

CHROMOSOMAL STUDIES OF BATS (MAMMALIA: CHIROPTERA)
FROM THAILANDCRAIG S. HOOD¹DUANE A. SCHLITZER
Curator, Section of MammalsJOAN I. GEORGUDAKI²SONGSAKDI YENBUTRA³ROBERT J. BAKER⁴
Research Associate, Section of Mammals

ABSTRACT

Chromosomal data are presented for 19 species that represent four families of bats collected during field studies in Thailand. The karyotypes of *Pteropus lylei*, *Megaerops niphanae*, *Emballonura monticola*, and *Megaderma spasma* are reported for the first time. The karyotype of *Pteropus lylei* ($2n = 40$, $FN = 72$) presents new diploid and fundamental numbers for the genus *Pteropus*. The chromosomal complement of *Megaerops niphanae* ($2n = 26$, $FN = 42$) is like that reported for Thailand populations of the closely related species, *M. ecaudatus*. Chromosomal data for *Emballonura monticola* ($2n = 24$, $FN = 44$) is the first reported for a species of the genus *Emballonura*. *Megaderma spasma* ($2n = 38$, $FN = 64$) and *M. lyra* ($2n = 54$, $FN = 104$) differ substantially in overall chromosomal morphology, and in G- and C-banding patterns. Karyotypes for the other chiropteran species examined were similar to those previously reported in the literature.

INTRODUCTION

The bat fauna of Thailand includes nine families, 33 genera, and approximately 93 species, ranking it as one of the world's most diverse chiropteran faunas (Lekagul and McNeely, 1977; Corbet and Hill, 1980). Despite this diversity, little is known concerning the systematics and distribution of the bats of Thailand (e.g., Thonglongya, 1974; Thonglongya and Hill, 1974; Hill, 1974; Hill and Thonglongya, 1972; Yenbutra and Felton, 1983). Undoubtedly, as scientific research continues in the country, new distributional records will be added and it is not unlikely that new forms may be discovered and described.

In the summer of 1983, the Carnegie Museum of Natural History, Hofstra University, Texas Tech University, Texas A&M University, and the Thailand Institute of Scientific and Technological Research supported field studies that resulted in a collection of 848 small mammals, including a large collection of bats.

¹ Department of Biological Sciences, Loyola University, New Orleans, LA 70118.

² Department of Biology, Faculty of Natural Science, University of Patras, Patras, Greece.

³ Thailand Institute of Scientific and Technological Research, 196 Phahonyothin, Bang Khen, Bangkok 9, Thailand.

⁴ Department of Biological Sciences and The Museum, Texas Tech University, Lubbock, TX 79409. Submitted 10 May 1987.

Table 1.—*Chromosomal data for bats examined in this study. Symbols are: 2n, diploid number; FN, fundamental number; SM, submetacentric; ST, subtelocentric; A, acrocentric.*

Taxon	Males	Females	2n	FN	X	Y	References
Family Pteropodidae							
<i>Rousettus amplexicaudatus</i>	2	1	36	68	SM	A	1, 2
<i>Pteorpus lylei</i>	2	0	40	72	SM	A	1
<i>Cynopterus sphinx</i>	8	14	34	58	SM	A	1, 3, 4
<i>Megaerops niphanae</i>	3	5	26	42	SM	A	1
<i>Eonycteris spelaea</i>	4	4	36	66	SM	SM	1, 5, 6
<i>Macroglossus sobrinus</i>	2	4	34	60	M	A	1, 5
Family Emballonuridae							
<i>Emballonura monticola</i>	0	2	24	44	—	—	1
<i>Taphozous melanopogon</i>	4	6	42	64	SM	A	1, 7, 8
Family Megadermatidae							
<i>Megaderma lyra</i>	3	5	54	104	SM	A	1, 7
<i>Megaderma spasma</i>	2	1	38	64	ST	A	1
Family Rhinolophidae							
<i>Rhinolophus acuminatus</i>	7	7	62	60	ST	ST	1, 4
<i>Rhinolophus affinis</i>	2	0	62	60	ST	ST	1, 9
<i>Rhinolophus coelophyllus</i>	2	1	62	60	ST	ST	1, 4
<i>Rhinolophus luctus</i>	0	1	32	60	ST	A	1, 9
<i>Rhinolophus malayanus</i>	3	2	62	60	ST	ST	1, 4
<i>Hipposideros armiger</i>	6	3	32	60	SM	ST	1
<i>Hipposideros fulvus</i>	0	1	32	60	SM	A	1, 7, 10
<i>Hipposideros larvatus</i>	5	6	32	60	SM	ST	1, 4
<i>Hipposideros lekaguli</i>	3	1	32	60	SM	ST	1, 4

References are: ¹ This study; ² Haiduk (1983); ³ Ray-Chaudhari et al. (1968); ⁴ Harada et al. (1982); ⁵ Yong and Dhaliwal (1976); ⁶ Ando et al. (1980b); ⁷ Ray-Chaudhari et al. (1971); ⁸ Hood and Baker (1986); ⁹ Harada, Yenbutra, Yosida and Takada (1985); ¹⁰ Harada, Yenbutra, Tsuchiya and Takada (1985).

Material from this collection has formed the basis for evolutionary studies utilizing anatomical, histological, and ultrastructural methods (Hood, 1986; Phillips et al., 1987). Molecular, biochemical, and chromosomal banding studies of rodents and bats are in progress.

Chromosomal studies of bats from Thailand have reported standard (non-differentially stained) karyotypes for 25 species representing five families (Harada et al., 1982; Harada, Yenbutra, Yosida and Takada 1985; Harada, Yenbutra, Tsuchiya and Takada, 1985). In this paper, we present chromosomal data for 19 species representing four chiropteran families (Table 1). In cases where our data are similar to those in the literature, we give the information in Table 1 and the Specimens Examined. Species accounts are presented for those species where new observations or conclusions were obtained. Chromosomal data for vespertilionid bats are not reported here, but have been treated elsewhere (Bickham et al., 1986; McBee et al., 1986).

MATERIALS AND METHODS

All specimens examined were obtained from natural populations. Standard, G-, and C-band chromosomal preparations were obtained by in vivo bone marrow (Lee and Elder, 1980; Baker et al., 1982) and tissue culture methods (from ear and lung biopsies, Baker and Bass, 1979). G- and C-banding followed Seabright

(1971) and Stefos and Arrighi (1971) according to the protocol of Baker and Qumsiyeh (in press). A minimum of ten complete spreads was scored for each specimen in the analysis of G- and C-band preparations. All figures presented in this paper represent the complete chromosomal complements of single cells.

Microscopic slides and tissue culture cell lines are deposited in The Museum, Texas Tech University. Voucher specimens are deposited in the Section of Mammals, The Carnegie Museum of Natural History (CM), The Museum, Texas Tech University (TTU), and the Texas Cooperative Wildlife Collection, Texas A&M University (TCWC).

SPECIMENS EXAMINED

Cynopterus sphinx.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Khao Nang Rum Wildlife Research Station, 15°29'N, 99°18'E (CM 88324, CM 87932, CM 87944, CM 87945, CM 88353, CM 88358, CM 88359, CM 88360, CM 88369, CM 88370, CM 99371); 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 88424, CM 88425, CM 88427, CM 88428); Huai Kha Khang Wildlife Research Station, 15°32'N, 99°17'E (CM 87957); Surat Thani Prov.; Muang Surat Thani Dist., Khao Tha Pet Nature Study Center, 5 km S, 2 km E Surat Thani, 09°06'N, 99°01'E (CM 87918, CM 87919, CM 87920, CM 87921, CM 87959).

Megaerops niphanae.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Khao Nang Rum Wildlife Research Station, 15°29'N, 99°18'E (CM 88444, CM 88448, CM 88449, CM 88452, CM 88672); 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 88457).

Rousettus amplexicaudatus.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Sap Fa Pha Wildlife Research Station, 15°32'N, 99°17'E (CM 88460); Huai Kha Khang Wildlife Sanctuary, 1.5 km W Khao Nang Rum Wildlife Research Station, 15°29'N, 99°17'E (CM 88461); Surat Thani Prov.; Tha Chang Dist., 15 km N, 23 km W Ban Maruan, 09°18'N, 98°58'E (CM 87974).

Pteropus lylei.—Chonburi Prov.; Panatnikom Dist., Wat Loung (CM 87972, CM 87973).

Eonycteris spelaea.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Khao Nang Rum Wildlife Sanctuary, Khao Nang Rum Wildlife Research Station, 15°29'N, 99°18'E (CM 87983, CM 87984, CM 87985, CM 87986, TCWC 47470); Surat Thani Prov.; Tha Chang Dist., 15 km N, 23 km W Ban Maruan, 09°18'N, 98°58'E (CM 87978, CM 87980).

Macroglossus minimus.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Khao Nang Rum Wildlife Research Station, 15°29'N, 99°18'E (CM 879932, TTU 41247, TCWC 47471); Surat Thani Prov.; Tha Chang Dist., 15 km N, 23 km W Ban Maruan, 09°18'N, 98°58'E (CM 87990, CM 87991, CM 87992).

Emballonura monticola.—Surat Thani Prov.; Muang Surat Thani Dist., Khao Tha Phet Nature Study Center, 5 km S, 2 km E Surat Thani, 09°06'N, 99°01'E (CM 87994, CM 87995).

Taphozous melanopogon.—Chumphon Prov.; Pathhiu Dist., 25 km E Ban Nimit Charoen, 10°54'N, 99°31'E (CM 88000, CM 88530, CM 88531, CM 88532, CM 88533, CM 88534, CM 88535, CM 88536, CM 88537).

Megaderma lyra.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Khao Nang Rum Wildlife Research Station, 15°29'N, 99°18'E (CM 88012); Huai Kha Khang Wildlife Sanctuary, Tam Khe Nok, 3.6 km N, 2.6 km W Sanctuary H.Q., 15°38'N, 99°18'E (CM 88008, CM 88011, CM 88538, CM 88540, CM 88541, TTU 41249, TCWC 47474).

Megaderma spasma.—Surat Thani Prov.; Muang Surat Thani Dist., Khao Tha Phet Nature Study Center, 5 km S, 2 km E Surat Thani, 09°06'N, 99°01'E (CM 88013, CM 88014, CM 88015).

Rhinolophus acuminatus.—Surat Thani Prov.; Muang Surat Thani Dist., Khao Tha Phet Nature Study Center, 5 km S, 2 km E Surat Thani, 09°06'N, 99°01'E (CM 88020, CM 88021, CM 88022, CM 88023, CM 88024, CM 88025, CM 88027, CM 88028, CM 88029, CM 88545, CM 88546); Tha Chang Dist., 15 km N, 23 km W Ban Maruan, 09°18'N, 98°58'E (CM 88016, CM 88017, CM 88018).

Rhinolophus affinis.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Khao Nang Rum Wildlife Research Station, 15°29'N, 99°18'E (CM 88033, CM 88034).

Rhinolophus coelophyllus.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, (CM 88039); Huai Kha Khang Wildlife Sanctuary, Tam Khe Nok, 3.6 km N, 2.6 km W Sanctuary H.Q., 15°38'N, 99°18'E (CM 88037, CM 88038).

Rhinolophus luctus.—Surat Thani Prov.; Tha Chang Dist., 15 km N, 23 km W Ban Maruan, 09°18'N, 98°58'E (CM 88040).

Rhinolophus malayanus.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Tam Khe Nok, 3.6 km N, 2.6 km W Sanctuary H.Q., 15°38'N, 99°18'E (CM 88044, CM 88046, CM 88558, CM 88559).

Hipposideros armiger.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Khao Nang Rum Wildlife Research Station, 15°29'N, 99°18'E (CM 88066); 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 88067, CM 88069); Huai Kha Khang Wildlife Sanctuary, Tam Khe Nok, 3.6 km N, 2.6 km W Sanctuary H.Q., 15°38'N, 99°18'E (CM 88053, CM 88055, CM 88060); Huai Kha Khang Wildlife Sanctuary, 1.5 km W Khao Nang Rum Wildlife Research Station, 15°29'N, 99°17'E (CM 88064); Chumphon Prov.; Pathiu Dist., 9 km N, 25 km E Ban Nimit Charoen, 10°59'N, 99°32'E (CM 88052).

Hipposideros fulvus.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Tam Khe Nok, 3.6 km N, 2.6 km W Sanctuary H.Q. 15°32'N, 99°18'E (CM 88081).

Hipposideros larvatus.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Khao Nang Rum Wildlife Research Station, 15°29'N, 99°18'E (CM 88086, CM 88087, CM 88089, CM 88090, CM 88091, CM 88092, CM 88095); Huai Kha Khang Wildlife Sanctuary, 1.5 km W Khao Nang Rum Wildlife Research Station, 15°29'N, 99°17'E (CM 88097, CM 88106); Huai Kha Khang Wildlife Sanctuary, Tam Khe Nok, 3.6 km N, 2.6 km W Sanctuary H.Q., 15°32'N, 99°18'E (CM 88610, CM 88611).

Hipposideros lekaguli.—Chumphon Prov.; Pathiu Dist., 9 km N, 25 km E Ban Nimit Charoen, 10°59'N, 99°32'E (CM 88109, CM 88110, CM 88111, CM 88113).

SPECIES ACCOUNTS

Rousettus amplexicaudatus (Geoffroy)

2n = 36; FN = 68

The karyotype of this species was first reported by Haiduk (1983) for specimens from Papua New Guinea. The chromosomal complement of our specimens, assigned to the subspecies *R. a. amplexicaudatus* following Rookmaaker and Bergmans (1981), appears to be identical to those reported from Papua New Guinea. Chromosomal evolution within the genus *Rousettus* is extremely conservative; only two rearrangements distinguish *R. aegyptiacus*, *R. amplexicaudatus*, and *R. (Lissonycteris) angolensis* (Haiduk et al., 1981). The karyotype of *R. leschenaulti*, which is apparently sympatric with *R. amplexicaudatus* in Thailand, has an identical 2n = 36, FN = 68 non-differentially stained morphology (Ray-Chaudhari et al., 1968; Harada et al., 1982).

Pteropus lylei Andersen

2n = 40; FN = 72

The karyotype of *Pteropus lylei* is reported for the first time. The autosomes of this species include 15 pairs of metacentric-submetacentric, and three pairs of subtelocentric chromosomes (Fig. 1A). The X is a large submetacentric and the Y a minute acrocentric element. This karyotype is unique for the genus *Pteropus*. All previously reported karyotypes have had a 2n = 38, FN = 72 chromosomal complement (*P. giganteus*, Ray-Chaudhari et al., 1968; Datta, 1977; *P. macrotis*, *admiraltilatum*, *neohibernicus*, Haiduk, 1983). The difference between these karyotypes appears to be the presence of an additional pair of small biarmed chromosomes in *P. lylei*. The nature of the rearrangements that were involved in this variation was not apparent in our comparisons of standard, G-, and C-band preparations. *Pteropus lylei* is a small form of *Pteropus*, endemic to Southeast Asia and found commonly in lowland areas of Thailand. Andersen (1912) noted that *P. lylei* was distinguished from other taxa within the *Pteropus vampyrus* species group (including *P. giganteus*, *vampyrus*, *ariel*, and *intermedius*), and may represent an indigenous continental form of the *vampyrus* group. In a group that exhibits extreme chromosomal conservation, the chromosomal data presented here support the notion that *P. lylei* is a distinct form.

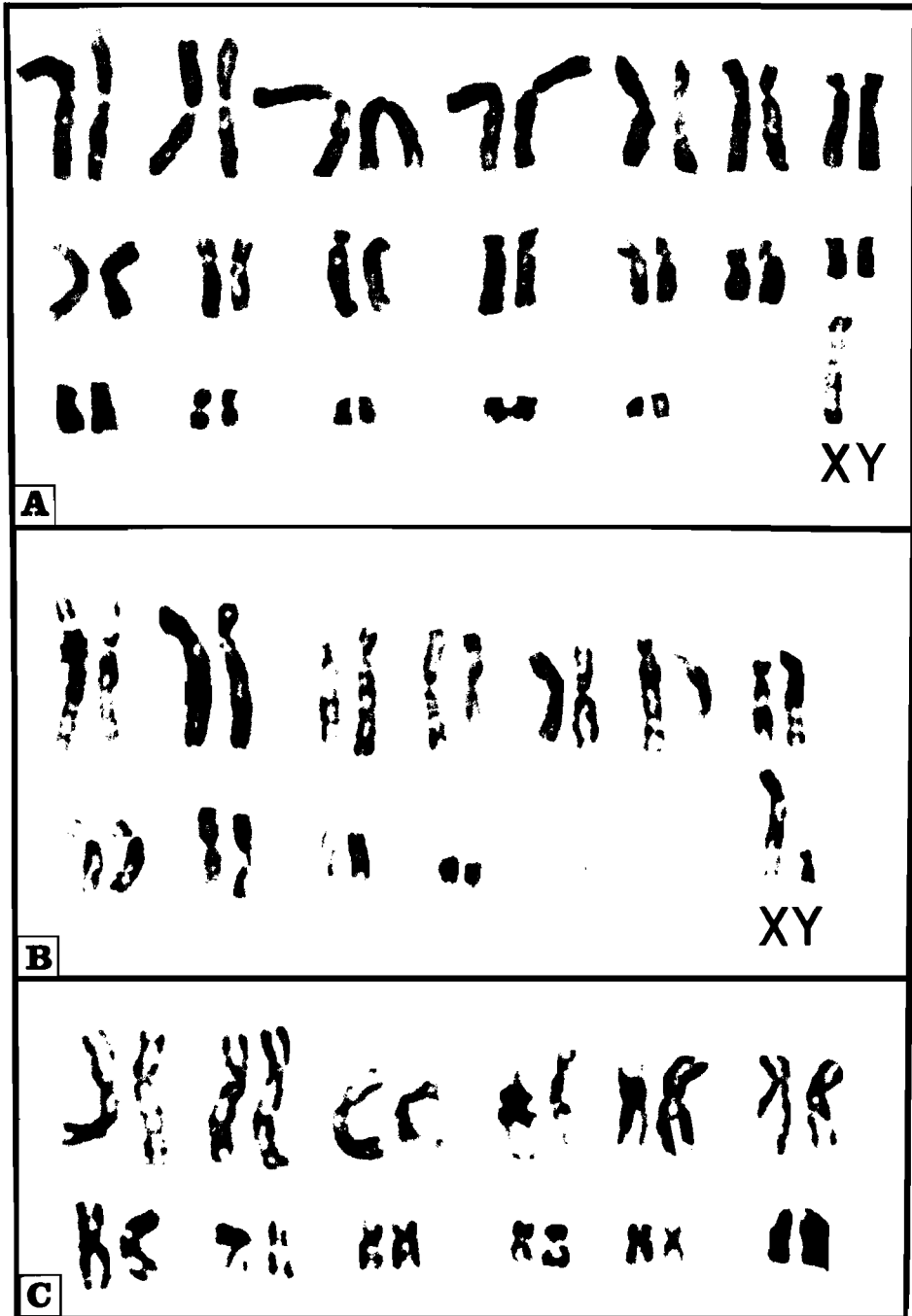


Fig. 1.—The standard karyotypes of: A) *Pteropus lylei*, male (CM 87973); B) *Megaerops niphanae*, male (CM 88672); C) *Emballonura monticola*, female (CM 87994).

Megaerops niphanae Yenbutra and Felton $2n = 26$; FN = 42

The karyotype of this recently described species is reported for the first time. The autosomes are comprised of nine pairs of metacentric-submetacentric, and three pairs of acrocentric chromosomes. The largest pair of autosomes has a prominent secondary constriction (Fig. 1B). The sex elements include a large submetacentric X and a small submetacentric or subtelocentric Y. This karyotype appears to be identical to that of some populations of the closely related species, *M. ecaudatus*. Populations of this species from central Thailand have a diploid number of 26, whereas bats from peninsular Malaysia are reported to have $2n = 24$ (Harada et al., 1982; Yong, 1984). Yong (1984) proposed that a Robertsonian translocation (fission/fusion event) involving the two largest acrocentric chromosomes of the $2n = 26$ karyotype accounts for the variation in diploid number. An alternative interpretation of the meaning of this chromosomal variation is that *M. ecaudatus* with the $2n = 26$ karyotype represents misidentified *M. niphanae*. In this case, the difference in diploid number represents differentiation between the two species. As currently understood, *M. ecaudatus* is restricted to peninsular Malaysia southward and *M. niphanae* is the proper specific epithet for *Megaerops* of central Thailand (Yenbutra and Felton, 1983).

Diploid and fundamental numbers are remarkably constant within the family Pteropodidae. Most pteropodids have diploid numbers of 34, 36, or 38 (Haiduk et al., 1980; 1981). However, the cynopterine taxa *Balionycteris* and *Megaerops* have radically departed from this trend with diploid numbers of 24 to 28 (Yong and Dhaliwal, 1976; Harada et al., 1982; Yong, 1984). Chromosomal banding data may provide a critical test of homology for these taxa.

Emballonura monticola Temminck $2n = 24$; FN = 44

Chromosomal data for *Emballonura monticola* is reported for the first time. Based on our examination of two female specimens, the karyotype is comprised of entirely biarmed chromosomes (Fig. 1C). Specific identification of the X and Y must await chromosomal data from a male. This is the first description of a karyotype of a bat of the genus *Emballonura*. Diploid numbers for the family Emballonuridae range from 22 to 32 for Neotropical taxa (Hood and Baker, 1986); four species of *Taphozous* examined to date all have $2n = 42$ (Ray-Chaudhari et al., 1971; Harada et al., 1982; Hood and Baker, 1986). C-band preparations showed that heterochromatin is restricted to centromeric regions, a pattern that has been found in most other emballonurids (Hood and Baker, 1986). Comparison of G-band patterns of *E. monticola* and other emballonurid genera failed to document any obvious banding homologies.

Megaderma lyra Geoffroy $2n = 54$; FN = 104

The karyotype of our specimens of *Megaderma lyra* (Fig. 2) appears to be identical to that reported for specimens from India (Ray-Chaudhari et al., 1971). C-band preparations show that C-positive material occurs extensively among the autosomes of this species. Heterochromatin was found in the long arms of six pairs (Fig. 2B). The incorporation of this magnitude of C-positive material is striking when compared with patterns of heterochromatin found in *M. spasma* (see below) and in other bat families. Heterochromatic material is primarily re-

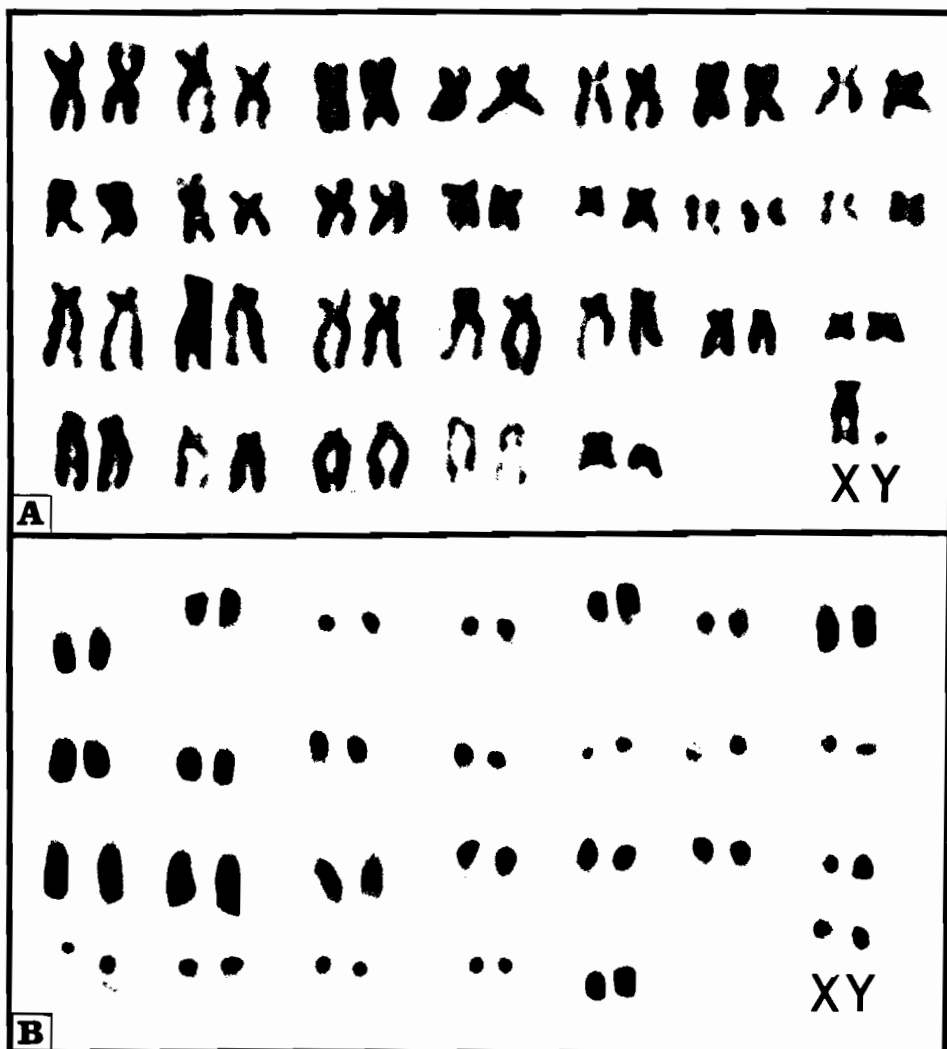


Fig. 2.—The standard and C-banded karyotypes of *Megaderma lyra*: A) male specimen (CM 88011); B) male specimen (CM 88012).

stricted to centromeric regions in Pteropodidae, Emballonuridae, Rhinopomatidae, Rhinolophidae, Phyllostomidae, Vespertilionidae, and Molossidae (Baker, 1979; Baker et al., 1982, 1987). Significant variation in the amount and placement of heterochromatin has been found in *Scotonycteris* (Pteropodidae, Haiduk et al., 1981), *Cormura* (Hood and Baker, 1986), and within the phyllostomids *Carollia*, *Choeroniscus*, *Tonatia*, and *Uroderma* (Baker, 1979; Baker et al., 1982).

Comparison of the G-banded karyotypes of *Megaderma lyra* and *M. spasma* showed that extensive G-band repatterning has occurred during the evolution of these species. The lack of G-band resolution may be due to the heterochromatinization of the autosomes in *M. lyra*, but may also reflect the fact that one or both

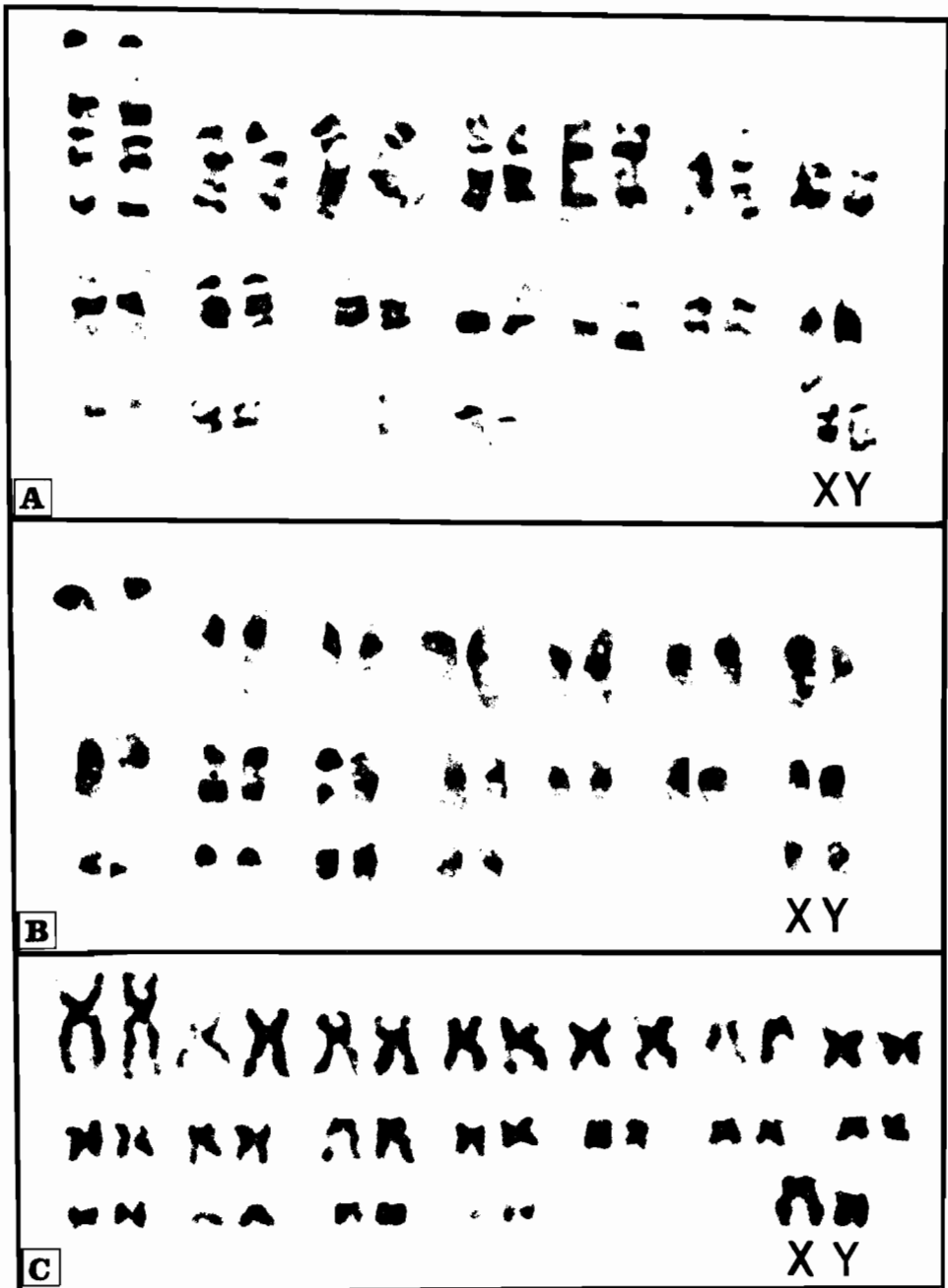


Fig. 3. — The karyotype of *Megaderma spasma*, male (CM 88015): A) G-banded karyotype; B) C-banded karyotype; C) standard karyotype.

taxa have undergone extensive euchromatic evolution since the establishment of ancestral generic conditions.

***Megaderma spasma* (Linnaeus)**

$2n = 38$; FN = 64

The karyotype of *Megaderma spasma* is reported for the first time. The autosomes of this species include 14 pairs of metacentric-submetacentric, and four pairs of acrocentric chromosomes (Fig. 3). The largest autosome is nearly two times the length of any of the other chromosomes in the karyotype. The sex chromosomes include a medium-sized subtelocentric X and an acrocentric Y.

Heterochromatin is restricted to centromeric regions in most autosomes; telocentric C-positive material is found in two autosomes (Fig. 3B). G- and C-band karyotypes were compared with those of *M. lyra*, as well as with representatives of the families Pteropodidae, Emballonuridae, and Rhinopomatidae (Haiduk et al., 1981; Qumsiyeh and Baker, 1985; Hood and Baker, 1986). As noted above in the account on *M. lyra*, G-band homologies could not be demonstrated between the karyotypes of the two species of *Megaderma*. Furthermore, comparisons with other chiropteran families failed to document any obvious G-band homologies. A better understanding of the type, magnitude, and direction of chromosomal evolution within the Megadermatidae must await critical examination of chromosomal banding data for other species within the family.

***Rhinolophus luctus* Temminck**

$2n = 32$; FN = 60

Two very different karyotypes have been reported for this species. Ando et al. (1980a) reported a diploid number of 52 for *Rhinolophus luctus* from Taiwan, whereas specimens from India and Thailand have been recorded as $2n = 32$ (Naidu and Gururaj, 1984; Harada, Yenbutra, Yosida and Takada, 1985). The karyotype of our female specimen from Ban Maruan is identical to that reported by Harada, Yenbutra, Yosida and Takada (1985) for specimens from Chiang Mai in northern Thailand. Harada, Yenbutra, Yosida and Takada (1985) suggested that the similarity in the karyotypes of *R. luctus* and species of *Hipposideros* ($2n = 36$) reflects chromosomal homology that may represent the ancestral karyotype for rhinolophids and hipposiderids. Given the large number of examples documenting that non-differentially stained karyotypes may be poor indicators of homology in bats (Haiduk et al., 1981; Baker et al., 1985, 1987; McBee et al., 1986) this conclusion seems premature. However, the differences between sub-specifically differentiated populations of *R. luctus* are striking. Intraspecific variation in bats usually involves one or a few rearrangements (Baker, 1979). Most examples of chromosomal polymorphism in bats have been associated with the hybridization of chromosomal races (Baker, 1979, 1984), or involve cases of cryptic species (Baker, 1984; Baker et al., 1985). The significance of chromosomal variation within *R. luctus* is not clear at this time.

***Hipposideros armiger* (Hodgson)**

$2n = 32$; FN = 60

The karyotype of this species was first reported by Ando et al. (1980a) for specimens from Taiwan. The chromosomal complement of our specimens from Thailand, assigned to the subspecies *H. a. armiger*, appears to be identical to that reported from Taiwan. As in all species of *Hipposideros* examined to date,

the autosomal complement of *H. armiger* consists of a graded series of biarmed chromosomes. The X is a large subtelocentric and the Y is a medium-sized acrocentric element.

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