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COMPARATIVE CYTOGENETICS OF THE NEW WORLD LEAF-NOSED BATS (PHYLLOSTOMATIDAE)

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SUMMARY. Karyotypic data on the New World Leaf-Nosed Bats have been summarized and discussed. Three sex determining systems are found within the family. The diploid number ranges from 16—46 and the fundamental number ranges from 20—68. Karyotypic data are available for 77 of the approximately 130 species and for 28 species the data are given for the first time. At phyletic tree for the subamily Stenoderminae based primarily on chromosome values has been constructed.

The family of new world leaf-nosed bats is the most complex in feeding divergence and cranial morphology. Associated with this adaptive radiation has been considerable divergence in karyotypic parameters. Three sex determining systems are found within the family, the diploid number ranges from 16—46 and the fundamental number ranges from 20—68. Karyotypic data are available for 77 of the approximately 130 species (Table 1). A discussion of these data are presented below.

Diploid number. The frequency of various diploid numbers reported for the family is presented in Figure 1. In Figures 1—4 the values for each chromosomal race of *Macrotus waterhousii*, *Uroderma bilobatum*, and *Vampyressa pusilla* are plotted. Although the range of the diploid numbers is wide (16—46) over 50 per cent of the species studied in this family have a diploid number of 30—32. Ten species have a number above 32, whereas 27 have a diploid value below thirty. When these values are plotted on normal probability graph paper, Figure 2, (a method for testing for normality of distribution 23), the distribution of these values is found to be skewed toward the lower values.

The diploid numbers of 30—32 are found in species of the subfamilies Phyllostomatinae, Glossophaginae, Stenoderminae, Phyllonycterinae, and Desmodontinae. In the only subfamily, Caroliinae, where no species have a 2N = 30—32, there are only two genera and the species of one genus, *Carollia* (2N = 20, 21, & 22), have a value lower than 30, and the species of the other genus, *Rhinophylla* (2N = 32—36), have values above 32. Because the 2N = 30—32 diploid value is so frequent and because this diploid value is widely distributed within the family, I suspect that a value of 30 or 32 is primitive for the family. Because the species with 2 N = 30 ♀♀, 31 ♂♂ appear to have been derived by a translocation of an autosome to the X chromosome (reducing the number from 32), I suspect that the primitive number for the family was 32.

If the above assumption is true, then thero has been a greater tendency to reduce the diploid value rather than to increase it (Figures 1 and 2).

Fundamental number. The frequency of the various FN values (in this case FN is defined to be the number of arms of the auto-

TABLE 1

CHROMOSOMAL DATA FOR PHYLLOSTOMATID BATS

SPECIES	2N	FN	X	Y	Authority
Subfamily Phyllostomatinae					
Chrotopterus auritus Peters	28	52	SM	A	Yonenaga, et al., (25)
Lonchorhina aurita Tomes	32	60	M	A	Baker & Hsu, (6)
Macrotus waterhousii Gray	40	60	SM	A	Osborne, (21)
	46	60	SM	A	Baker, (1)
	40	60	M	SM	Kniaseff, et al., (17) & Nelson Rees, et al., (20)
Micronycteris megalotis Gray	40	68	ST	A	Baker, (1)
Micronycteris schmidtorum Sanborn	38	66	ST	A	This paper
Micronycteris nicefori Sanborn	28	52	M	A	Baker & Hsu, (6)
Micronycteris hirsuta (Peters)	28	32	A	A	This paper
Micronycteris minuta (Gervais)	28	50	ST	A	This paper
Mimon crenulatum (E. Geoffroy St.-Hilaire)	32	—	—	—	Baker & Hsu, (6)
	32	58—60	M	A	Baker, et al., (4)
Phylloderma stenops Peters	32	58	—	—	Baker & Hsu, (6)
	32	58	M	A	This paper
Phyllostomus discolor Wagner	32	60	SM	A	Baker, (2)
	32	60	SM	A	Kiblisky, (16)
	32	60	—	—	Yonenaga, et al. (25)
Phyllostomus hastatus Pallas	32	58	SM	A	Yonenaga, et al., (25)
	32	58	SM	A	Baker & Hsu, (6)
	32	58	SM	A	Kiblisky, (16)
Phyllostomus elongatus E. Geoffroy St-.Hilaire	32	58	SM	A	This paper
Tonatia minuta Goodwin	30	56	SM	A	Baker & Hsu, (6)
Tonatia bidens Spix	16	20	M	A	Baker & Hsu, (6)
Trachops cirrhosus Spix	30	56	ST	A	Baker, (1)
Vampyrum spectrum (Linnaeus)	30	56	—	—	Baker & Hsu, (6)
	30	56	SM	A	This paper
Subfamily Glossophaginae					
Anoura geoffroyi Gray	30	56	SM	A	Baker, (1)
	30	56	SM	A	Baker & Hsu, (6)

Table 1 continued

SPECIES	2N	FN	X	Y	Authority
Anoura caudifer (E. Geoffroy St.-Hilaire)	30	56	SM	A	This paper
Choeroniscus godmani Thomas	19	32	SM	ST-A	Baker, (1), and Hsu, et al., (14)
Choeroniscus intermedius (J. A. Allen and Chapman)	20		?	?	This paper
Choeronycteris mexicana Tschudi	16	24	?	?	Baker, (1)
	16	24	SM	SM	This paper
Hylonycteris underwoodi Thomas	16	24	—	—	This paper
Glossophaga soricina Pallas	32	60	M	A	Baker, (1)
	32	60	M	A	Baker & Hsu, (6)
Glossophaga alticola Davis	32	60	M	A	Baker, (1)
Glossophaga commissarisi Gardner	32	60	M	A	Baker, (1)
Leptonycteris sandborni Hoffmeister	32	60	M	A	Baker, (1)
Leptonycteris nivalis (Saussure)	32	60	—	—	This paper
Lichonycteris obscura Thomas	28	50	SM	A	This paper
Lonchophylla thomasi J. A. Allen	30	(34)	—	—	This paper
Lonchophylla robusta Miller	28	50	SM	A	This paper
Monophyllus redmani Leach	32	60	SM	A	Baker & Lopez, (7)
Subfamily Carolliinae					
Carollia subrufa Hahn	20—21	36	ST	A-A	Baker, (1)
	20—21	36	ST	A-A	Baker & Bleier, (3)
Carollia perspicillata Saussure	20—21	36	ST	A-A	Baker, (1), and Hsu, et al., (14)
	20—21	36	ST	A-A	Yonenaga, et al., (25)
	20—21	36	ST	A-A	Kiblisky, (16)
	20—21	36	ST	A-A	Baker & Hsu, (6)
	20—21	36	ST	A-A	Baker & Bleier, (3)
Carollia castanea H. Allen	20—21	36	ST	A-A	Baker & Bleier, (3)
	22	36	SM	A	Patton & Gardner, (22)
Rhinophylla pumilio Peters	36	62	M	A	Baker & Bleier, (3)
Rhinophylla fischerae Carter	34	56	SM	A	Baker & Bleier, (3)
Subfamily Stenoderminae					

Table 1 continued

SPECIES	2N	FN	X	Y	Authority
Artibeus phaeotus (Miller) 6 = *A. turpis*	30	56	ST	SM	Baker, (1)
Artibeus cinereus Gervais 7	30—31	56	ST	SM-M	Baker & Hsu, (6)
Artibeus toltecus Saussure 7	30—31	56	ST	A-A	Baker, (1)
Artibeus aztecus Andersen 7	30—31	56	ST	A-A	This paper
Artibeus literatus Lichtenstein 7	30—31	56	ST	A-A	Baker, (1)
	30—31	56	ST	A-A	Kiblisky, (16)
	30—31	56	ST	A-A	Yonenaga et al., (25)
	30—31	56	ST	A-A	Baker & Hsu, (6)
Artibeus hirsutus Andersen 7	30—31	56	ST	ST-A	This paper
Artibeus jamaicensis Leach 7	30—31	56	ST	A-A	Baker, (1)
	30—31	56	ST	A-A	Becak et al., (9)
	30—31	56	ST	A-A	Kiblisky, (16)
	30—31	56	ST	SM-A	Baker & Hsu, (6)
	30—31	56	ST	A-A	Baker & Lopez, (7)
Artibeus watsoni Thomas 6	30	56	ST	SM	This paper
Centurio senex Gray 17	28	52	?	?	Baker, (1)
	28	52	ST	SM	Baker & Hsu, (6)
Chiroderma salvini Dobson 9	26	48	ST	SM	This paper
Chiroderma trinitatum Goodwin 9	26	48	ST	SM	Baker & Hsu, (6)
Chiroderma villosum Peters 9	26	48	ST	SM	Baker, (1)
	26	48	ST	SM	Baker & Hsu, (6)
Enchisthenes hartii Thomas 23	30	56	?	?	Baker, (1)
	30—31	56	ST	SM-A	Baker & Hsu, (6)
Mesophylla macconnelli Thomas	21—22	24	A	?	Baker & Hsu, (6)
Sphaeronycteris toxaphyllum Peters 18	28	52	ST	SM	This paper
Stenoderma rufum Desmarest 15	30—31	56	ST	A-A	Baker & Lopez, (7)
Sturnira bidens Thomas 2	30	56	ST	A	Gardner & O'Neill, (12)
Sturnira lilium Geoffroy 3	30	56	ST	SM	Baker, (1)
	30	56	ST	SM	Kiblisky, (16)
Sturnira ludovici Anthony 3	30	56	ST	SM	Baker, (1)
Sturnira tildae de la Torre 3	30	56	ST	SM	Baker & Hsu, (6)
Sturnira erythromous (Tschudi) 2	30	56	ST	A	Gardner & O'Neill, (12)
Sturnira mordax Goodwin 3	30	56	—	—	This paper
Uroderma bilobatum Peters 27	44	48	ST	SM	Baker, (1)

Table 1 continued

SPECIES	2N	FN	X	Y	Authority
25	38	44	ST	SM	Baker & Lopez, (7)
26	42	50	ST	SM	Baker & Lopez, (7)
Uroderma magnirostrum Davis 25	36	62	ST	SM	Baker & Lopez, (7)
Vampyressa brocki Peterson 10	24	44	?	?	Baker et al., (5)
Vampyressa nymphaea (Thomas) 8	26	48	ST	SM	This paper
Vampyressa pusilla (Wagner) 11	23—24	22	ST	?	This paper
Vampyressa pusilla (Wagner) 12	18	20	ST	SM	This paper
Vampyrodes caraccioli Thomas 5	30	56	ST	SM	Baker & Hsu, (6)
Vampyrodes major G. M. Allen 5	30	56	ST	SM	This paper
Vampyrops dorsalis Thomas 4	30	56	ST	SM	This paper
Vampyrops brachycephalus Rouk and Carter 4	30	56	ST	SM	This paper
Vampyrops vittatus (Peters) 1	30	56	ST	A	This paper
Vampyrops helleri Peters 4	30	56	ST	SM	Baker, (1)
	30	56	ST	SM	Baker & Hsu, (6)
Subfamily Phyllonycterinae					
Erophylla bombifrons Miller	32	60	?	?	Baker & Lopez, (7, 8)
Brachyphylla cavernarum Gray	32	60	SM	A	Baker & Lopez, (7, 8)
Subfamily Desmodontinae					
Desmodus rotundus Geoffroy	28	52	SM	A	Hsu & Benisrchke (15)
	28	52	SM	A	Forman et al., (16)
	28	52	SM	A	Yonenaga et al., (25)
Diaemus youngi Jentink	32	60	SM	A	Forman et al., (11)
Diphylla ecaudata Spix	28	52	SM	A	This paper

somal complement) are shown in Figure 3. Although there is a wide range of values, over 50 per cent of the species have a FN of 56—60. For the most part, these are the same species that have the 2N = 30—32 karyotype as most of these species have autosomal complements composed entirely of biarmed elements. A fundamental number of 56, 58, or 60 is found in all six of the subfamilies. Because the fundamental numbers of 56 and 60 are so frequent, and because it is found in all subfamilies, I believe the primitive FN for the family is 56 or 60. In light of the possibility of 2N = 32 being primitive to the 2N = 30 karyotype (see Diploid Number), then the primitive FN is 60.

Four species have a FN greater than 60, whereas thirty-one have a value lower than 56. As with the diploid number, the distribution of FN values does not appear normal (Figure 4). Clearly, there has been a greater tendency toward a reduction in the total arms of the auto-

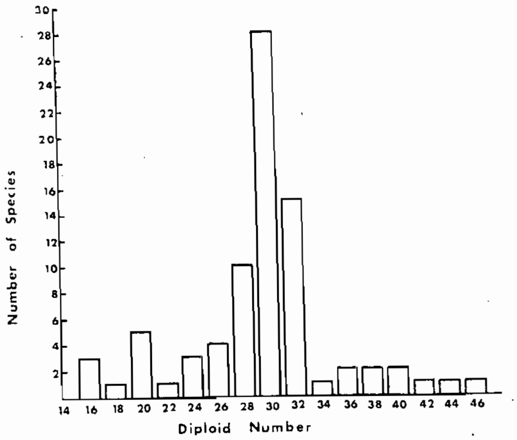

FIGURE 1. — Frequency histogram of diploid numbers of species of phyllostomatid bats.

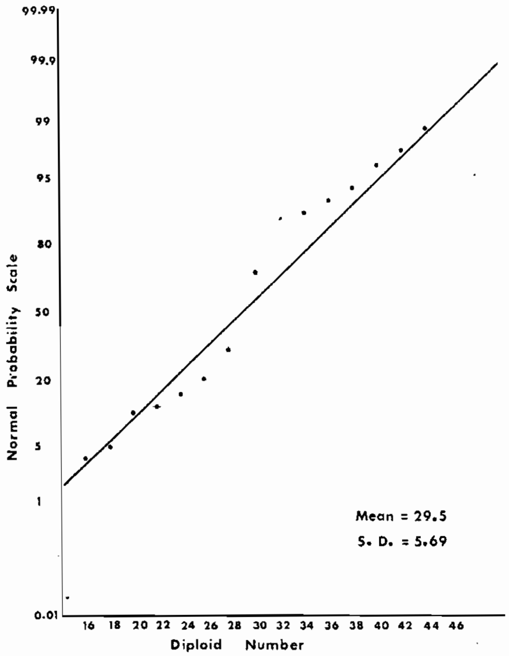

FIGURE 2. — Accumulative normal probability diagram for frequency of diploid numbers of species of phyllostomatid bats.

If the above suppositions concerning the primitive karyotype are true, then the ancestral stock would have had a 2N = 32 with all biarmed autosomes; a karyotype similar to that characteristic of *Phyllostomus discolor* (Phyllostominae), *Glossophaga soricina* (Glossophaginae), *Desmodus rotundus* (Desmodontinae), and *Erophylla bombifrons* (Phyllonycterinae). In most cases involving mammalian karyotypes where there is a reduction in the diploid number, it is generally explained by centric fusions. Because the karyotype of most phyllostomatids contains only

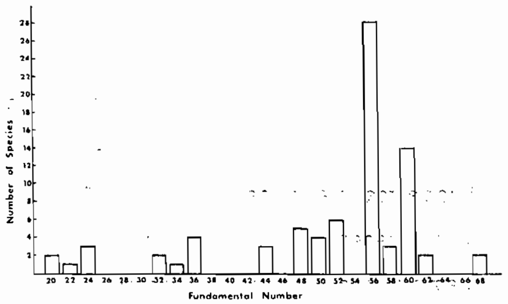

FIGURE 3. — Frequency histogram of fundamental numbers of species of phyllostomatid bats.

zation of centromeres) is required before centric fusion could reduce the diploid number. On the other hand, any series of centric fissions (with no intermediate steps required) of the autosomes would cause an increase in the diploid numbers. I believe that this is what has occurred in the case of *Macrotus waterhousii* (2N = 40 and 46), *Micronycteris megalotis* (2N = 40), and *M. schmidtorum* (2N = 38) of the Phyllostominae, *Rhinophylla fischerae* and *pumilio* (2N = 34 and 36) of the Carolliinae, and *Uroderma magnirostrum* (2N = 36) of the Stenoderminae. The karyotypes of all four genera contain acrocentrics which could be the product of fissions. However, the process of lowering the diploid and fundamental numbers has been more successful.

There are two ways to explain this phenomenon. One, it is more difficult for a centric fission to occur than it is for a centromere terminalization and subsequent centric fusion to occur. Some workers have suggested that centric fission is rare because it is difficult to evolve the additional centromere. Or, two, these spontaneous aberrations occur at equal rates, but selection favors the survival of species with lower values.

Figure 5 is a phyletic tree of the subfamily Stenoderminae. In some cases only chromosome values were used in constructing this tree; however, in some cases other morphological features were used. I am fully aware of the dangers of constructing a phyletic tree based primarily on a single character. Further, it is clear that in some cases, the chromosomal characteristics do not reveal distinct divergences (like between the genera *Sturnira* and *Vampyrops*) and in other cases chromosomal divergence implies a greater degree of divergence than is obviously the case (as within the species *Uroderma bilobatum*). There is value to such a presentation because other workers can readily grasp the interpretation of these karyotypic data,

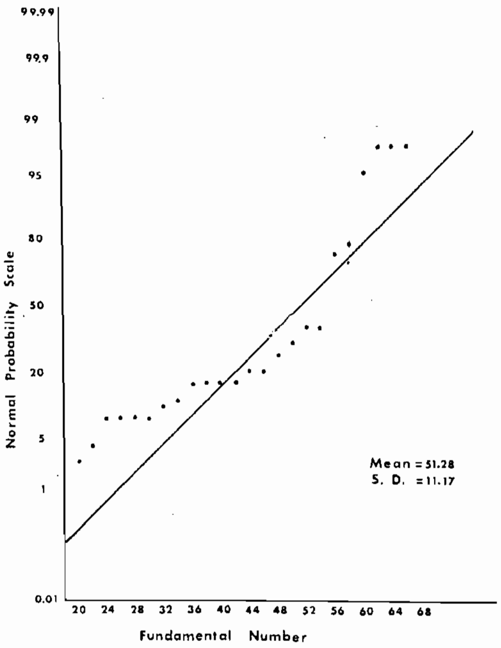

FIGURE 4. — Accumulative normal probability diagram for frequency of fundamental numbers of species of phyllostomatid bats.

conclusions. At any rate, I do not feel that there is anything sacred about this hypothetical tree, and like other workers, I will strive to determine the inaccuracies in it. All genera of the Stenoderminae are included. Where no chromosomal data are available, the genus is placed near the genera to which it is morphologically similar.

The number following each specific name of Stenoderminae in Table 1 identifies where that species is placed in Figure 5 (the number before each genus). The diploid number and fundamental number are given in parentheses and are separated by a semicolon. The number of species given after the parentheses indicates the number of species of that genus that have that specific karyotype.

As indicated in the above discussions on diploid number and fundamental number, the basal stock is believed to have had a karyotype similar to groups 1—7. The species involved in groups 1—7 have similar autosomal complements and the divisions are based on the Y element(s). Species of groups one and two have a single acrocentric Y element, species of groups 3—6 have a biarmed Y and species of group seven have two Y chromosomes. There is some Y chromosomal variation within group 7 (14).

The proposed line 9—14 involves a series of decreasing diploid and fundamental numbers. This line could have evolved from any of the basal stocks 1—7, but because they do not have two Y elements, I associated this line with groups 1—6. Groups 8—10 have karyotypes with all biarmed autosomes, and in species where the sex chromosomes are known the system is XX/XAAy. In 12 the sex chromosomes appear to be the classical XX/XY. I have associated *Ectophylla* (no chromosomal data available) with the end of this line because of its morphological similarity to *Mesophylla* (13, 24).

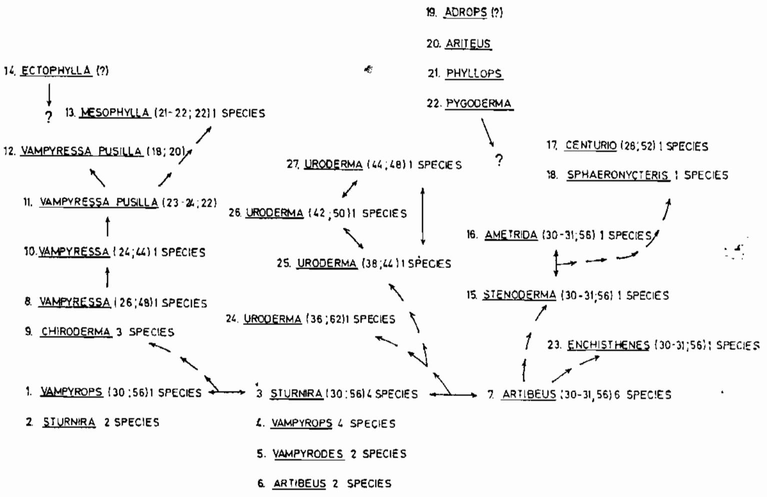

FIGURE 5. Phyletic tree of the subfamily Stenoderminae based upon karyotypes. See text for details. Diploid number and Fundamental number are in parenthesis beside the first genus in each group. Where no chromosomal data are available a

The *Uroderma* line (24—27) has a lot of chromosomal divergence but involves only two species (10). Number 24 is clearly most like groups 1—7; however, it is unclear if the descending fundamental numbers or if the the increasing diploid numbers reveal the primitive versus the derived forms of 25—27.

The line involving 15—23 involves a group of monotypic genera that are characterized by white spots on their shoulders and shortened rostra. The chromosomal values of 17 and 18 seem to quality them for the line 9—13; however, their morphological characteristics clearly identify them with numbers 15 and 16. Relative to what I believe is the basal karyotypic numbers 17 and 18 are the derived forms. *Stenoderma* is distinguished from number 7 because it has fewer subtelocentric autosomes. *Ametrida* has a larger biarmed Y element than either *Artibeus* (in group 7) or *Stenoderma.*

Since *Enchisthenes* does not share morphological characteristics with line 15—18, and because it has a greater (not fewers as in *Stenoderma)* number of subtelocentric autosomes, it is placed as a separate offbranch. Genera 19—22 are morphologically much like genera 15—18 and are associated with this line on this basis.

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USPOREDNA CITOGENETIKA KRPONOSACA (PHYLLOSTOMATIDAE) IZ NOVOG SVIJETA

SAŽETAK. Sabrani su i diskutirani podaci o građi kariotipa u krponosaca iz Novog Svijeta. Unutar te porodice pronađena su tri načina određivanja spola. Diploidni je broj kromosoma od 16 do 46, a fundamentalni od 20 do 68. Do sada su poznati kariotipovi za 77 od 130 postojećih vrsta. Za 28 vrsta daju se po prvi put podaci u ovom radu. Napravljeno je filogenetsko stablo za potporodicu Stenoderminae, i to djelomično samo na osnovi kromosomskih parametara, djelomično i uz pomoć drugih morfoloških značajki.