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STANDARD KARYOLOGY OF NINE SPECIES OF VESPERTILIONID BATS (CHIROPTERA: VESPERTILIONIDAE) FROM THAILAND

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ABSTRACT

Karyotypes of nine species of vespertilionid bats from Thailand are described. *Pipistrellus mimus* (2n = 34, FN = 46), *Tylonycteris robustula* (2n = 32, FN = 50), *Murina leucogaster* (2n = 44, FN = 50), and *Miniopterus schreibersi* (2n = 46, FN = 52) have karyotypes essentially identical to ones previously reported from other regions. *Pipistrellus pulveratus* (2n = 32, FN = 50) is reported for the first time and differs by six Robertsonian fission/fusion events from the primitive *Myotis*-like karyotype. Karyotypes

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for *Hesperoptenus tickelli* (2n = 32, FN = 50) and *H. blanfordi* (2n = 34, FN = 60) are reported for the first time and parallel the extreme morphological differences between the two species. *Harpiocephalus mordax* (2n = 40, FN = 62) is very distinct from other members of the subfamily Murininae but is apparently derived from a *Murina*-like ancestor. *Kerivoula papillosa* (2n = 38, FN = 52) though considered little differentiated from primitive vespertilionines has a relatively highly derived karyotype similar to *Vespertilio.*

INTRODUCTION

The family Vespertilionidae is distributed worldwide in temperate and tropical regions. It is the largest family in the order Chiroptera including approximately 33 genera and 313 Recent species (Koopman, 1984). Thirteen genera and 34 species are known to occur in Thailand (Lekagul and McNeely, 1977).

Previous karyotypic studies led Pathak and Sharma (1969) to suggest that the family has two very different patterns of chromosomal variability. Some genera such as *Myotis* exhibit remarkable homogeneity with all examined species having 2n = 44, FN = 50 or 52. Others such as *Pipistrellus* (2n = 26, 28, 30, 32, 34, 36, 38, 42, 44 and FN = 44, 46, 48, 50, 52) are much more heterogeneous. These studies, however, mostly have been restricted to New World (Baker and Patton, 1967; Bickham, 1979*a,* 1979*b*) and European (Bovey, 1949; Capanna and Civitelli, 1970; Fedyk and Fedyk, 1970; Zima, 1978) species. Karyotypic data for African, Australian, and Asian vespertilionids are sparse. For example, karyotypes have been reported for only one species of vespertilionids from Thailand (Harada et al., 1982*b*).

This study presents standard karyotypes of nine species in seven genera and four subfamilies from Thailand. Karyotypes of five of these species have been reported from other regions (Pathak and Sharma, 1969; Manna and Talukdar, 1965; Yong et al., 1971; Bickham and Hafner, 1978; Harada and Kobayashi, 1980; Harada, 1973; Ando et al., 1977). New data are presented for four species and one subfamily.

MATERIALS AND METHODS

All animals were collected in Thailand using mist nets. Upon capture, all animals were subcutaneously injected with a weak solution of baker's yeast, sugar, and water (Lee and Elder, 1980) to stimulate bone marrow mitosis. Twenty-four hours later, animals were sacrificed and humeri removed. Karyotypes were prepared in the field from bone marrow cells suspended in a hypotonic solution (0.075 M KCl) for approximately 25 min and then fixed in a 3:1 solution of methanol : glacial acetic acid (Baker et al., 1982). Three to four drops of the fixed cell suspension were dropped onto clean, dry microscope slides and ignited with a match. After the flaming suspension extinguished itself, any remaining liquid was carefully drained away and slides were stained in a 2% solution of Geimsa in 0.01 M phosphate buffer. Diploid (2n) and fundamental (FN) numbers were determined from counts of a minimum of 10 mitotic spreads. Description of chromosome morphology follows the nomenclature of Patton (1967). All specimens were prepared as

museum skins and skulls or alcoholics and are housed in the Carnegie Museum of Natural History (CM), the Texas Cooperative Wildlife Collection, Texas A&M University (TCWC), or The Museum, Texas Tech University (TTU).

Specimens Examined

Pipistrellus mimus.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, 15°29′N, 99°18′E (CM 88129 M, 88130 F); Huai Kha Khang Wildlife Sanctuary, 2.7 km S Khao Nang Rum Wildlife Research Station, 15°27′N, 99°18′E (CM 88132 M); Huai Kha Khang Wildlife Sanctuary, 1.5 km W Khao Nang Rum Wildlife Research Station, 15°29′N, 99°17′E (CM 88131 M).

Pipistrellus pulveratus.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, 3.7 km S, 1 km E Khao Nang Rum Wildlife Research Station, 15°27′N, 99°18′E (CM 88134 F, CM 88136 F).

Tylonycteris robustula.—Surat Thani Prov.; Tha Chang Dist., 15 km N, 23 km W Ban Maruan, 09°18′N, 98°58′E (CM 88149 F, CM 88151 F, CM 88152 F, CM 88140 F, TTU 41257 F, TK 21416 F).

Hesperoptenus blanfordi.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, 15°19′N, 99°18′E (CM 88114 M, TTU 41255 F); Huai Kha Khang Wildlife Sanctuary, 1.5 km W Khao Nang Rum Wildlife Research Station (TK 21279 F).

Hesperoptenus tickelli.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, 3.7 km S, 1 km E Khao Nang Rum Wildlife Research Station, 15°27′N, 99°18′E (CM 88119 M, TK 21193 M); Huai Kha Khang Wildlife Sanctuary, 2.0 km S Khao Nang Rum Wildlife Research Station, 15°30′N, 99°16′E (CM 88117 M).

Kerivoula papillosa.—Surat Thani Prov.; Tha Chang Dist., 15 km N, 23 km W Ban Maruan, 09°18′N, 90°58′E (CM 88164 F).

Miniopterus schreibersi haradai.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, 2.7 km S Khao Nang Rum Wildlife Research Station, 15°30′N, 99°16′E (CM 88156 M); Huai Kha Khang Wildlife Sanctuary, 3.7 km S, 1 km E Khao Nang Rum Wildlife Research Station, 15°27′N, 99°18′E (CM 88157 M).

Murina leucogaster.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Khao Nang Rum Wildlife Research Station, 15°29′N, 99°18′E (CM 88162 F, CM 88163 F).

Harpiocephalus mordax.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Khao Nang Rum Wildlife Research Station, 15°29′N, 99°18′E (CM 88159 F).

Results

Table 1 is a summary of the known standard karyotypic data for the family Vespertilionidae including those reported here. The standard karyotypes of eight species representing seven genera and four subfamilies are presented in Figs. 1–3. A brief description of these karyotypes follows.

Subfamily Vespertilioninae

Pipistrellus mimus (2n = 34, FN = 46; Fig. 1a).—Four animals examined have a karyotype that consists of six pairs of large metacentric to submetacentric chromosomes and one large subtelocentric pair. There are nine pairs of acrocentric chromosomes ranging in size from medium

Table 1.—*A summary of known standard karyotypic data for the family Vespertilionidae. SM—submetacentric, M—metacentric, ST—subtelocentric, and A—acrocentric.*

Taxon	2n	FN	X	Y	Authority
Subfamily Vespertilioninae					
Myotis auriculus	44	52	SM	A	Bickham, 1979*b*
Myotis austroriparius	44	50	SM	SM	Baker and Patton, 1967
	44	50	SM	A	Bickham, 1979*b*
Myotis bechsteini	44	52	M	A	Zima, 1978
Myotis blythi	44	52	SM	A	Baker, 1970
	44	50	SM	A	Baker et al., 1974
Myotis brandti	44	50	SM	A	Zima, 1982
Myotis californicus	44	50	SM	SM	Baker and Patton, 1967
Myotis capaccinii	44	50	—	—	Manfreddi Romanini et al., 1975
Myotis dasycneme	44	52	M	A	Zima, 1978
Myotis daubentonii	44	50–52	SM	A	Bovey, 1949
	44	54	SM	—	Fedyk and Fedyk, 1970
	44	52	M	A	Zima, 1984
Myotis elegans	44	50	SM	SM	Baker and Patton, 1967
Myotis emarginatus	44	50	SM	A	Bovey, 1949
	44	56	M	A	Radjhabli et al., 1969, 1970
	44	52	M	A	Zima, 1978
Myotis evotis	44	50	SM	SM	Baker and Patton, 1967
	44	52	SM	A	Bickham, 1979*b*
Myotis fortidens	44	50	SM	A	Osborne, 1965
Myotis frater	44	50	SM	A	Harada and Yoshida, 1978
Myotis grisescens	44	50	SM	A	Baker and Patton, 1967
	44	50	SM	A	Bickham, 1979*b*
Myotis horsfieldi	44	50	SM	A	Harada and Kobayashi, 1980
Myotis hosonoi	44	52	SM	A	Harada, 1973
	44	50	SM	A	Harada and Yoshida, 1978
Myotis keaysi	44	50	SM	A	Bickham, 1979*b*
	44	50	—	—	Baker and Bickham, 1980
Myotis keenii	44	50	SM	SM	Baker and Patton, 1967
	44	50	SM	A	Bickham, 1979*b*
Myotis leibii	44	50	SM	SM	Baker and Patton, 1967
Myotis lucifugus	44	50	SM	SM	Baker and Patton, 1967
Myotis macrodactylus	44	52	SM	A	Harada, 1973
	44	52*	SM	A	Obara et al., 1976*a*
	44	50	SM	A	Harada and Yoshida, 1978

Table 1.—*Continued.*

Taxon	2N	FN	X	Y	Authority
Myotis milleri	44	52	SM	—	Reduker et al., 1983
Myotis myotis	44	50	M	A	Bovey, 1949
	44	50	SM	A	Bickham and Hafner, 1978
	44	50	SM	A	Iliopoulou-Georgudaki and Giagia, 1984
Myotis mystacinus	44	56	M	A	Radjhabli et al., 1969, 1970
Myotis nattereri	44	50	SM	—	Ando et al., 1977
	44	50	SM	—	Harada and Yoshida, 1978
	44	52	SM	A	Zima, 1978
Myotis nigricans	44	50	SM	SM	Baker and Patton, 1967
	44	50	SM	A	Bickham, 1979*b*
	44	50	SM	A	Baker and Bickham, 1980
Myotis oxygnathus	44	56	M	A	Radjhabli et al., 1969, 1970
	44	50	SM	A	Bickham and Hafner, 1978
Myotis pruinosus	44	52	SM	ST	Harada and Uchida, 1982
Myotis sodalis	44	50	SM	—	Baker and Patton, 1967
	44	50	SM	A	Bickham, 1979*b*
Myotis thysanodes	44	50	SM	SM	Baker and Patton, 1967
	44	52	SM	A	Bickham, 1979*b*
Myotis velifer	44	50	SM	SM	Baker and Patton, 1967
	44	50	SM	A	Bickham, 1979*b*
Myotis (*Pizonyx*) *vivesi*	44	50	SM	SM	Baker and Patton, 1967
Myotis volans	44	50	SM	SM	Baker and Patton, 1967
Myotis yumanensis	44	50	SM	—	Baker and Patton, 1967
	44	50	SM	A	Bickham, 1979*b*
Lasionycteris noctivagans	20	28	SM	A	Baker and Patton, 1967
	20	28	SM	A	Bickham, 1979*a*
Pipistrellus abramus	26	44	ST	A	Takayama, 1959
	26	44	A	A	Harada, 1973
	26	44	A	A	Obara et al., 1976*b*, 1976*c*
Pipistrellus affinus	36	50	SM	A	Pathak and Sharma, 1969
Pipistrellus babu	36	50	M	A	Dulic, 1981
Pipistrellus endoi	38	50	A	—	Ando et al., 1977
	38	50	A	—	Ando et al., 1980
Pipistrellus hesperus	28	46	SM	A	Baker and Patton, 1967
Pipistrellus kuhli	44	50	SM	A	Capanna, 1968
	44	50	SM	—	Baker et al., 1974
	44	50	SM	A	Zima, 1982
Pipistrellus mimus	34	—	—	—	Manna and Talukdar, 1965

Table 1.—*Continued.*

Taxon	2N	FN	X	Y	Authority
	38	48	M	A	Pathak and Sharma, 1969
	34	46	SM	A	This study
Pipistrellus mordax	34	46	M	A	Pathak and Sharma, 1969
Pipistrellus nanus	36	50	M	A	Peterson and Nagorsen, 1975
Pipistrellus nathusii	44	51	SM	A	Bovey, 1949
	42	50	M	—	Fedyk and Ruprecht, 1976
	42	50	M	A	Zima, 1978
Pipistrellus pipistrellus	42	51	M	A	Bovey, 1949
	44	50	M	—	Fedyk and Ruprecht, 1976
	44	50	M	A	Zima, 1978
	44	50	SM	A	Zima, 1982
	44	52	M	A	Zima, 1984
Pipistrellus savii	44	50	SM	A	Capanna, 1968
	44	50	—	—	Park and Won, 1978
	44	50	SM	A	Zima, 1982
Pipistrellus pulveratus	32	50	SM	—	This study
Pipistrellus subflavus	30	56	SM	A	Baker and Patton, 1967
	30	50	SM	—	Bickham, 1979*a*
Nyctalus furvus	44	50	SM	A	Ando et al., 1977
	44	50	SM	A	Harada et al., 1982*a*
Nyctalus lasiopterus	42	50	SM	A	Tsuchiya et al., 1972
	42	50	SM	A	Harada, 1973
	42	50	SM	A	Ando et al., 1977
	42	50	SM	A	Harada et al., 1982*a*
Nyctalus leisleri	46	54	SM	—	Fedyk and Fedyk, 1970
Nyctalus noctula	42	50	SM	A	Dulic et al., 1967
	42	50	SM	A	Vorontsov, 1969
	42	50	M	A	Zima, 1978
	42	50	M	M	Zima, 1984
Eptesicus andinus	50	48	SM	A	Baker and Patton, 1967
Eptesicus brasiliensis	50	48	SM	A	Baker and Patton, 1967
	50	48	SM	A	Baker et al., 1982
Eptesicus capensis	32	50	SM	A	Peterson and Nagorsen, 1975
Eptesicus circumdatus	50	48	SM	—	Heller and Volleth, 1984
Eptesicus diminutus	50	48	SM	A	Williams, 1978
Eptesicus furinalis	50	48	SM	A	Baker and Patton, 1967
	50	48	SM	A	Williams, 1978
Eptesicus fuscus	50	48	SM	A	Baker and Patton, 1967
	50	48	SM	A	Bickham, 1979*a*
Eptesicus guadeloupensis	50	48	SM	A	Genoways and Baker, 1975

Table 1.—*Continued.*

Taxon	2N	FN	X	Y	Authority
Eptesicus hottentotus	50	48	SM	—	Peterson and Nagorsen, 1975
Eptesicus japonensis	50	48	SM	SM	Ando et al., 1977
Eptesicus lynni	50	48	SM	A	Bickham, 1979*a*
Eptesicus nilssoni	50	48	—	—	Ando et al., 1977
	50	50	M	A	Zima, 1978
	50	48	M	—	Zima, 1982
Eptesicus serontinus	50	48	SM	A	Baker and Patton, 1967
	50	48	SM	A	Vorontsov, 1969
	50	52	SM	SM	Fedyk and Fedyk, 1970
	50	48	SM	—	Baker et al., 1974
	50	48	SM	A	Bickham, 1979*a*
	50	48	SM	—	Baker and Bickham, 1980
Vespertilio murinus	38	50	M	A	Vorontsov, 1969
	38	54	M	A	Zima, 1978
	38	50	—	—	Obara and Saitoh, 1977
Vespertilio orientalis	38	50	M	A	Ando et al., 1977
	38	50	SM	A	Obara and Saitoh, 1977
Vespertilio superans	38	50	M	A	Vorontsov, 1969
	38	50	M	A	Zima, 1978
Histiotus montanus	50	48	SM	A	Williams and Mares, 1978
Tylonycteris pachypus	46	52	A	M	Yong et al., 1971
Tylonycteris robustula	32	52	A	M	Yong et al., 1971
	32	52	A	M	This study
Hesperoptenus blanfordi	34	60	A	—	This study
Hesperoptenus tickelli	32	46	ST	M	This study
Nycticeius humeralis	46	48	SM	A	Baker and Patton, 1967
	46	48	SM	A	Bickham, 1979*a*
Scotoecus hindei	30	50	ST	SM	Nagorsen et al., 1976
Rhogeessa genowaysi	42	50	SM	SM	Baker, 1984
Rhogeessa parvula	44	50	SM	SM	Baker and Patton, 1967
	44	50	SM	—	Bickham and Baker, 1977
Rhogeessa tumida	42	50	SM	SM	Baker and Patton, 1967
	30	50	—	—	Baker, 1970
	42	50	SM	SM	Bickham and Baker, 1977
	34	50	SM	SM	Bickham and Baker, 1977
	32	50	SM	SM	Bickham and Baker, 1977
	30	50	SM	ST	Bickham and Baker, 1977
	34	50	—	—	Baker and Bickham, 1980
	30	50	—	—	Baker and Bickham, 1980
	52	52	—	—	Honeycutt et al., 1980
	34	50	SM	—	Baker et al., 1985
	32N	50	SM	—	Baker et al., 1985
	32B	50	SM	—	Baker et al., 1985
	30	50	SM	A	Baker et al., 1985

Table 1.—*Continued.*

Taxon	2N	FN	X	Y	Authority
Scotophilus dinganii	36	52	A	M	Schlitter et al., 1980
	36	62[1]	—	—	Peterson and Nagorsen, 1975
Scotophilus heathi	36	52	M	A	Sharma et al., 1974
Scotophilus kuhlii	36	52	M	A	Pathak and Sharma, 1969
	36	48	M	A	Harada et al., 1982*b*
Scotophilus temminckii	36	52	SM	A	Pathak and Sharma, 1969
	36	48	SM	A	Harada and Kobayashi, 1980
Scotophilus viridis	36	54	A	M	Schlitter et al., 1980
Lasiurus borealis	28	46	SM	A	Baker and Patton, 1967
	28	48	SM	A	Baker and Mascarello, 1969
	28	48	SM	A	Bickham, 1979*a*
Lasiurus cinereus	28	46	SM	A	Baker and Patton, 1967
	28	48	SM	A	Bickham, 1979*a*
Lasiurus ega	28	48	SM	A	Bickham, 1979*a*
Lasiurus ega panamensis	28	46	A	A	Baker and Patton, 1967
Lasiurus ega xanthinus	28	46	SM	A	Baker and Patton, 1967
Lasiurus intermedius	26	40	SM	A	Baker and Patton, 1967
	26	42	A	A	Baker, 1970
Lasiurus seminolus	28	48	SM	A	Baker and Mascarello, 1969
	28	48	SM	A	Bickham, 1979*a*
Barbastella barbastellus	32	52	—	—	Matthey and Bovey, 1948
	32	50	M	A	Bovey, 1949
	32	50	SM	A	Capanna et al., 1968
	32	52	SM	A	Zima, 1978
Barbastella leucomelas	32	50	SM	A	Ando et al., 1977
Plecotus auritus	32	52	—	—	Matthey and Bovey, 1948
	32	50	M	A	Bovey, 1949
	32	54	SM	A	Fedyk and Fedyk, 1970
Plecotus auritus auritus	32	54	M	A	Ando et al., 1977
	32	52	M	A	Zima, 1978
Plecotus auritus sacrimontis	32	50	M	A	Harada, 1973
Plecotus austriacus	32	50	SM	A	Baker, 1970
	32	54	SM	A	Fedyk and Fedyk, 1970
	32	50	SM	A	Baker et al., 1974
	32	52	M	A	Zima, 1978
Plecotus phyllotis	30	50	—	—	Baker and Patton, 1967
	30	50	SM	A	Baker and Mascarello, 1969
Idionycteris phyllotis	30	50	SM	—	Bickham, 1979*a*
	30	50	SM	—	Stock, 1983

Table 1.—*Continued.*

Taxon	2N	FN	X	Y	Authority
Plecotus rafinesquii	32	50	A	A	Baker and Mascarello, 1969
Plecotus townsendi	32	48	—	—	Baker and Patton, 1967
	32	50	A	A	Baker and Mascarello, 1969
	32	50	A	A	Bickham, 1979*a*
	32	50	A	A	Stock, 1983
Euderma maculatum	30	50	SM	A	Williams et al., 1970
	30	50	SM	—	Stock, 1983
Subfamily Miniopterinae					
Miniopterus australis	46	50	SM	A	Harada and Kobayashi, 1980
Miniopterus magnater	46	50	SM	A	Harada and Kobayashi, 1980
Miniopterus schreibersi	46	50	—	—	Matthey and Bovey, 1948
	46	50	SM	A	Baker et al., 1974
	46	50	SM	A	Bickham and Hafner, 1978
	46	50	SM	A	Bickham, 1979*a*
	46	50	SM	A	Harada and Kobayashi, 1980
Miniopterus schreibersi haradai	46	52	SM	A	This study
Miniopterus schreibersi fuliginosus	46	52	SM	A	Harada, 1973
Subfamily Murininae					
Murina aurata	44	60	SM	A	Ando et al., 1977
Murina leucogaster	44	50	—	—	Harada, 1973
	44	58	SM	A	Ando et al., 1977
	44	50	SM	A	This study
Harpiocephalus mordax	40	62*	—	—	This study
Subfamily Kerivoulinae					
Kerivoula papillosa	38	52**	—	—	This study
Subfamily Nyctophilinae					
Antrozous pallidus	56	50	SM	A	Bickham, 1979*a*
Bauerus dubiaquercus	44	52	SM	A	Engstrom and Wilson, 1981

* Obara et al., 1976*a*, report on inversion polymorphism in chromosome 5.
** Includes sex chromosomes in FN.
[1] Examination of the figure in Peterson and Nagorsen (1975) gives a FN = 52. This probably represents a typographical error.

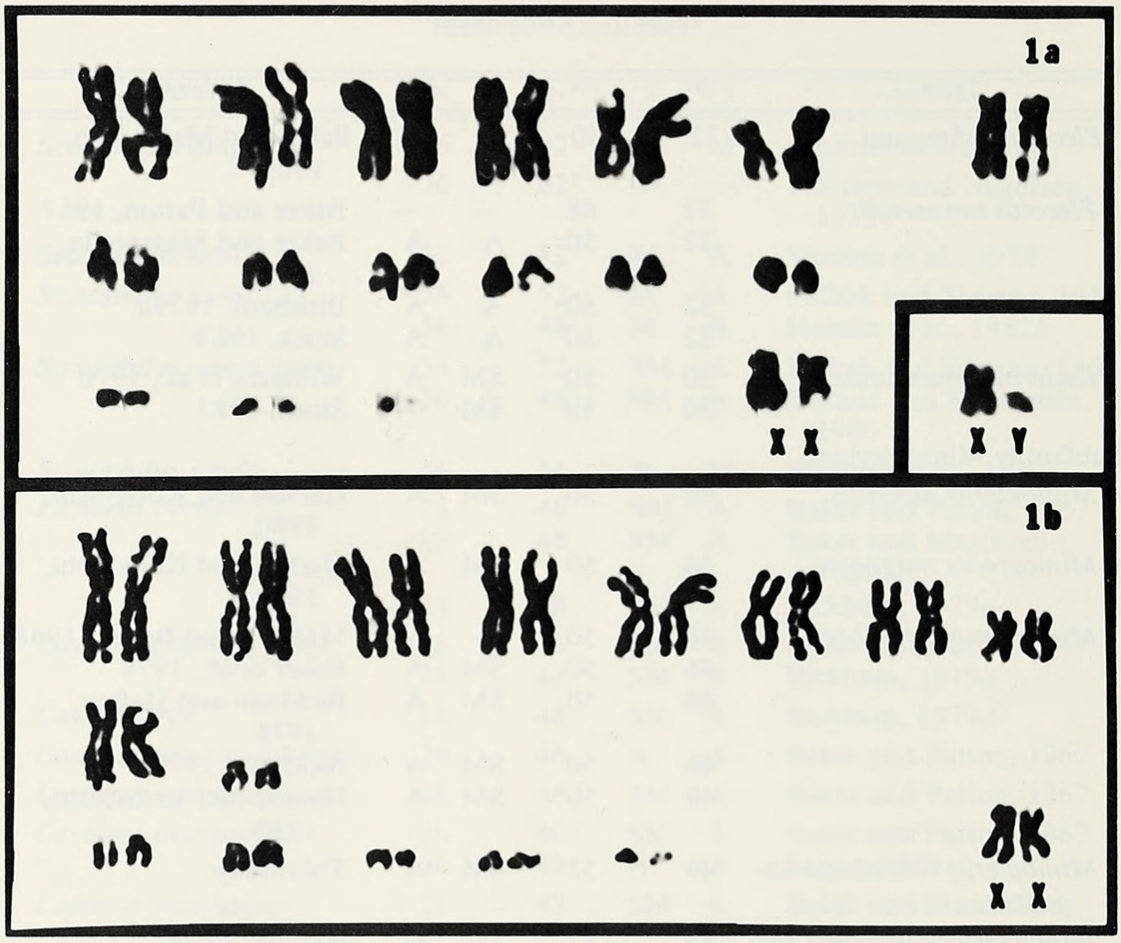


Fig. 1.—The standard karyotypes of: a) *Pipistrellus mimus* F (CM 88135), 2n = 34, FN = 46, inset *P. mimus* M (CM 88131); b) *Pipistrellus pulveratus* F (CM 88136), 2n = 32, FN = 50.

to minute. The X is medium-sized and submetacentric and the Y is small and acrocentric.

Pipistrellus pulveratus (2n = 32, FN = 50; Fig. 1b).—The autosomal complement includes eight pairs of metacentric or submetacentric chromosomes ranging in size from large to medium. There is one large pair and one small pair of subtelocentric chromosomes, and five pairs of acrocentric chromosomes ranging from medium-sized to small. The X is medium-sized and submetacentric.

Tylonycteris robustula (2n = 32, FN = 50; Fig. 2a).—The karyotype shown here is similar to that reported by Yong et al. (1971), but there are slight differences. Both studies report 2n = 32 with nine pairs of metacentric to submetacentric chromosomes. However, our specimens had one pair of medium-sized subtelocentric chromosomes and five pairs of acrocentric chromosomes ranging from medium-sized to minute, whereas Yong et al. (1971) reported two pairs of subacrocentric

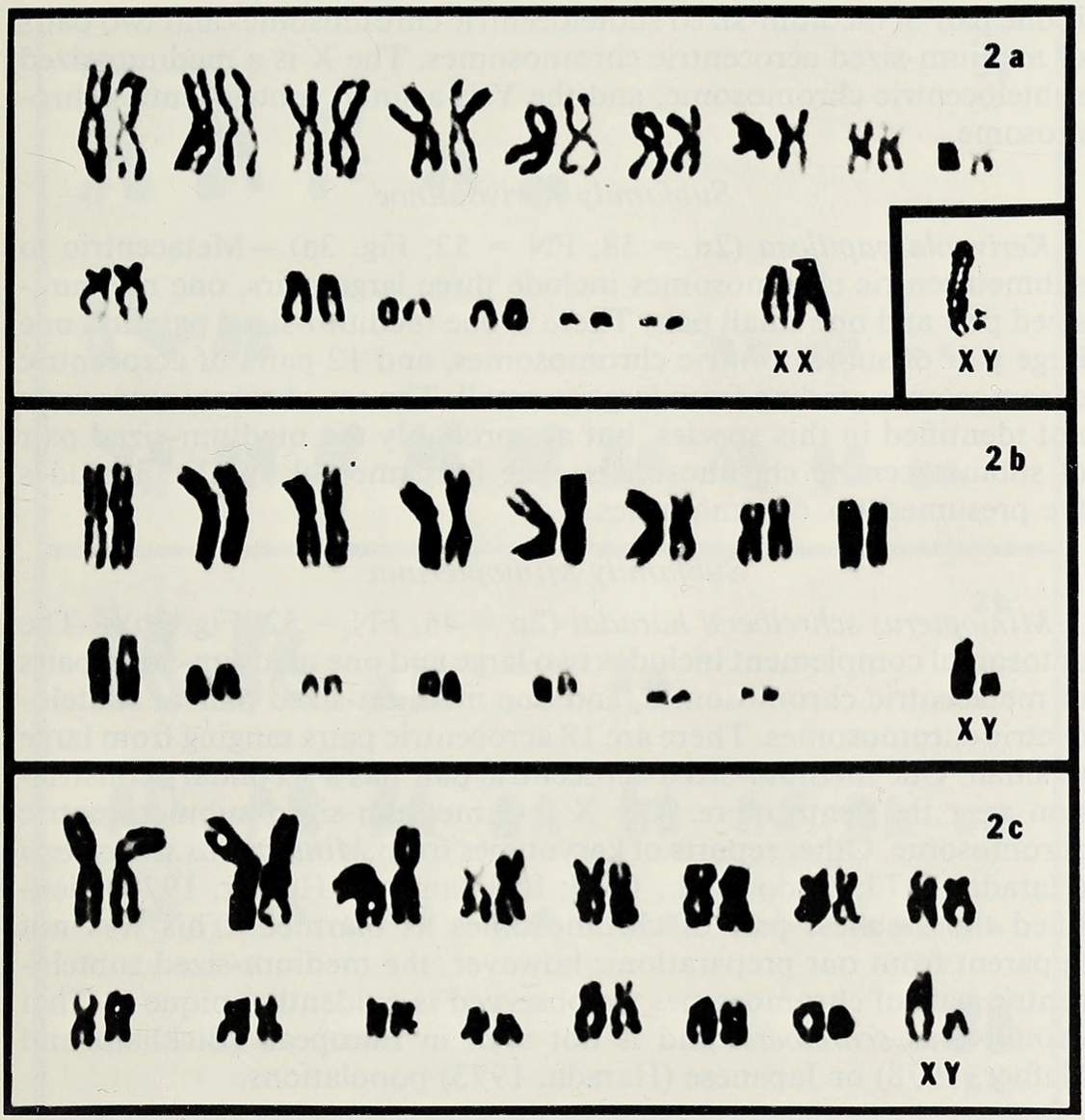


Fig. 2.—The standard karyotypes of: a) *Tylonycteris robustula* F (TK 21416), 2n = 32, FN = 50; inset *T. robustula* M. (CM 88152); b) *Hesperoptenus tickelli* M (TCWC 47481), 2n = 32, FN = 46; c) *Hesperoptenus blanfordi* F (CM 88114), 2n = 34, FN = 60.

and two pairs of acrocentric chromosomes. The X is large and acrocentric and the Y is a small metacentric chromosome.

Hesperoptenus tickelli (2n = 32, FN = 46; Fig. 2b).—The autosomal complement contains eight pairs of metacentric to submetacentric chromosomes ranging from large to medium-sized. There also are seven pairs of medium-sized to minute acrocentric chromosomes. The X is a large subtelocentric and the Y is a small metacentric chromosome.

Hesperoptenus blanfordi (2n = 34, FN = 60; Fig. 2c).—The autosomal complement includes 13 pairs of metacentric to submetacentric chromosomes gradually decreasing in size from large to small. There

is one pair of medium-sized subtelocentric chromosomes and two pairs of medium-sized acrocentric chromosomes. The X is a medium-sized subtelocentric chromosome, and the Y is a small subtelocentric chromosome.

Subfamily Kerivoulinae

Kerivoula papillosa (2n = 38, FN = 52; Fig. 3a).—Metacentric to submetacentric chromosomes include three large pairs, one medium-sized pair and one small pair. There is one medium-sized pair and one large pair of subtelocentric chromosomes, and 12 pairs of acrocentric chromosomes grading from large to small. The sex chromosomes were not identified in this species, but are probably the medium-sized pair of submetacentric chromosomes. The fundamental number includes the presumed sex chromosomes.

Subfamily Miniopterinae

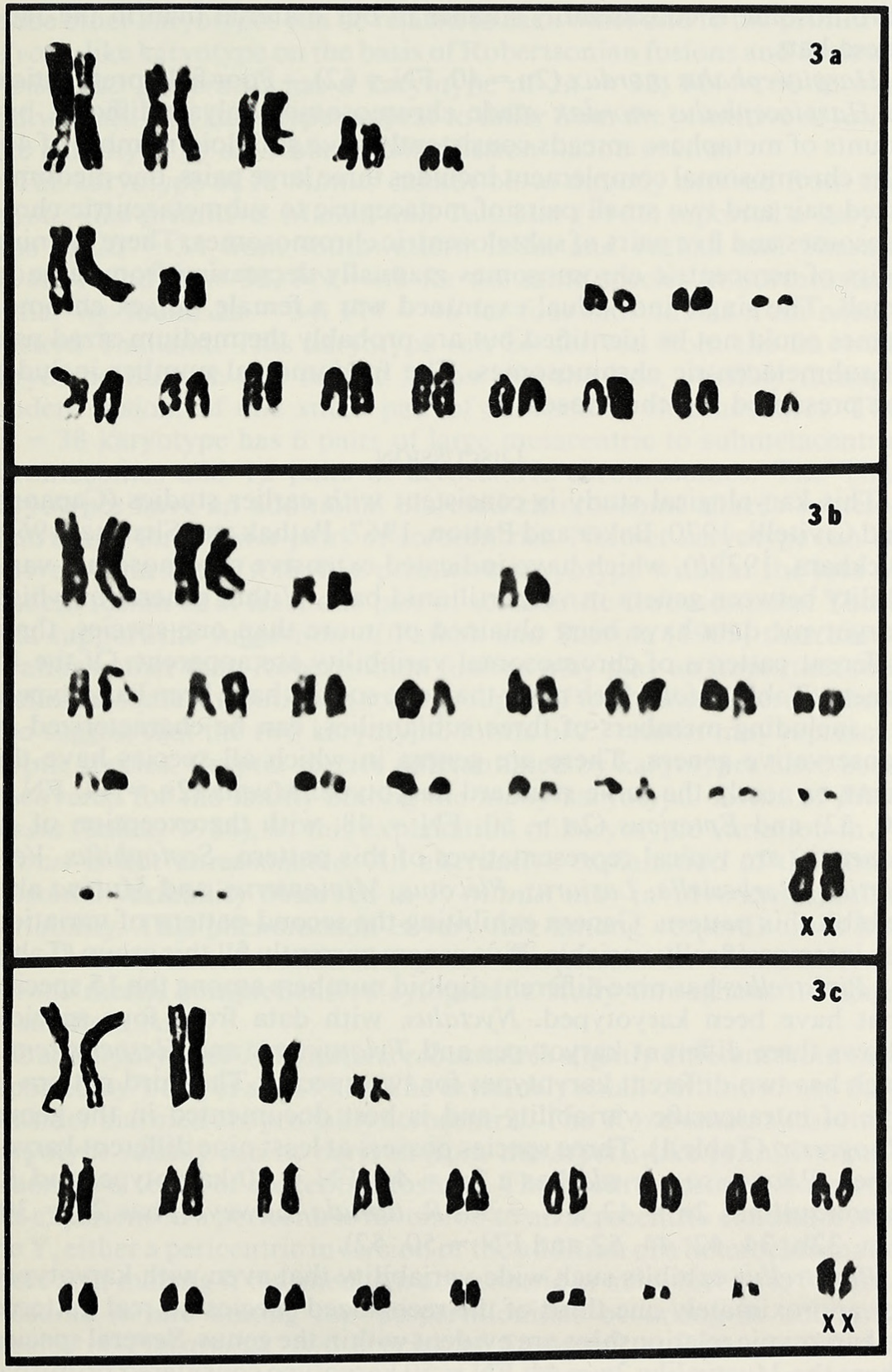
Miniopterus schreibersi haradai (2n = 46, FN = 52; Fig. 3b).—The autosomal complement includes two large and one medium-sized pairs of metacentric chromosomes, and one medium-sized pair of subtelocentric chromosomes. There are 18 acrocentric pairs ranging from large to small. One medium-sized acrocentric pair has a secondary constriction near the centromere. The X is a medium-sized submetacentric chromosome. Other reports of karyotypes from *Miniopterus schreibersi* (Harada, 1973; Ando et al., 1977; Bickham and Hafner, 1978) identified the smallest pair of chromosomes as biarmed. This was not apparent from our preparations; however, the medium-sized subtelocentric pair of chromosomes we observed is evidently unique to Thai *Miniopterus schreibersi* and is not seen in European (Bickham and Hafner, 1978) or Japanese (Harada, 1973) populations.

Subfamily Murininae

Murina leucogaster (2n = 44, FN = 50; Fig. 3c).—There are two pairs of large metacentric, and two pairs of medium-sized to small submetacentric autosomes. The autosomal complement is completed by 17 acrocentric pairs ranging from large to small. The X is medium-sized and submetacentric. This karyotype is similar to that of *Murina leucogaster* from Atesu, Japan (Harada, 1973), but the third largest

→

Fig. 3.—The standard karyotypes of: a) *Kerivoula papillosa* F (CM 88164), 2n = 38, FN = 52 (FN includes sex chromosomes); b) *Miniopterus schreibersi haradai* F (CM 88157), 2n = 46, FN = 52; c) *Murina leucogaster* F (CM 88163), 2n = 44, FN = 50.


3a
3b
XX
3c
XX

chromosome is considerably smaller in our material than in the Japanese bats.

Harpiocephalus mordax (2n = 40, FN = 62).—Poor field preparation of *Harpiocephalus mordax* made chromosome analysis difficult, but counts of metaphase spreads consistently gave a diploid number of 40. The chromosomal complement includes three large pairs, one medium-sized pair and two small pairs of metacentric to submetacentric chromosomes and five pairs of subtelocentric chromosomes. There are nine pairs of acrocentric chromosomes gradually decreasing from large to small. The single individual examined was a female, so sex chromosomes could not be identified but are probably the medium-sized pair of submetacentric chromosomes. The fundamental number includes the presumed sex chromosomes.

DISCUSSION

This karyological study is consistent with earlier studies (Capanna and Civitelli, 1970; Baker and Patton, 1967; Pathak and Sharma, 1969; Bickham, 1979*b*), which have indicated extensive chromosomal variability between genera in vespertilionid bats. Within genera for which karyotypic data have been obtained on more than one species, three different patterns of chromosomal variability are apparent. Of the 15 genera (Table 1) for which more than one species have been karyotyped, 11, including members of three subfamilies, can be characterized as conservative genera. These are genera in which all species have the same or nearly the same standard karyotype. *Myotis* (2n = 44, FN = 50, 52) and *Eptesicus* (2n = 50, FN = 48, with the exception of *E. capensis*) are typical representatives of this pattern. *Scotophilus, Vespertilio, Barbestella, Lasiurus, Plecotus, Miniopterus,* and *Murina* also exhibit this pattern. Genera exhibiting the second pattern of variation are interspecifically variable. Five genera currently fill this group (Table 1). *Pipistrellus* has nine different diploid numbers among the 15 species that have been karyotyped. *Nyctalus,* with data from four species, shows three different karyotypes and *Tylonycteris* and *Hesperoptenus* each has two different karyotypes for two species. The third pattern is one of intraspecific variability and is best documented in the genus *Rhogeessa* (Table 1). Three species possess at least nine different karyotypes. *Rhogeessa parvula* has a 2n = 44, FN = 50 karyotype, and *R. genowaysi* has 2n = 42, FN = 50. *R. tumida,* however, has 2n = 30, 32a, 32b, 34, 42, 44, 52 and FN = 50, 52).

Pipistrellus exhibits such wide variability that even with karyotypes for approximately one third of the recognized species no real patterns of karyotypic relationships are evident within the genus. Several species share the *Myotis*-like 2n = 44, FN = 50 karyotype considered primitive for the family (Bickham, 1979*a,* 1979*b*; Baker and Patton, 1967). Many

of the other karyotypes can be related to each other and to the primitive *Myotis*-like karyotype on the basis of Robertsonian fusions and fissions. *Pipistrellus pulveratus* has a karyotype of 2n = 32, FN = 50 in two individuals. The karyotypes appear to differ from the primitive *Myotis*-like karyotype by six Robertsonian fission-fusion events.

The karyotype of *P. mimus* cannot be so directly derived from the *Myotis*-like primitive. Manna and Talukdar (1965) reported a karyotype of 2n = 34 from southwestern India and Pathak and Sharma (1969) found 2n = 38, FN = 48 for the same species in northeastern India. We found 2n = 34, FN = 46 for four individuals from northwestern Thailand. This karyotype can be derived from the 2n = 38 karyotype through one centric fusion and the loss, possibly through tandem fusion, of one small pair of acrocentric chromosomes. The 2n = 38 karyotype has 6 pairs of large metacentric to submetacentric chromosomes and 12 pairs of acrocentric chromosomes. The Thai karyotypes have an additional biarmed chromosome that is subtelocentric and three fewer pairs of acrocentrics. Neither karyotype can be derived from the *Myotis*-like primitive karyotype without the loss or tandem fusion of at least one pair of acrocentric chromosomes. These data support the suggestion of Pathak and Sharma (1969) that translocations other than Robertsonian fusions may play an important role in chromosomal evolution in some groups of *Pipistrellus*. These authors also suggest that the two karyotypic forms of *P. mimus* may represent cryptic species. Cryptic species differentiated by karyotypes have been discovered for the family among the many karyotypic forms of *Rhogeessa* (Baker, 1984), so this explanation of karyotypic variation in *P. mimus* is not unreasonable. An alternative explanation of the chromosomal variability observed in *P. mimus* may involve intraspecific variability. This phenomenon is very rare among vespertilionids but is well documented within the genus *Rhogeessa*. In either case, *P. mimus* merits comprehensive cytogenetic study throughout its range in southern Asia.

Our karyotype of *Tylonycteris robustula* is slightly different from that reported by Yong et al. (1971). The extremely small chromosomes they consider biarmed are probably acrocentric. The *T. robustula* autosomal karyotype readily can be derived from the *Myotis*-like primitive condition by a series of six centric fusions. The X chromosome, however, has experienced a pericentric inversion to an acrocentric condition and the Y, either a pericentric inversion or the addition of a heterochromatic short arm making it biarmed. An acrocentric or subtelocentric X chromosome is rare among the Vespertilionidae occurring in only two species of *Pipistrellus*, two species of *Scotophilus*, *Scotoecus hindei*, two species of *Lasiurus*, two species of *Plecotus*, and two species of *Hesperoptenus* (Table 1). *Tylonycteris robustula* also has diploid and

fundamental numbers in common with the two *Plecotus*. The karyotypes are at least superficially the same, except both *Plecotus* have acrocentric rather than biarmed Y chromosomes. Assumptions of homology on the basis of standard karyotypes must be made with caution, however (Bickham and Baker, 1977; Baker et al., 1985; Haiduk and Baker, 1982). The similarities between the plecotine genus, *Plecotus,* and the vespertilionine genus *Tylonycteris* are likely the result of convergence. Tate (1942) considered *Tylonycteris* and *Philetor* as derived from an ancestor similar to the *Pipistrellus joffrei* group. Neither *Philetor* nor any members of the *P. joffrei* group have been karyotyped for comparison, however.

The genus *Hesperoptenus* is poorly understood systematically. Four species are currently recognized, two of which are known from only a few specimens. The more common forms, *H. tickelli* and *H. blanfordi,* are very different from one another morphologically. Tate (1942) commented that if the genus was not polyphyletic it at least contained strongly differentiated species. *Hesperoptenus blanfordi* and *H. tickelli* also are karyologically distinct. Whereas the two species have similar diploid numbers, *H. blanfordi* has one of the highest FNs reported for the family, and *H. tickelli* has an FN of 52, among the most commonly found in the family. To derive one karyotype from the other would require one fission/fusion event and five pericentric inversions or heterochromatic additions. The *H. tickelli* karyotype can be derived from the *Myotis*-like primitive karyotype through four Robertsonian fusions and the loss or tandem fusion of two pairs of acrocentrics. There also has been a pericentric inversion changing the primitive biarmed X to a derived subtelocentric configuration. The Y is a derived small metacentric chromosome, either through pericentric inversion or heterochromatic addition. The *H. blanfordi* karyotype is more difficult to derive from the *Myotis*-like primitive requiring at least five Robertsonian fusions and five pericentric inversions in the autosomal complement. The X chromosome also is inverted to an acrocentric condition. The more parsimonious scenario might consist of *H. tickelli* diverging from the *Myotis*-like ancestor with *H. blanfordi* being a highly divergent offshoot of *H. tickelli.* Chromosomal data support the conclusion that *H. tickelli* and *H. blanfordi,* at best, are only distantly related. Ryan (1966) and Koopman (1971) thought *Hesperoptenus* was closely related to *Glauconycteris* and *Chalinolobus.* Hill (1976) considered dental differences between the three genera to be too great and considered *Hesperoptenus* more closely aligned with the genus *Scotophilus. Hesperoptenus tickelli* and some *Scotophilus* have FN and uniarmed X chromosomes in common. *H. tickelli* has one fewer pair of biarmed chromosomes and one fewer pair of acrocentric chromosomes

than *Scotophilus,* however. No species of *Glauconycteris* or *Chalinolobus* have been karyotyped for comparison.

Our karyotype of *Miniopterus schreibersi haradai* agrees well with previous reports. Miniopterinae is considered the most derived subfamily of the Vespertilionidae, even being accorded familial status by some authors (Mein and Tupinier, 1977) yet the karyotype found throughout this subfamily differs from the primitive *Myotis*-like karyotype by a single Robertsonian fission and two pericentric inversions (Bickham and Hafner, 1978). Harada (1973) found in *M. s. fuliginosus,* and we found in *M. s. haradai,* a medium-sized subtelocentric chromosome apparently unique to Thai members of the species.

Members of the subfamily Murininae have been regarded as a specialized offshoot of an early *Myotis*-like ancestor (Miller, 1907). The subfamily contains two genera, *Murina* and *Harpiocephalus.* All members of *Murina* karotyped so far have had a standard karyotype essentially identical to the 2n = 44 *Myotis*-like primitive, agreeing with the early divergence of Murininae from the vespertilionine line. Tate (1941) considered the second genus, *Harpiocephalus,* as a very specialized offshoot of the line leading to *Murina,* and Miller (1907) termed *Harpiocephalus* as one of the most aberrant genera of the family. The *Harpiocephalus* karyotype is derived from the primitive *Myotis*-like karyotype and the *Murina* karyotype by two possible pericentric inversions indicating that *Harpiocephalus* probably evolved from a *Murina*-like ancestor rather than diverging earlier from the line leading to *Murina.*

The subfamily Kerivoulinae has been considered the least specialized of the vespertilionid subfamilies being closely related to the "least progressive" genera of the subfamily Vespertilioninae (Tate, 1941). The karyotype of *Kerivoula papillosa* can be derived from the primitive *Myotis*-like karyotype through two Robertsonian fusions and the loss or tandem fusion of one pair of acrocentric chromosomes.

Within the Vespertilionidae, *Kerivoula* shares a similar standard karyotype with the Japanese *Pipistrellus endoi* and members of the genus *Vespertilio.* In the past, the entire genus *Pipistrellus* has been considered a part of *Vespertilio,* but Zima (1978) considers the distinctive karyotype of *Vespertilio* as justification for separate generic status. Ando et al. (1980) suggest *P. endoi* may be a link between the genus *Vespertilio* and its *Pipistrellus*-like ancestor. The subfamily Kerivoulinae may have a similar link to its *Pipistrellus*-like ancestor here. There are no other data to link the three, however, and postulation of a common origin is only speculative.

Unquestionably, Robertsonian fusions and fissions have played a major role in chromosomal evolution of the family Vespertilionidae

(Bickham, 1979*a*). However, the standard karyotypes reported here indicate a greater importance for non-Robertsonian rearrangements such as inversions and translocations as evolutionary mechanisms than was previously thought (Bickham, 1979*a*; Bickham and Baker, 1977). Pericentric inversions, tandem fusions, or heterochromatic additions apparently have occurred in *Tylonycteris robustula, Miniopterus schreibersi haradai, Kerivoula papillosa,* and *Harpiocephalus mordax* in their evolution from the 2n = 44 ancestral karyotype. *Hesperoptenus tickelli* and *H. blanfordi* may show an especially high incidence of pericentric inversions, requiring up to five possible inversion events to be derived from the ancestral karyotype. Examination of these standard karyotypes emphasizes how poorly understood are vespertilionid karyological relationships. Speculations about relationships based on standard karyotypes can be misleading, however. G-band analysis has indicated that constant genera such as *Myotis* are indeed as constant as was assumed from standard karyotypes (Bickham, 1979*b*). It also has pointed out extreme chromosomal differences where standard karyotypes indicated homology (Baker et al., 1985). Chromosomal banding analysis should allow a more accurate assessment of the mechanisms of chromosomal evolution seen in the family Vespertilionidae. G-banding also will provide a means to test apparent homologies between groups such as *Kerivoula* and *Vespertilio.* The extensive variability between, and possibly within, species of *Pipistrellus* also will be much better characterized by G-banding. Comparison of conserved and derived chromosome sequences revealed by G-banding is imperative to an understanding of systematic relationships among the Vespertilionidae.

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