus* (*Phyllostomatinae*)

All of these genera have a high F.N. (50-60), diploid number of 30 or greater, and similar karyotypes lacking telocentric chromosomes, except for *Macrotus*. Centric fusion of the telocentrics in this genus could produce a karyotype similar to that of the others. The differences in F.N. and diploid number among these genera are important and indicate that significant chromosomal changes have occurred since their derivation from a proposed common ancestor.

d) *Anoura* (*Glossophaginae*)

This genus has a karyotype that is not related to any other in any obvious way.

e) *Micronycteris* (*Phyllostomatinae*)

The large F.N. (68) and unusually large number of subtelocentrics indicate extensive inversions from the karyotype of an ancestral stock. This karyotype is also not clearly related to another genus in this family.

f) *Sturnira* (*Sturnirinae*), *Artibeus*, *Vampyrops*, *Chiroderma*, *Euchisthenes* and *Centurio* (*Stenoderminae*)

Sturnira, *Artibeus*, and *Vampyrops* have identical autosomes. The XY_1Y_2 mechanism in *Artibeus* has been discussed above. *Sturnira* and *Vampyrops* have subtelocentric single Y chromosomes. These may have been derived from a centric fusion of Y_1 and Y_2 , or the double Y mechanism in *Artibeus* may have been formed by the centric fission of an original biarmed Y chromosome as present in the first two genera. In either case, *Sturnira* is closely related to the other genera of *Stenoderminae*, and *Sturnirinae* does not represent a separate subfamily.

Euchisthenes has a karyotype similar to that of *Sturnira*. *Centurio* and *Chiroderma* are less closely related to the others in the group and have undergone extensive rearrangements of their chromosomes during species differentiation.

TABLE I a
The Chromosomes of the Bats by Families
 Les Chromosomes des Chauves Souris rangées par familles

Taxa	2n*	FN	M et SM	ST	A	T	MI	X	Y	References
ORDER CHIROPTERA										
SUBORDER MEGACHIROPTERA										
Family <i>Pteropodidae</i>										
<i>Cynopterus sphinx gangeticus</i>	34	58	11	2	3	—	—	ST	A	46, 47
<i>Eidolon helvum</i>	34	—	—	—	—	—	—	—	—	27
<i>Pteropus giganteus</i>	38	—	—	—	—	—	—	—	—	26
<i>P. giganteus giganteus</i>	38	72	15	3	—	—	—	ST	A	46, 47
<i>P. dasymallus inopinatus</i>	38	70	17	—	—	I	—	SM	MI	24
<i>Rousettus leschenaulti</i>	36	68	13	4	—	—	—	ST	A	42
SUBORDER MICROCHIROPTERA										
Family <i>Desmodontidae</i>										
<i>Desmodus rotundus murinus</i>	28	52	13	—	—	—	—	SM	T	19a
Family <i>Emballonuridae</i>										
<i>Balanopteryx plicata</i>	32	—	—	—	—	—	—	—	—	45
<i>Taphozous longimanus</i>	42	—	—	—	—	—	—	—	—	46
<i>T. longimanus longimanus</i>	42	—	—	—	—	—	—	—	—	46, 47
<i>T. melanopogon</i>	42	—	—	—	—	—	—	—	—	46, 47
Family <i>Hipposideridae</i>										
<i>Hipposideros ater ater</i>	32	—	—	—	—	—	—	—	—	46
<i>H. bicolor</i>	32	—	—	—	—	—	—	—	—	48
<i>H. bicolor bicolor</i>	32	—	—	—	—	—	—	—	—	48
<i>H. fulvus</i>	32	—	—	—	—	—	—	—	—	46
Family <i>Megadermatidae</i>										
<i>Megaderma lyra lyra</i>	54	92	20	—	6	—	—	SM	T	43, 44

TABLE I b
The Chromosomes of the Bats by Families
 Les Chromosomes des Chauves Souris rangées par familles

Taxa	2n*	FN	M et SM	ST	A	T	MI	X	Y	References
Subfamily Glossophaginae.										
<i>Anoura geoffroyi</i>	30	56	7	7	—	—	—	SM	MI	2, 20
<i>Choeromiscus godmani</i>	♂19	32	3	5	—	—	—	M	Y ₁ ST Y ₂ A	2, 20
<i>Choeronycteris mexicana</i>	♀16	24?	4	2	2	—	—	?	?	2, 20
<i>Glossophaga allicola</i>	32	60	13	2	—	—	—	SM	MI	2
<i>G. comissarisii</i>	32	60	13	2	—	—	—	SM	MI	2, 20
<i>G. soricina</i>	32	60	13	2	—	—	—	SM	MI	2, 20
<i>Leptonycteris sanborni</i>	32	60	13	2	—	—	—	SM	MI	2, 20
Subfamily Sturnirinae										
<i>Sturnira lilium</i>	30	56	10	4	—	—	—	ST	SM	2, 19c, 20, 22, 45
<i>S. ludovici</i>	30	56	10	4	—	—	—	ST	SM	2, 20, 22, 45
Subfamily Stenoderminae										
<i>Artibeus jamaicensis</i>	♂31, ♀30	56	10	4	—	—	—	ST	Y ₁ MI	A 2, 19b, 20
<i>A. jamaicensis jamaicensis</i>	♂31, ♀30	56	10	4	—	—	—	ST	Y ₂ Y ₁ MI	A 22
<i>A. lituratus</i>	♂31, ♀30	56	10	4	—	—	—	ST	Y ₂ Y ₁ MI	A 2, 19b, 20
<i>A. lituratus lituratus</i>	♂31, ♀30	56	10	4	—	—	—	ST	Y ₂ Y ₁ MI	A 6
<i>A. lituratus palmarum</i>	♂31, ♀30	56	10	4	—	—	—	ST	Y ₂ Y ₁ MI	A 22

	♂31, ♀30	56	10	4					ST	Y ₁ Y ₂ SM	A ²⁰ MI
<i>A. toltecus</i>				4					—		
<i>A. turpis</i>	30	56	10	4					ST		2, 20
<i>A. turpis namus</i>	30	—	—	—					—		45
<i>Centurio senex</i>	♀28	52?	10	4					?		2, 20
<i>Chiroderma villosum</i>	26	48	9	4					ST	SM	2, 20
<i>Enchisthenes hartii</i>	♀30	56?	8	7					?		2, 20
<i>Uroderma bilobatum</i>	44	48	1	2	18				ST	SM	2, 20
<i>Vampyrops helleri</i>	30	56	10	4					ST	SM	2, 20
Family Rhinolophidae											
<i>Rhinolophus blasii</i>	58	—	—	—					—		16
<i>R. euryale</i>	58	60	2	—	24			2	SM	MI	7, 9
<i>R. ferrum-equinum</i>	58	60	2	—	24			2	SM	MI	7, 9
<i>R. ferrum-equinum nippon</i>	58	60	2	?	?			?	T	MI	24
<i>R. hipposideros</i>	58	60	3	—	22			2	M	MI	7, 13, 31
<i>R. mehelyi</i>	58	64	4	—	24			—	SM	MI	18
Family Rhinopomatidae											
<i>Rhinopoma hardwickei</i>	36	68	15	2				—	SM	A	46, 47
Family Vespertilionidae											
Subfamily Miniopterinae											
<i>Miniopterus schreibersi</i>	46	50	3	—	17			2	M	MI	7, 10, 31
Subfamily Nyctophilinae											
<i>Antrozous pallidus</i>	46	50	3	—	19			—	SM	MI	3, 19b, 45
Subfamily Vespertilioninae											
<i>Barbastella barbastellus</i>	32	50	10	—	3			2	M	MI	7, 15, 31
<i>Eptesictus andamanis</i>	50	48	—	—	24			—	SM	A	3
<i>E. furinalis</i>	50	48	—	—	24			—	SM	A	3

<i>Nyctalus noctula</i>	42	50	5	—	12	—	3	M	A	17
<i>Nycticeus humeralis</i>	46	48	2	—	20	—	—	SM	A	3, 45
<i>Pipistrellus affinis</i>	36	50	7	1	9	—	—	M	A	44, 46
<i>P. hesperus</i>	28	46	10	—	3	—	—	SM	A	3, 45
<i>P. kuhlii</i>	44	50	4	—	15	—	2	M	A	11
<i>P. mimus</i>	38	48	6	—	12	—	—	M	A	44, 46
<i>P. mordax</i>	34	46	7	—	9	—	—	M	A	44, 46
<i>P. nathusii</i>	44	—	—	—	—	—	—	—	—	7, 24
<i>P. pipistrelli</i>	42	—	—	—	—	—	—	—	—	7, 24
<i>P. savii</i>	44	50	4	—	15	—	2	M	A	17
<i>P. subflavus</i>	30	56	14	—	—	—	—	SM	A	3, 45
<i>P. subflavus subflavus</i>	30	56	11	3	—	—	—	M	SM	19a
<i>P. tralatus abramus</i>	26	44	10	—	—	2	—	ST	T	51
<i>Plecotus auritus</i>	32	—	—	—	—	—	—	—	—	7
<i>P. phyllotis</i>	30	50	11	—	3	—	—	SM	A	3, 4
<i>P. rafinesquii</i>	32	50	10	—	5	—	—	A	A	4
<i>P. townsendii</i>	32	50	10	—	5	—	—	A	A	3, 4, 45
<i>Rhogeessa gractlis</i>	44	50	3	1	17	—	—	SM	SM	3
<i>R. parvula</i>	44	50	3	1	17	—	—	SM	SM	3
<i>R. tumida</i>	42	50	3	2	15	—	—	SM	SM	3

(*) Legend:

- ²ⁿ Diploid number.
- FN Fundamental number (See text for definition).
- M Metacentric pairs.
- SM Submetacentric pairs.
- ST Subtelocentric pairs.
- A Acrocentric pairs.
- T Telocentric pairs.
- M Minute pairs.
- X Morphology of the X chromosome.
- Y Morphology of the Y chromosome.

g) *Uroderma* (*Stenoderminae*)

The presence of eighteen acrocentric pairs makes this karyotype unique within the family. Until other species of this genus are karyotyped, it must represent a separate group. The genus may represent a primitive karyotype that has been maintained without gross changes while the rest of the phyllostomid stock continued to evolve chromosomally.

FAMILY DESMODONTIDAE

Taxonomically this family is closely related to *Phyllostomatidae* (23). The karyotype of *Desmodus rotundus murinus* is the only reported one for this family, but it is superficially similar to those of *Centurio* and *Chiroderma* in *Stenoderminae*. More karyotypes must be reported before any more definitive relationship can be established.

FAMILY RHINOLOPHIDAE

The karyotypes of *Rhinolophus euryole* and *ferrum-equinum* are essentially identical. *R. hipposideros* has two less chromosomes than these species but the same F.N. The large pair of metacentrics in *hipposideros* could have been formed by the centric fusion of two pairs of acrocentrics in the ancestor of these species (9). The derivation of *meheyli* from *euryole* is more complex, and the relationship cannot be clearly defined on the basis of chromosomes alone.

FAMILY VESPERTILIONIDAE

This has been the most extensively studied family in the order. BAKER and PATTON (3) have reported a large number of karyotypes from this family and have organized their results into four groups based on similar karyotypes. Species reported by other workers fit reasonably well into this tentative schema.

- a) *Myotis*, *Rhogeësa*, *Eptescius*, *Nyctalus*, and *Nyctecius* (*Vespertilioninae*),
Miniopterus (*Miniopterinae*), and *Antrozous* (*Nyctophilinae*)

This group is characterized by a high diploid number (42-50), stable F.N. (48-50), and a large number of acrocentric chromosomes.

All of the reported North American *Myotis* have the same karyotype and must have developed from the same line (3). Two European species, *M. myotis* and *capaccinii*, differ by having a metacentric X and an acrocentric Y. A pericentric inversion in each of the sex chromosomes could change one karyotype into the other.

- b) *Plecotus*, *Euderma*, and *Barbastella* (*Vespertilioninae*)

These three genera are closely related. *Barbastella* is considered to be the representative of the ancestral karyotype with diploid number of 32 and a submetacentric X. Centric fusions and pericentric inversions could produce *Euderma* with its subtelocentric X and autosome pair, and diploid number of 30. Similar events could have produced the separate species of *Plecotus* (56).

- c) *Lasiurus* and *Pipistrellus* (*Vespertilioninae*)

The genus *Lasiurus* presents examples of both intrageneric and intraspecific karyotypic variation. *L. borealis*, *cinerus*, *ega panamensis*, *ega xanthinus*, and *seminolus* have the same

diploid number (28) and F.N. (46) and very similar karyotypes. *L. borealis blossevillii* and *ega argentinus* have lower diploid numbers (22-24) and F.N. ten less than the first species. *L. ega intermedius* and *intermedius* have diploid numbers (26) and F.N. (40-42) in between these two extremes. *L. borealis blossevillii* is thus cytologically more closely related to *ega argentinus* than to its general species.

Pipistrellus is a large genus with more than fifty species. More karyotype reports are needed before any meaningful relationships can be defined within this genus.

d) *Lasionycteris* (*Vespertilioninae*)

The one genus in this group is characterized by low diploid number (20) and F.N. (38). Its karyotype is unlike that of any known vespertilionid bats and awaits future explanation.

Using chromosome numbers and morphology, tentative groupings of genera within several families of the bats have been defined. This approach to taxonomy, based solely on the appearance of the chromosomes, is useful but must not be overextended. The Tobacco Mouse (*Mus paschivinus*, $2n = 26$) from Switzerland differs from the Common Mouse (*Mus musculus*, $2n = 40$) by seven Robertsonian fusions. There are no known intermediate species, and the two share biochemical gene loci (38). The Indian Muntjac (*Muntiacus muntjak*) has diploid number 6 in the male and 7 in the female, while closely related species and genera have diploid numbers from 46 to 70 (57, 58).

These results support the contention that certain types of chromosomal rearrangements may play a role in species formation, but that there does seem to be a degree of independence between organic and chromosomal evolution such that changes in the karyotype are not necessarily the cause of speciation (34, 54, 55). In *Chiroptera* the karyotype is generally conservative at the generic level. The widespread genera such as *Myotis* appear to maintain one karyotype despite diverse evolutionary pressures. Anomalous groups such as *Lasiurus* accentuate the weakness of all such generalities. Before more definitive statements can be made regarding relationships within the family, more karyotypes must be reported. Above all, the chromosomal data must be correlated with traditional taxonomic evidence in order that intrafamilial relationships may be more meaningfully defined. It is hoped that this review will stimulate continued effort to obtain karyotypes of more species of *Chiroptera*.

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RÉSUMÉ

CYTOTAXONOMIE ET ÉVOLUTION CHROMOSOMIQUE
DE LA CHAUVÉ-SOURIS (*MAMMALIA-CHIROPTERA*)

Une compilation extensive a fourni le nombre diploïde des chromosomes de 110 espèces de Chauves-Souris. A partir de 87 caryotypes connus, on s'est efforcé d'établir les relations cytologiques existant à l'intérieur des familles suivantes : *Pteropodidae*, *Rhinopomatidae* et *Vespertilionidae*. Pour établir des relations interfamiliales absolument certaines, la connaissance du caryotype de nouvelles espèces est encore nécessaire.

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