STUDIES OF TAXONOMY AND GEOGRAPHIC

VARIATION IN PLECOTINE BATS

OF NORTH AMERICA

By

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yet here I can but verbally acknowledge their patience,
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CHAPTER I

INTRODUCTION

This thesis is composed of 4 manuscripts written in
formats suitable for submission to selected scientific
journals. Each manuscript is complete without supporting
materials. Chapter II, "Bats of the genus Plecotus in
Mexico: Discrimination and distribution", is written in the
format of the Occasional Papers, The Museum, Texas Tech
University. Chapters III and IV, "Geographic variation in
the Mexican big-eared bat, Idionycteris phyllotis, with
descriptions of subspecies" and "Parsimony analysis of the
phylogeny of the Plecotine bats (Chiroptera:
Vespertilionidae)" are written in the format of the JOURNAL
OF MAMMALOGY. Chapter V, "Toward optimum wing size in
Plecotine bats: Ontogenetic adjustments in size of bony
elements" is written in the format of EVOLUTION.

CHAPTER II

BATS OF THE GENUS PLECOTUS IN MEXICO:
DISCRIMINATION AND DISTRIBUTION

Renn Tumlison

Three taxa of the genus Plecotus occur in Mexico. Allen
(1916) described Plecotus mexicanus, a species endemic to
Mexico, and Handley (1955) described Plecotus townsendii
australis, an endemic subspecies which intergrades with P.
t. pallescens (Miller, 1897) in northern Coahuila. Since
Handley's (1959) revision of the North American Plecotini,
essentially all of the published information on big-eared
bats in Mexico has dealt with distributions. Many range
extensions have been published for various Mexican states,
yet several important records represented in museums are
unknown in the literature. Further, some published records
are based on misidentified specimens. The purposes of this
paper are: 1) to provide additional morphological
information useful in identification of these bats; 2) to
consolidate information on distribution and co-occurrence of
Plecotus taxa in Mexico; 3) to correct some
misidentifications in the literature; and 4) to document new
records which expand considerably our understanding of the
distribution of Plecotus in Mexico.

MATERIALS AND METHODS

<u>Morphology</u>

I borrowed 235 museum specimens of <u>Plecotus</u> taxa
collected in Mexico and identified them on the basis of hair
color, size, and occurrence of an accessory cusp on the
first incisor (Allen, 1916; Handley, 1959). Eighteen skull
characters (Fig. 1) were measured with a Lasico digitizer
and recorded to the nearest 0.1 mm. Skull measurements were
total length (TL), zygomatic breadth (ZB), cranial breadth
(CB), mastoid breadth (MB), width of interorbital
constriction (IOC), length of maxillary toothrow (MT),
palatal length (PL), basicranial length (BL), auditory bulla
length (ABL), intercanine width (ICW), palatal breadth
across the third molars (PBM3), interpterygoid width (IPW),
cranial depth (CD), dentary length (DL), moment arm of the
temporal (MAT), moment arm of the masseter (MAM), coronoid
to angle distance (CA), and mandibular fossa to condyle
distance (FC). Nine skin characters were measured with dial
calipers and recorded to the nearest 0.1 mm. Skin
measurements (Fig. 2) were forearm length (FA), tibia length
(TIB), length of third metacarpal (M3), length of first
phalanx off third metacarpal (M3P1), length of second
phalanx off third metacarpal (M3P2), length of fourth
metacarpal (M4), length of first phalanx off fourth
metacarpal (M4P1), length of fifth metacarpal (M5), and
length of first phalanx off fifth metacarpal (M5P1). Data
were collected on adults only, i.e., specimens having fused

epiphyses in wing bones. Damaged specimens which could not be measured for all characters were excluded from multivariate analyses. Sex was recorded from specimen labels; see acknowledgments for list of museums providing specimens.

I performed a two-way analysis of variance (ANOVA) on each character stratified by taxon and sex. The two-way analysis was selected because sexual dimorphism is known to occur in this genus (Handley, 1959). I treated sexes separately and used pairwise comparisons (protected least significant difference (LSD) tests, Sokal and Rohlf, 1981:244) to identify variables that would help distinguish the three taxa.

Discriminant function analysis (DFA) was used to provide objective identifications of specimens examined. Because sexual dimorphism could reduce the power of discrimination of taxa, the "zwitter" approach of Schnell et al. (1985) was used to reduce the effect of sex. Correction terms used to factor out the effect of sex on skull and skin measurements were based on differences between sexes assessed within taxa. One-half the difference between means for each character was added to the smaller sex (males) and subtracted from the larger sex (females). A two-way analysis of variance for taxon and sex completed after application of correction terms indicated that this procedure had removed sex effects from all variables

(p>0.62) while leaving differences between taxa unaffected.

Sex-adjusted data were transformed to log10 values and
principal components (PCs) were extracted from the
variance-covariance matrices of cranial characters and of
skin characters. Skulls and skins were treated separately
in the multivariate analyses to allow evaluation of skull or
skin only specimens, and because the two data sets may not
provide equal levels of discrimination. Because the
assumption of equal covariance matrices was violated, within
group covariance matrices were used in the discriminant
function analyses.

Distribution

I examined 235 of the specimens identified and reported
in the literature. Identifications were checked in the DFA
analyses, and all specimen records were plotted on a map of
Mexico. Unpublished and misidentified specimens were noted,
and collections simultaneously containing P. mexicanus and
P. townsendii were identified.

RESULTS and DISCUSSION

Fifteen of the 18 skull characters were sexually
dimorphic (p<0.01); the exceptions were cranial breadth,
cranial depth, and width of the interorbital constriction.
All skin variables were dimorphic (p<0.004). The
contribution of sex to the model variance was generally an
order of magnitude less than the contribution of taxon.

Means for all skull variables except CD were significantly different (ANOVA, $p<0.05$) across taxa for females, and all variables except CD and MAM were different for males. Plecotus mexicanus was smallest for most skull measurements and was most similar in size to P. townsendii pallescens; P. t. australis was overall the largest (Table 1). Plecotus mexicanus and P. t. australis are partially sympatric, but size alone was generally sufficient to distinguish individuals. Handley (1959:137) used length of skull (>15.7 mm for P. townsendii) and length of maxillary tooth row (>4.9 mm for P. townsendii) in his key to distinguish the species, and noted (p. 143) that P. mexicanus has a smaller auditory bulla and shorter rostrum, although no measurements were provided. These characters are particularly good for univariate discrimination: in regions of sympatry, bulla lengths of <4.0 mm and palatal lengths <5.2 mm usually represent P. mexicanus while larger measurements represent P. townsendii. I stress sympatry because P. t. pallescens is smaller than P. t. australis and not as easily distinguished by measurements alone. However, sympatry of P. mexicanus and P. t. pallescens is not known to occur except in northern Chihuahua (Anderson, 1972).

All skin variables were significantly different across taxa for both sexes ($p<0.0001$). In contrast to skull data, skins of P. t. pallescens were typically smallest while P. mexicanus was of intermediate size. The first phalanx off the fifth metacarpal provided the only major contrast, in

which P. mexicanus was smallest.

The effect of sexual dimorphism was factored out using correction terms calculated for each taxon (Table 2), producing a "sexless" data set. Principal components analysis indicated structure in those data for both skulls and skins (Fig. 2), and subsequent multivariate analysis of variance (MANOVA) demonstrated that all taxa were different (p<0.0001). The first three PC axes for skulls accounted for 54.7%, 10.0%, and 7.7% of the total sample variance, respectively. The PCI axis is interpreted to represent size because all character loadings were positive and small to moderate in magnitude (Table 2). Clusters corresponding with each of the three taxa are evident, although some overlap exists, especially between the subspecies of P. townsendii (Fig. 3). Overlap of P. t. pallescens with P. mexicanus is due to similarity in overall body size.

Palatal length, intercanine width, coronoid-angle distance, and especially moment arm of the masseter distance contributed most to PC II. The contrast between the first two characters probably indicates a differently shaped rostrum, while the latter two reflect a longer angular process on the dentary. PC II helps distinguish P. mexicanus from P. townsendii, due primarily to differences in the masticatory apparatus.

The first three PCs for skins accounted for 64.9%, 17.2%, and 4.7%, respectively, of the total sample variance. Three

clusters are again apparent but overlap was greater than in the skull analysis. The first PC reflects size, with P. mexicanus being intermediate (Fig. 3). Character loadings for PC II suggest a contrast between metacarpals and first phalanxes, with greater emphasis on the first phalanx of the fifth digit. PC II separates P. mexicanus from both subspecies of P. townsendii.

Discriminant analysis assigned 98.1% of 216 skulls and 84.5% of 219 skins into taxa to which they were initially allocated on the basis of hair color and morphological characters (Allen, 1916; Handley, 1959). No skulls classified a priori as P. t. australis were misclassified, but 3 specimens treated as P. t. pallescens were grouped with P. t. australis . All of the misclassified specimens were from Sonora, and inspection of the posterior probabilities of group membership indicated that, for each subspecies, specimens with > 10% probability of belonging to the alternative subspecies typically were from northern Mexico. Handley (1959:188) suggested that P. t. australis and P. t. pallescens exhibited a zone of intergradation in northern Coahuila and western Texas. Thus, specimens in these areas may be intermediate between the larger P. t. australis and the smaller P. t. pallescens. In my analyses, both skulls and skins from eastern Mexico clustered with P. t. australis, although variation was greater for skins. Specimens of P. t. pallescens from Baja California were not available at the time of Handley's study. Skulls of those I

examined were smaller than specimens referable to P. t.
pallescens from northern Sonora and Chihuahua.

I re-evaluated taxonomic affinity of specimens of P.
townsendii from northern Sonora, Chihuahua, Coahuila, and
northern Durango. Skulls of P. t. pallescens from southern
Arizona and New Mexico (n=110) and of P. t. australis from
southern Mexico (Zacatecas and south) (n=61) were used as
reference specimens. The discriminant function correctly
identified 90.1% of the 171 reference skulls: 82.0% of the
P. t. australis and 94.6% of the P. t. pallescens were
correctly identified. A similar analysis of skins (108 P.
t. pallescens; 68 P. t. australis) resulted in correct
identification of 72.7% of the reference skins: 97.1% of the
P. t. australis but only 57.4% of P. t. pallescens were
correctly identified. Thus, skulls of P. t. pallescens but
skins of P. t. australis are most likely to be accurately
identified. Analysis of skins and skulls from Sonora,
Chihuahua, Coahuila, and Durango indicated that specimens
from northern Sonora and Chihuahua were typical P. t.
pallescens while specimens from southern Chihuahua, northern
Durango, and central Coahuila often had skins more like P.
t. australis and skulls more like P. t. pallescens. The
intergrade zone through northern Coahuila and western Texas
indicated by Handley (1959:188) apparently extends westward
to include southern Chihuahua and northern Durango.

Plecotus mexicanus occurs primarily in higher, more humid mountain areas between 4800-10500 ft. (usually above 6000 ft.), while P. t. australis occurs in the arid interior mountain ranges between 1800-9500 ft. (but most collections were between 4000-7000 ft.) in central and northern Mexico (Handley, 1959:141,185). Still, some sampling locations provided specimens of both species. Burt (1938) treated a series of nine specimens from Saric (Sonora) as P. t. pallescens. One of these specimens "agrees in both skin and skull characters with Allen's description of mexicanus", prompting Handley (1959:148) to suggest that both species might have been present. Handley (1959) also noted both species in samples from Sonora (El Tigre Mountains, p. 148), Guanajuato (Santa Rosa, p. 151, 189), and Zacatecas (Sierra del Valparaíso, p. 151, 189). Further, Wilson et al. (1985) documented both species from Coahuila (Sierra del Carmen), and Matson and Patten (1975) and Matson and Baker (1986) from Zacatecas (3 mi. N Ciudad Cuauhtémoc, 8 mi. NW Nochistlán). Jones and Webster (1976) reported P. townsendii from Zacatecas (Laguna Valderrama), but my analysis indicated that both species were present in their sample. The range in elevation of collection sites producing both species is 6600-9500 ft. (2010-2900 m).

Species Accounts

Plecotus mexicanus (G. M. Allen, 1916)

Specimens referable to P. mexicanus were previously
reported from Chihuahua (Knobloch, 1942; Anderson, 1972),
Coahuila (Wilson et al., 1985), Jalisco (Watkins et al.,
1972), México (Davis, 1944), Michoacán (Miller, 1897; Hall
and Villa-R., 1949), Puebla (Koopman, 1974), Quintana Roo:
Isla Cozumel (Koopman, 1974), Queretaro (Baumgardner et al.,
1977), San Luis Potosí (Wilson et al., 1985), Sonora (Burt,
1938), Veracruz (Ward, 1904; Hall and Dalquest, 1963),
Yucatan (Koopman, 1974), and Zacatecas (Matson and Patten,
1975; Matson and Baker, 1986). Handley (1959) listed
specimens from Chihuahua, Guanajuato, México, Michoacán,
Morelos, Nuevo León, Puebla, Sonora, Veracruz, and
Zacatecas, and Villa-R. (1966) added material from Distrito
Federal, México, and Morelos. Additional records are herein
reported (see specimens examined) for Chihuahua, Jalisco,
Queretaro, and Zacatecas (Fig. 4). The new Zacatecas record
was published by Jones and Webster (1976) as P. townsendii
but I found specimens representing both species in their
sample. In addition, I report here the first state records
for Colima, Hidalgo, Sinaloa, and Tlaxcala. The Colima
records extend the range slightly from western Jalisco
(Watkins et al., 1972), but the Sinaloa specimens represent
the greatest range extension.

Specimens Examined.--Total 77, "*" indicates unpublished
records.

CHIHUAHUA: Barranca del Cobre, 23 mi. S, 1.5 mi. E Creel, 2 (KU); near Pacheco (Sierra de Breña, 8000 ft.), 2 (USNM); Sisoguichic, 8500 ft., 1 (OU)*; Mojarachic (=Mafuarachic), 1 (USNM). COAHUILA: Sierra del Carmen, 1 mi. N of summit, 1 (USNM). COLIMA: Cerro Grande, 7800 ft., 16 (LACM)*; 10 mi. NW Comala, 6800 ft., 1 (LACM)*. GUANAJUATO: Santa Rosa, 9500 ft., 1 (USNM). HIDALGO: 12 mi. W Tulancingo, 8850 ft., 5 (KU)*. JALISCO: Volcán de Colima, N slope Cerro Nevado, 8500 ft., 3 (LACM)*; Cueva del Aquacate, 4 km E Soyatlán del Oro, 3 (UA)*; N slope Nevado de Colima (Volcán de Nieve), 8000 ft., 2 (UA)*; 15 mi. S, 9 mi. E Talpa de Allende, 6900 ft., 1 (KU); 7 mi. S Tapalpa, 6800 ft., 1 (KU). MEXICO: Monte Río Frío, 55 km ESE México City, 10500 ft., 1 (TCWC). NUEVO LEÓN: 33 km SE Monterrey, 2 (MCZ). PUEBLA: between Mexico City and Puebla, E side of Continental Divide, 10300 ft., 3 (AMNH). QUERETARO: Piñal de Amoles, 1 (TCWC); 20 km NW (by road) San Joaquin, 3 (TCWC); Rancho Agua Frío, 9.5 mi. W Maconi, 5 (TCWC)*. SAN LUIS POTOSÍ: 14 mi. S San Francisco, Cueva de la Joya de Lapuente, 1 (USNM). SINALOA: ca. 2 mi. NW Palmito, 3 (UA)*. TLAXCALA: 5 km E, 3 km N Tlaxcala, 2300 m., 1 (TTU)*. VERACRUZ: 4 km E Las Vigas, 8500 ft., 6 (KU); 6 km WSW Zacualpilla, 6500 ft., 1 (KU). YUCATAN: 8 km from Tixpehual on Hwy to Tixkokob, 1 (AMNH). ZACATECAS: 3 mi. N Ciudad Cuauhtémoc, 6600 ft., 4 (LACM); 8 mi. NW Nochistlán, 6600 ft., 1 (LACM); 10 mi. NW Yahualica (Jalisco), 7100 ft., 1 (LACM); 40 mi. W Fresnillo, Laguna Valderrama, 2 (CAS)*.

Additional records:

CHIHUAHUA: 3 mi. S and 10 mi. E Pacheco (Anderson, 1972). DISTRITO FEDERAL: Cañada de San Bernabé, Contreras, 2280 m; Facultad de Ciencas, Ciudad Universitaria, 2260 m (Villa-R., 1966). JALISCO: 4.5 mi. NE Comanja de Corona, 8000 ft.; 12 mi. S Toliman, 7700 ft. (Watkins et al., 1972). MÉXICO: Criadero de Fauna Cinegética, San Cayetano; Cueva en el Paso Oyamecalco, 25 km N Cuatepec Harinas; Barranca de los Idolos, 35 km W Mexico, D.F. (Villa-R., 1966). An unpublished record housed at TCWC was collected 5.5 mi. E Amecameca, on the road to Paso de Cortes. MICHOACAN: 2 mi. N Pátzcuarco (Miller, 1897; Hall and Villa-R., 1949). MORELOS: no exact locality (Handley, 1959:151); Cueva del Murciélago, Cerro El Fraile, 6.5 km NW Tres Cumbres, 3400 m (Villa-R., 1966). PUEBLA: Hacienda de Miguel Sesma, 2 mi. NW Esperanza (Handley, 1959:151). QUERETARO: 3.8 km W El Madrono (near El Lobo) (Baumgardner et al., 1977). QUINTANA ROO: Isla Cozumel. On geographic grounds, Koopman (1959) discredited a specimen collected by Gaumer (housed at KU and listed as collected on the Island of Cozumel off the Yucatan Peninsula) but later (Koopman, 1974) noted that a specimen from Yucatan supports the Cozumel record. SAN LUIS POTOSÍ: 12 km W, 6.4 km N Río Verde (Wilson et al., 1985). SONORA: Santa María Mine, El Tigre Mountains (Handley, 1959:151); Saric (Burt, 1938; Handley 1959:151). TAMAULIPAS: Cueva Chica de la Perra, 8 mi. NW Gómez Farías, Sierra de Guatemala, 7000 ft. (Mollhagen, 1971). VERACRUZ: Jico (5500

ft.) (Handley, 1959:151). ZACATECAS: Sierra del Valparaíso
(13 mi. W Valparaíso, 8200 ft.) (Handley, 1959:151; Matson
and Baker, 1986).

Plecotus townsendii australis (Handley, 1955)

Specimens referable to P. t. australis were previously
reported from Aguascalientes (Urbano-Vidales et al., 1987),
Chihuahua (Anderson, 1972), Coahuila (Baker, 1956; Easterla
and Baccus, 1973; Wilson et al., 1985), Durango (Baker and
Greer, 1962; Gardner, 1965), Guerrero (Davis and Carter,
1962), Hidalgo (Davis, 1944; Hooper, 1955; Carter and Jones,
1978), Jalisco (Allen, 1890; Watkins et al., 1972), Nuevo
León (Wilson et al., 1985), Oaxaca (Goodwin, 1969),
Queretaro (Baumgardner et al., 1977), San Luis Potosí
(Dalquest, 1953; Wilson et al., 1985), Tamaulipas (Alvarez
and Ramirez-P., 1972; Baumgardner et al., 1977; Schmidly and
Hendricks, 1984), and Zacatecas (Jones and Webster, 1976;
Matson and Patten, 1975; Matson and Baker, 1986). Handley
(1955, 1959) listed specimens from Coahuila, Distrito
Federal, Durango, Guanajuato, Hidalgo, Jalisco, México,
Morelos, Oaxaca, San Luis Potosí, and Zacatecas, and
Villa-R. (1966) added material from Distrito Federal,
Guanajuato, Guerrero, Hidalgo, Jalisco, México, and
Michoacán. Additional records are herein reported for
Aguascalientes, Chihuahua, Coahuila, Nuevo León, San Luis
Potosí, and Zacatecas (Fig. 5). The new Zacatecas records
were reported by Matson and Baker (1986) as P. mexicanus

based on 3 specimens housed at OU. These specimens are referable to P. t. australis on the basis of size, absence of the accessory cusp on the first incisor, and discriminant analysis.

A specimen from near La Mariposa, Coahuila (KU 44759) was mentioned by Handley (1959:149) as a possible intergrade because it possessed many characteristics of P. mexicanus. Discriminant analysis assigned the skull of this specimen to P. mexicanus with a posterior probability of membership of 1.0000, but the skin was discriminated as P. townsendii. The specimen was collected northwest of the nearest records of P. mexicanus from Nuevo Leon but lies intermediate in geographic position with a record from northern Coahuila (Wilson et al., 1985). This record would lower the elevational limit from 4800 ft. (Handley, 1959:141) to 2300 ft. (700 m) for P. mexicanus. I suggest that the skin is probably the correct specimen for the locality data, but the skull apparently does not belong with the skin.

Specimens Examined.--Total 96, "*" indicates new records. AGUASCALIENTES: mine above San Pedro de Cobre, 0.2 mi. S, 12 mi. E Rincon de Romos, 1 (MVZ)*. CHIHUAHUA: 3 mi. E San Francisco del Oro, 6900 ft., 1 (TCWC)*; 14.3 mi. S Santa Elena, 1 (ROM)*; 1 mi. N, 1 mi. W Salaices, 2 (KU). COAHUILA: 4 mi. W Hacienda La Mariposa, 2300 ft., 1 (KU); Cuatrociéngas, 2250 ft., 1 (TCWC); 8 mi. W Nadadores, 2100 ft., 1 (MSU)*; 1 mi. S, 4 mi. W Bella Unión, 7000 ft., 1 (KU); 0.5 mi. N Muralla, 4500 ft., 2 (KU); 9 mi. W, 4 mi. S

San Buenaventura, 2000 ft., 2 (KU); Sierra Guadalupe, 10 mi.
S, 5 mi. W General Cepeda, 7800 ft., 1 (KU); 1 mi. N, 2.5
mi. W El Cedrito, 2400 m., 1 (USNM); 1 mi. N Cuatrociéngas,
1 (USNM); Sierra del Carmen, 1 mi. N Summit, 1 (USNM).
DURANGO: 7 mi. N Campaña, 3750 ft., 1 (MSU); San Juan, 12
mi. W Lerdo, 3800 ft., 2 (UMMZ); near Ojito, ca. 50 km W on
Vergel Road from Hidalgo de Parral, 7600 ft., 2 (LACM); ca.
72 km W on Vergel Road from Hidalgo de Parral, 6100 ft., 3
(LACM) 2 (UA). GUANAJUATO: Santa Rosa (9500 ft.), 1 (USNM);
Charcas, 1 (USNM). GUERRERO: 1 mi. SSE Almolonga, ca. 5600
ft., 2 (TCWC). HIDALGO: Jacala, 1 (YPM); 3 km W Jacala,
5500 ft., 1 (USNM); Río Tasquillo, 26 km E Zimapán, 5200
ft., 1 (TCWC); Grutas Xoxafí, 11 km SE Yoltepec, 1 (KU).
JALISCO: San Andrés, 10 mi. W Magdalena (4900 ft.), 3
(UMMZ); San Pedro, Guadalajara, 1 (AMNH). MÉXICO: Lago
Texcoco, 7500 ft., 1 (USNM). NUEVO LEÓN: Grutas de Garcia,
1 (MWSU)*; Mina del Taco, 3.5 mi. N Aramberri, 3900 ft., 3
(KU)*; 5 mi. W Sabinas Hidalgo, Cueva sin Nombre, 1 (USNM);
0.5 mi. W La Joya, Cerro Potosí, 1 (USNM). QUERETARO: Río
Galindo, 1 (TCWC). SAN LUIS POTOSÍ: 21.5 km N Huizache, 1
(TTU)*; Presa de Guadalupe (4000 ft.), 1 (LSUMZ); San Pedro,
1 (USNM). TAMAULIPAS: 2 mi. ESE San Carlos, San Carlos
Mountains, 3 (TCWC). ZACATECAS: 6 km W San Rafael, 2170 m.,
1 (MSU); 12 mi. SE Concepción del Oro, 7450 ft., 3 (MSU); 16
km SW Concepción del Oro (near La Laja), 2400 m., 1 (MSU);
10 mi. SW Concepción del Oro, 7600 ft., 15 (LACM); 9.7 mi.
NW Cuauhtémoc, 7100 ft., 1 (OU)*; 3 mi. N Ciudad Cuauhtémoc,

6600 ft., 18 (LACM); 6 mi. NNW Pinos, 7900 ft., 1 (MSU); 8
mi. NW Nochistlán, 6600 ft., 1 (LACM); Laguna Valderrama, 40
mi. W Fresnillo, 7800 ft., 1 (CAS); Hacienda El Lobo, 10 km
ENE Loreto, 7350 ft., 1 (OU)*; 7 mi. E Moyahua, 5500 ft., 1
(OU)*.

Additional records:

AGUASCALIENTES: Cerro de los Gallos, 14 km S, 6 km E
Aguascalientes City (Urbano-Vidales et al., 1987).
COAHUILA: mina abandonada de flourita, Sierra del Carmen
(Wilson et al., 1985); Fronteriza Mountains, 28°58'N, 102°
26'W, northwestern Coahuila (Easterla and Baccus, 1973).
DISTRITO FEDERAL: Desierto de los Leones (Handley,
1959:189); Osario Común, Pantéon de Dolores, 2260 m
(Villa-R., 1966). GUANAJUATO: Apaseo, 1805 m (Villa-R.,
1966). GUERRERO: Cueva Tecabra, Aguacatitlán, 1400 m
(Villa-R., 1966). An unpublished record housed at USNM was
collected 5 mi. E Omilteme, 6200 ft. HIDALGO: Barranca
Punta Rosa, 1 km from Escandón (Villa-R., 1966). JALISCO:
El Salto, 24 mi. W Guadalajara, 4500 ft. (Watkins et al.,
1972); Cueva de las Garrochas, 17 km NNW Soyatlán del Oro
(Villa-R., 1966). MÉXICO: Convento de Acolman, 9 mi. N
México, Distrito Federal (Handley, 1959:189); Cueva del
Diablo, 1880 m, La Peña, Valle de Bravo (Villa-R., 1966).
An unpublished record housed at USNM was collected 5 mi. S
Raices, Nevado de Toluca. MICHOACÁN: Cueva de la Arena, 5
km SW Jacona (Villa-R., 1966). MORELOS: Cuernavaca (4900
ft.) (Handley, 1955, 1959:189). OAXACA: Tlacolula, Mitla;

Tehuantepec, Tehuantepec (Goodwin, 1969); Oaxaca (Motne
Albán, 3 mi. SW Oaxaca, 6500 ft.) (Handley, 1955, 1959:189;
Goodwin, 1969). SAN LUIS POTOSÍ: Bledos (6200 ft.)
(Dalquest, 1953; Handley, 1955, 1959:189); Hacienda La
Parada, 6000 ft. (Miller, 1897; Handley, 1959:189).
TAMAULIPAS: 7 km S Marcela, 2400 m; 5 km S Miquihuana, 2150
m (Alvarez and Ramirez-P., 1972). ZACATECAS: Sierra de
Valparaíso (13 mi. W Valparaíso, 8200 ft.) (Handley, 1955,
1959:189).

Plecotus townsendii pallescens (Miller, 1897)

Specimens of Plecotus townsendii pallescens have been
documented from Baja California (Huey, 1963; Orr and Banks,
1964; Woloszyn and Woloszyn, 1982:86, Sanchez-H., 1986),
Chihuahua (Anderson, 1972), and Sonora (Burt, 1938; Dingman,
1964). Handley (1959:194-195) listed specimens from
Chihuahua and Sonora, and Villa-R. (1966) added material
from Baja California. Additional records are herein
reported for Baja California, Chihuahua, and Sonora (Fig.
6). This is the least well documented form of Plecotus in
Mexico. It has been collected throughout most of Baja
California and at least western and northern Sonora and
northern Chihuahua, and on several of the islands in the
Gulf of California. However, only one record (Dingman,
1964) has been reported for southwestern Sonora; four
additional records are documented here. The specimens from
that area are more similar in size to those from Baja

California than they are to P. t. pallescens from northern
Sonora and Chihuahua. Small specimens from the island of
Tiburon in the Gulf of California suggest a link between
populations in Baja California Norte and southern Sonora.
This may indicate a dual origin of populations in Sonora,
the southern population originating from Baja and the
northern population from Arizona and New Mexico.

Specimens Examined.--Total 62, "*" indicates new records.
BAJA CALIFORNIA: 11 mi. N San Antonio de mar, cave on sea
coast, 1 (LACM)*; 14 mi. NNE Punta Prieta, Desengaño Mine,
16 (CAS); mine de San Juan, 18 km NE San Gregorio, 4000 ft.,
1 (UA)*; Mina La Republica, 31°51'N, 116°04'W, 4000 ft., 10
(MVZ)*; Valladares, 2700 ft., 4 (MVZ)*; Arroyo San Luis, 9
mi. W Calmallí, 800 ft., 2 (MVZ)*; El Carrizalito, 5 mi. N
Santiago, 1400 ft., 2 (MVZ)*. CHIHUAHUA: 25 mi. SW Santa
Elena, SE slope Santa Elena Mountains, 1 (USNM)*. SONORA:
Isla Tiburón, Tecomaté, 10 (MSB)*; 5 mi. NW San Carlos, 1
(MSB)*; Bahia San Carlos, N of Guaymas, 4 (LACM)*; 0.5 mi. E
cemetery at Alamos, 1 (MSB)*; 5 mi. W Alamos, Minas Nuevas,
1600 ft., 1 (UA); 0.25 mi. E Bacerac, 3268 ft., 1 (UA)*;
Pilares, 1 (UMMZ); 5 mi. S Naco, 1 (CSULB)*; Sierra los
Cenizas, 11 mi. SE Agua Prieta, 1 (USNM)*; 11 mi. E Imuris,
Hwy 2, 1 (MSB)*; El Tigre Mts., Santa María Mine, 3 (UMMZ).

Additional records:
BAJA CALIFORNIA: Isla San José (Sanchez-H., 1986); Isla
Santa Catalina (Orr and Banks, 1964); Calmallí (Huey, 1963);
25 mi. N Punta Prieta (Huey, 1963); Las Cuevas, Santiago

(Villa-R., 1966); Sierra de La Laguna (Woloszyn and Woloszyn, 1982:86). Unpublished records housed at MVZ were collected at Los Gavilanes, 23 mi. N Laguna Hanson, Sierra Juárez, and at San Antonio mine, 10 mi. SE San José, near latitude 31°N. CHIHUAHUA: La Republica, 3900 ft. (Anderson, 1972); Tinaja de Ponce, 2600 ft., Sierra de Ponce, 12 mi. SW Santa Helena (Handley, 1959:194); Casas Grandes (Handley, 1959:195). SONORA: Saric (Burt, 1938).

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APPENDIX

Specimens examined of P. t. pallescens (n=114) from
southern Arizona and New Mexico, USA, used for comparison
with P. townsendii from northern Mexico.

ARIZONA: COCHISE COUNTY: location unknown, 2 (YPM);
Huachuca Mts., Ramsey Canyon, 1 (OSUFW); Huachuca Mts.,
Hunter Canyon, Short Mine, 2 (FMNH); Huachuca Mt. foothills,
Anderson Mine, Canelo, 1 (JMM); Huachuca Mts., 0.8 mi. N
Montezuma Pass, 1 (UA); Chiricahua Mts., 1.5 mi. N Portal, 1
(TTU); mine NW Portal, 4 (MSU); Guadalupe Canyon at AZ-MEX
border, 1 (MSB); Davis Mt., 6 mi. N Portal, Cochise Mine, 1
(LACM); Cochise, 7 (LACM); 3 mi. E, 17 mi. S San Simon, base
of Chiricahua Mts., 2 (ASUMZ); 13 mi. S Bowie, 1 (ISUVC);
0.5 mi. NW Portal, 1 (UMMZ); El Tigre Mine, Piney Canyon,
Chiricahua Mts., 1 (LSUMZ) 2 (UA); Cochise, Redbird Mine, 4
(LACM); 2.1 mi. E Portal, 1 (TTU); mine 1 mi. N Paradise, 1
(UA); Commonwealth Mine, 0.5 mi. E Pierce, 1 (UA); Crystal
Cave, 1 (AMNH) 1 (UA); Virture Mine, near Portal, 1 (UA); W
Turkey Creek, El Coronado Ranch, Chiricahua Mts., 1 (UA);
Barfoot Park, Chiricahua Mts., 1 (UA).

NEW MEXICO: DONA ANA COUNTY: 3.9 mi. N, 10.1 mi. W Las
Cruces, 1 (FSM); 1.8 mi. W, 0.4 mi. N Picacho Mt., vic. Las
Cruces, 6 (NMSU); W side Organ Mts., 1 (NMSU); Ruby Hayner
Mine, 4.2 mi. S Organ, 1 (NMSU); Dripping Spring, 1 (NMSU);
Organ Mts., 0.5 mi. W Rabbit Ears, 1 (NMSU). EDDY COUNTY:
McKittrick Hill, Dry Cave, 1 (UTEP); 18 mi. SW Carlsbad, 1

(KU). GRANT COUNTY: 14 mi. S, 6.5 mi. W Glenwood, 3 (MSB); NW of American Mine, S35,T27S,R16W, 8 (MSB); 1 mi. S Georgetown, 3 (UTEP); 13.5 mi. S, 0.5 mi. W Cliff, mouth of Bear Canyon on Gila River, 1 (MSB); 2.5 mi. N jct. NM527 and NM61, 1 (MSB); 4 mi. E, 6 mi. N San Lorenzo, Silver Creek, Teal Mine, 1 (WNMU); 2 mi. S Cliff, 1 (WNMU); 7 mi. NE Silver City, Cleveland Mine, 1 (WNMU). HIDALGO COUNTY: 12.6 mi. N Stiens, Peincillo Mts., 1 (UTEP); Thicket Spring, S23,T33S,R15W, 1 (NMSU); 7.1 mi. W, 4.2 mi. S Cloverdale, Guadalupe Canyon, 2 (NMSU); 17 mi. E Hilo Park, 1 (NMSU); NW 1/4, S34,T30S,R16W, 1 (MSB); Alamo Hueco Mts., Peterson Well, S7,T33S,R14W, 1 (WNMU); Aspen Spring, 0.9 mi. S, 0.4 mi. E Animas Peak, 1 (NMSU); Sycamore Well, SW 1/4, S31,T33S,R14W, 2 (MSB); W side Hachita Peak, S34,T28S,R16W, 1 (MSB); Occidental Mines, Sierra Rica, S25,T29S,R14W, 1 (MSB); Clanton Canyon, SW 1/4, S16,T32S,R21W, 1 (MSB); Howell's Well, S24,T28S,R16W, 1 (MSB); Dog Springs, S13,T34S,R15W, 1 (WNMU). LUNA COUNTY: 15.4 mi. S, 8.7 mi. E Deming, 1 (NMSU); 12.2 mi.S, 9.0 mi. E Deming, 1 (NMSU); 29.9 mi. S, 2.2 mi. W Deming, 1 (CSULB); 10 mi. SE Deming, 4 (WNMU). OTERO COUNTY: Mayhill Community Center, 1 (MSB); 3 mi. NW Oro Grande, 1 (UTEP); 2 mi. W, 0.5 mi. N Oro Grande post office, 1 (UTEP); mines W Oro Grande, 2 (UTEP); Oro Grande, 9 (UTEP); Jarilla Mts., 2 (UTEP); Ruidoso, Fort Stanton Cave, 2 (NMSU); Sacramento Mts., Hubell Canyon, T18S,R12E, 1 (MSB); Alamo Mt., T26S,R31E, 1 (MSB).

Table 1. Means and standard deviations () by sex for skull
measurements of Plecotus mexicanus (PMX), P. townsendii
australis (PTA), and P. t. pallescens (PTP) from
Mexico. Means with different letters (A, B, or C) are
significantly different (LSD, p<0.05). Comparative
measurements for P. t. pallescens from Arizona and New
Mexico, USA, are also given. See text for explanation
of character abbreviations.

FEMALES

SKULLS

	PMX (n=40)	PTA (n=50)	PTP (n=36) (Mexico)	PTP (n=70) (USA)
TL	15.13(0.22)A	16.09(0.21)B	15.46(0.28)C	15.85(0.28)
ZB	8.29(0.15)A	8.92(0.19)B	8.51(0.20)C	8.83(0.22)
CB	7.53(0.15)A	7.73(0.15)B	7.48(0.17)A	7.65(0.16)
MB	8.84(0.16)A	9.26(0.18)B	8.88(0.18)A	9.17(0.17)
IOC	3.39(0.11)A	3.62(0.12)B	3.45(0.10)C	3.57(0.10)
MT	4.75(0.10)A	5.10(0.13)B	5.02(0.12)C	5.06(0.13)
PL	5.02(0.13)A	5.50(0.15)B	5.35(0.18)C	5.42(0.23)
BL	11.99(0.22)A	12.90(0.22)B	12.54(0.23)C	12.76(0.30)
ABL	3.78(0.07)A	4.14(0.10)B	3.99(0.09)C	4.11(0.09)
ICW	2.21(0.09)A	2.25(0.10)B	2.16(0.07)C	2.25(0.09)
PBM3	5.70(0.12)A	5.90(0.16)B	5.68(0.11)A	5.87(0.14)
IPW	2.32(0.06)A	2.42(0.11)B	2.34(0.10)A	2.43(0.12)
CD	5.78(0.14)A	5.78(0.22)A	5.73(0.15)A	5.72(0.23)

Table 1. Continued.

FEMALES

| | SKULLS | | | |
	PMX (n=40)	PTA (n=50)	PTP (n=36) (Mexico)	PTP (n=70) (USA)
DL	9.44(0.22)A	10.05(0.29)B	9.68(0.21)C	9.90(0.28)
MAT	2.55(0.09)A	2.82(0.11)B	2.66(0.11)C	2.78(0.13)
MAM	2.36(0.10)A	2.29(0.10)B	2.24(0.12)C	2.31(0.11)
CA	3.80(0.17)A	4.07(0.15)B	3.89(0.13)C	4.05(0.13)
FC	3.03(0.13)A	3.30(0.17)B	3.16(0.11)C	3.27(0.14)

| | SKINS | | | |
	n=40	n=54	n=38	n=66
FA	41.53(1.20)A	42.81(0.99)B	40.24(1.08)C	42.20(1.27)
TIB	19.00(0.84)A	19.05(0.59)A	18.01(0.66)B	18.72(0.68)
M3	37.86(1.30)A	38.30(0.99)A	35.03(1.21)B	37.24(1.02)
M3P1	12.45(0.67)A	13.20(0.42)B	12.24(0.63)A	13.05(0.57)
M3P2	17.57(0.79)A	18.28(0.61)B	16.79(0.61)C	17.87(0.72)
M4	36.87(1.28)A	37.35(1.07)A	34.44(1.30)B	36.57(1.05)
M4P1	9.97(0.38)A	10.44(0.46)B	9.55(0.54)C	10.27(0.43)
M5	38.20(1.32)A	38.86(1.03)B	35.94(1.27)C	38.04(1.10)
M5P1	8.80(0.38)A	9.66(0.43)B	9.12(0.46)C	9.65(0.40)

Table 1. Continued.

MALES

SKULLS

	PMX (n=34)	PTA (n=36)	PTP (n=23) (Mexico)	PTP (n=43) (USA)
TL	15.07(0.26)A	15.84(0.26)B	15.23(0.31)C	15.73(0.31)
ZB	8.18(0.18)A	8.77(0.18)B	8.40(0.28)C	8.73(0.24)
CB	7.48(0.15)A	7.65(0.18)B	7.55(0.18)A	7.62(0.16)
MB	8.72(0.17)A	9.10(0.15)B	8.80(0.23)A	9.05(0.19)
IOC	3.38(0.13)A	3.59(0.09)B	3.42(0.18)A	3.54(0.12)
MT	4.71(0.11)A	5.08(0.11)B	4.95(0.11)C	5.01(0.12)
PL	4.95(0.14)A	5.46(0.10)B	5.32(0.12)C	5.36(0.12)
BL	11.85(0.22)A	12.77(0.19)B	12.34(0.29)C	12.66(0.21)
ABL	3.75(0.10)A	4.11(0.09)B	3.94(0.12)C	4.10(0.09)
ICW	2.15(0.09)A	2.21(0.12)B	2.08(0.09)C	2.18(0.10)
PBM3	5.57(0.13)A	5.82(0.16)B	5.58(0.15)A	5.76(0.13)
IPW	2.25(0.09)A	2.36(0.14)B	2.25(0.12)A	2.36(0.13)
CD	5.78(0.18)A	5.72(0.15)A	5.70(0.18)A	5.69(0.17)
DL	9.22(0.25)A	9.87(0.21)B	9.53(0.22)C	9.79(0.27)
MAT	2.53(0.10)A	2.72(0.10)B	2.59(0.11)C	2.69(0.11)
MAM	2.27(0.14)A	2.25(0.10)A	2.20(0.11)A	2.26(0.13)
CA	3.71(0.13)A	3.96(0.15)B	3.77(0.15)A	3.93(0.14)
FC	2.99(0.15)A	3.19(0.15)B	3.05(0.13)A	3.17(0.13)

Table 1. Continued.

MALES

<div style="text-align:center">SKINS</div>

	n=34	n=37	n=18	n=42
FA	40.19(0.99)A	41.62(0.88)B	39.13(1.13)C	41.16(1.01)
TIB	18.73(0.60)A	18.70(0.60)A	17.92(0.56)B	18.60(0.59)
M3	36.68(1.02)A	37.07(0.89)A	33.85(1.46)B	35.96(3.27)
M3P1	12.06(0.48)A	12.85(0.49)B	12.10(0.54)A	12.79(0.43)
M3P2	16.95(0.69)A	17.66(0.53)B	16.73(0.67)A	17.50(0.67)
M4	35.74(1.065A	36.19(0.91)A	33.21(1.48)B	35.80(0.96)
M4P1	9.61(0.43)A	10.08(0.47)B	9.49(0.33)A	10.00(0.39)
M5	37.19(1.18)A	37.58(0.91)A	34.82(1.21)B	37.13(1.05)
M5P1	8.59(0.32)A	9.42(0.42)B	9.16(0.36)C	9.33(0.40)

Table 2. Correction factors for removal of sex effects, and
loadings of morphological variables on the first three
principal components (PCs) in the analysis of <u>Plecotus</u>
taxa from Mexico.

SKULLS	Correction factor			Principal Component		
	PMX	PTA	PTP	I	II	III
TL	0.026	0.125	0.115	0.199	-0.064	-0.012
ZB	0.053	0.075	0.055	0.259	-0.023	0.034
CB	0.025	0.040	-0.035	0.114	0.050	0.085
MB	0.065	0.080	0.040	0.186	0.036	0.074
IOC	0.005	0.015	0.015	0.255	0.016	0.135
MT	0.020	0.010	0.035	0.254	-0.161	-0.070
PL	0.035	0.020	0.015	0.318	-0.244	-0.159
BL	0.070	0.065	0.100	0.248	-0.147	-0.063
ABL	0.015	0.015	0.025	0.310	-0.141	-0.063
ICW	0.030	0.020	0.040	0.179	0.301	0.549
PBM3	0.065	0.040	0.045	0.162	0.068	0.159
IPW	0.035	0.030	0.045	0.213	0.150	0.547
CD	0.000	0.030	0.015	0.037	0.158	0.131
DL	0.110	0.090	0.075	0.245	-0.055	-0.039
MAT	0.010	0.050	0.045	0.332	0.005	-0.287
MAM	0.045	0.020	0.020	0.012	0.804	-0.349
CA	0.045	0.055	0.060	0.282	0.256	-0.279

Table 2. Continued.

SKULLS	Correction factor			Principal Component		
	PMX	PTA	PTP	I	II	III
FC	0.020	0.055	0.055	0.322	0.086	−0.057
SKINS						
FA	0.670	0.595	0.555	0.266	0.076	0.067
TIB	0.135	0.175	0.045	0.222	0.257	0.279
M3	0.590	0.615	0.590	0.358	0.357	−0.114
M3P1	0.195	0.175	0.070	0.368	−0.315	−0.660
M3P2	0.310	0.310	0.030	0.325	0.070	0.520
M4	0.565	0.580	0.615	0.356	0.318	−0.065
M4P1	0.180	0.180	0.030	0.403	−0.233	−0.150
M5	0.505	0.640	0.560	0.332	0.287	−0.058
M5P1	0.105	0.120	−0.020	0.335	−0.677	0.410

Fig. 1. Skull variables used in the analysis of taxa of
  Plecotus collected in Mexico. Refer to text for
  explanation of characters.

Fig. 2. Skin variables used in the analysis of taxa of
  Plecotus collected in Mexico. Refer to text for
  explanation of characters.

Fig. 3. Principal components analysis of skulls (upper)
  and skins (lower) of specimens of _Plecotus_ from Mexico.
  Open circles = _P_. _t_. _australis_, closed circles = _P_. _t_.
  pallescens, and triangles = _P_. _mexicanus_.

Fig. 4. Distribution of _Plecotus_ _mexicanus_. Filled circles
  = new records, open circles = literature records,
  circled dots = published records examined during this
  study, and half-filled circles = unpublished museum
  records not examined.

Fig. 5. Distribution of _Plecotus_ _townsendii_ _australis_.
  Symbols are as in Fig. 4.

Fig. 6. Distribution of _Plecotus_ _townsendii_ _pallescens_ in
  Mexico. Symbols are as in Fig. 4.

PC 2

PC 1

Skins

PC 2

PC 1

Skulls
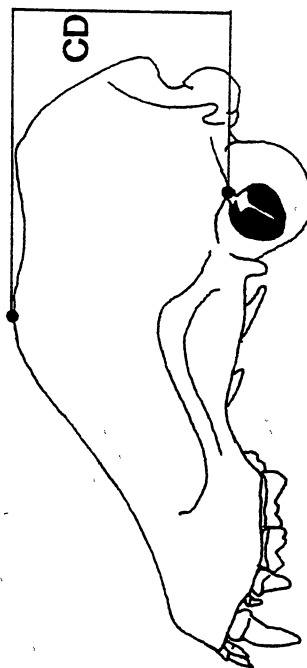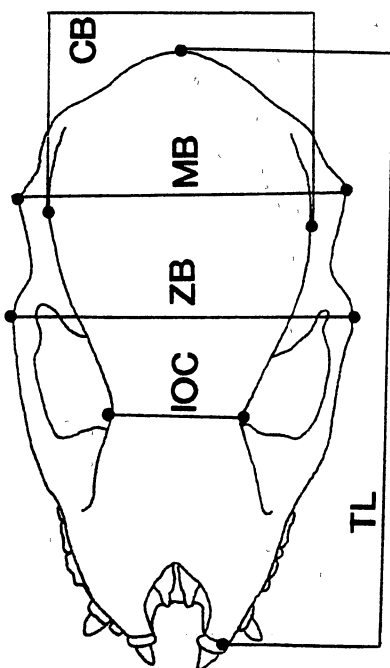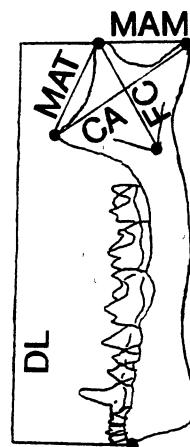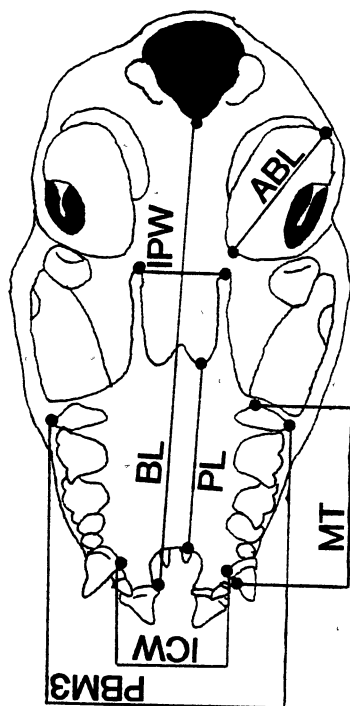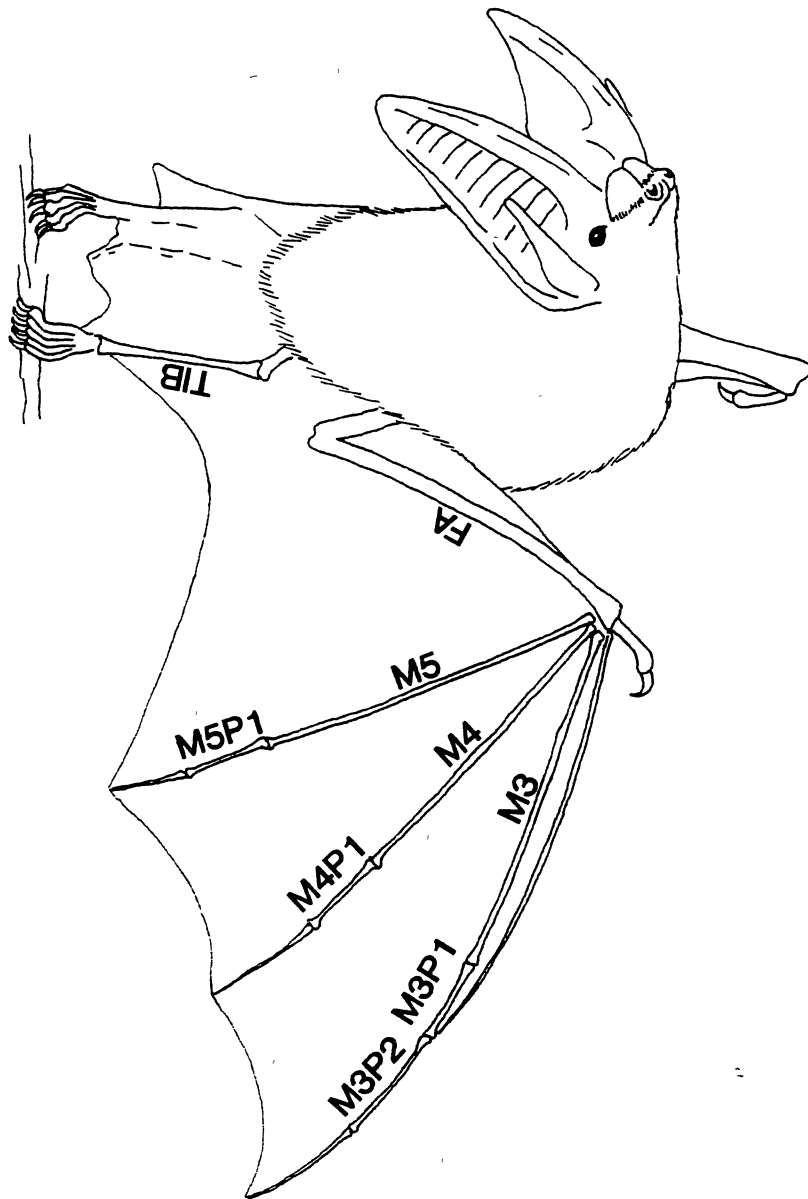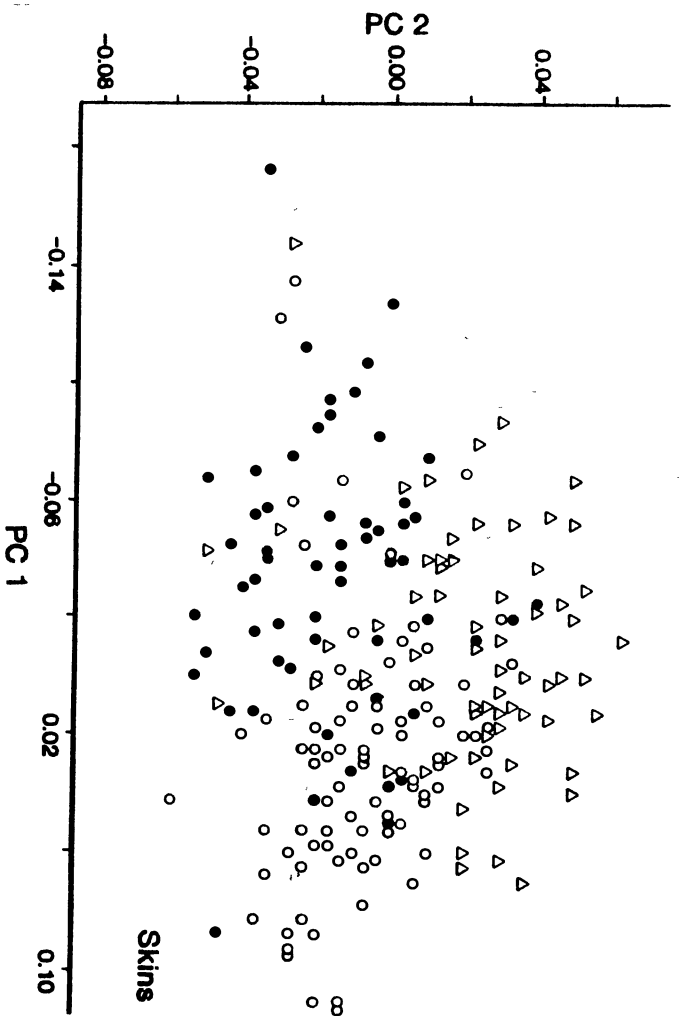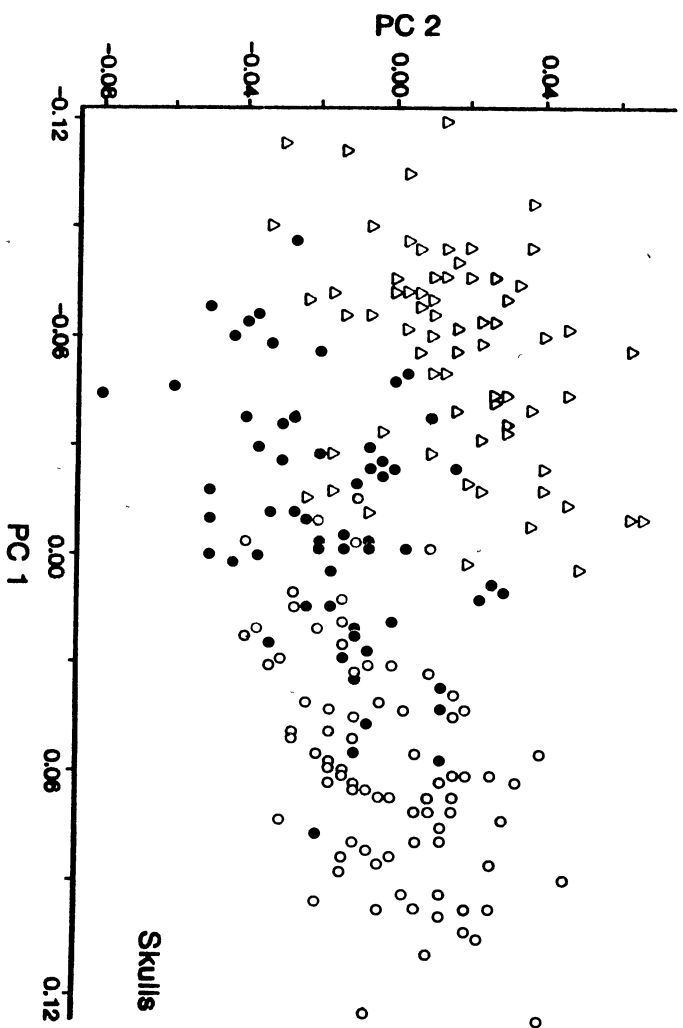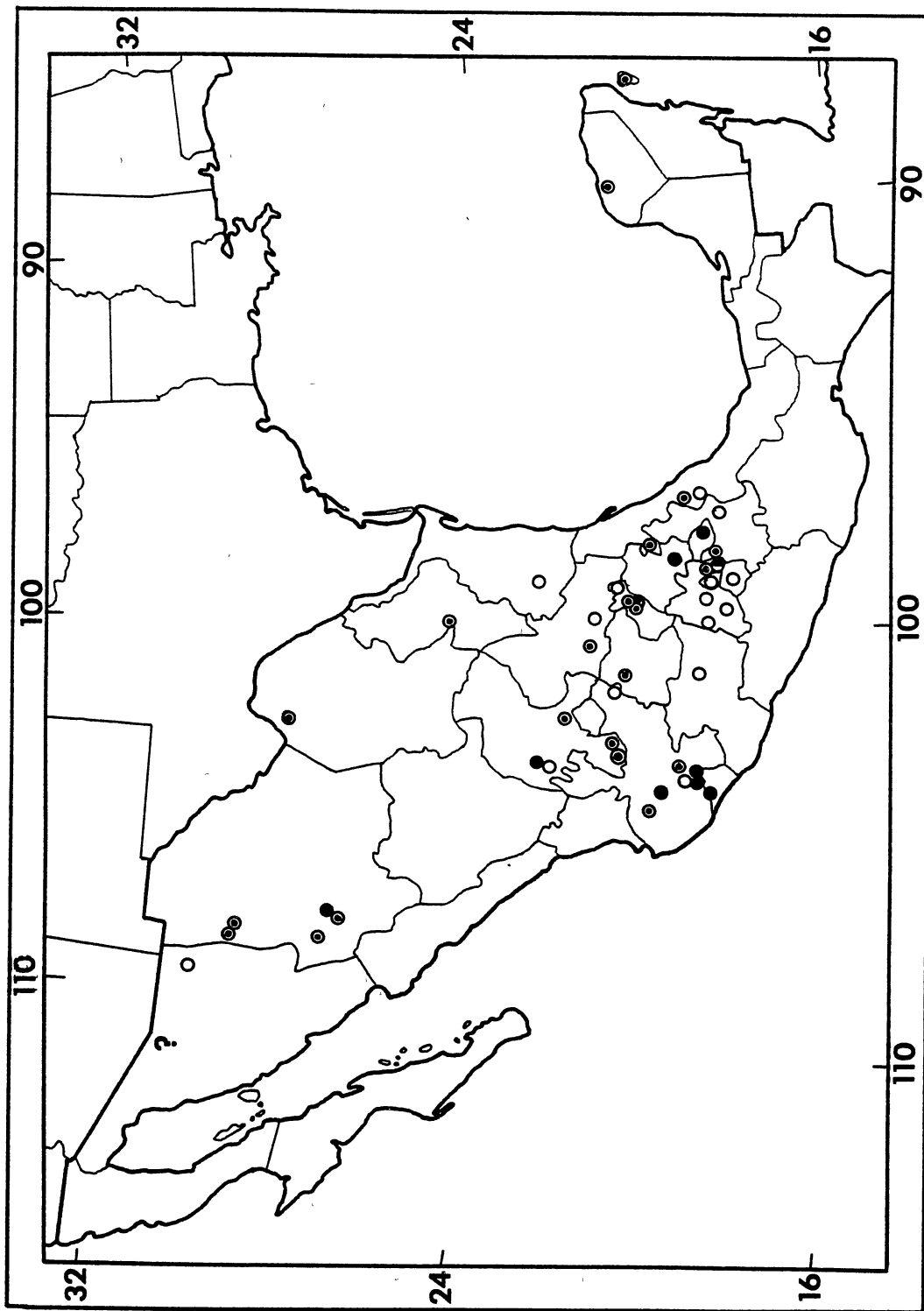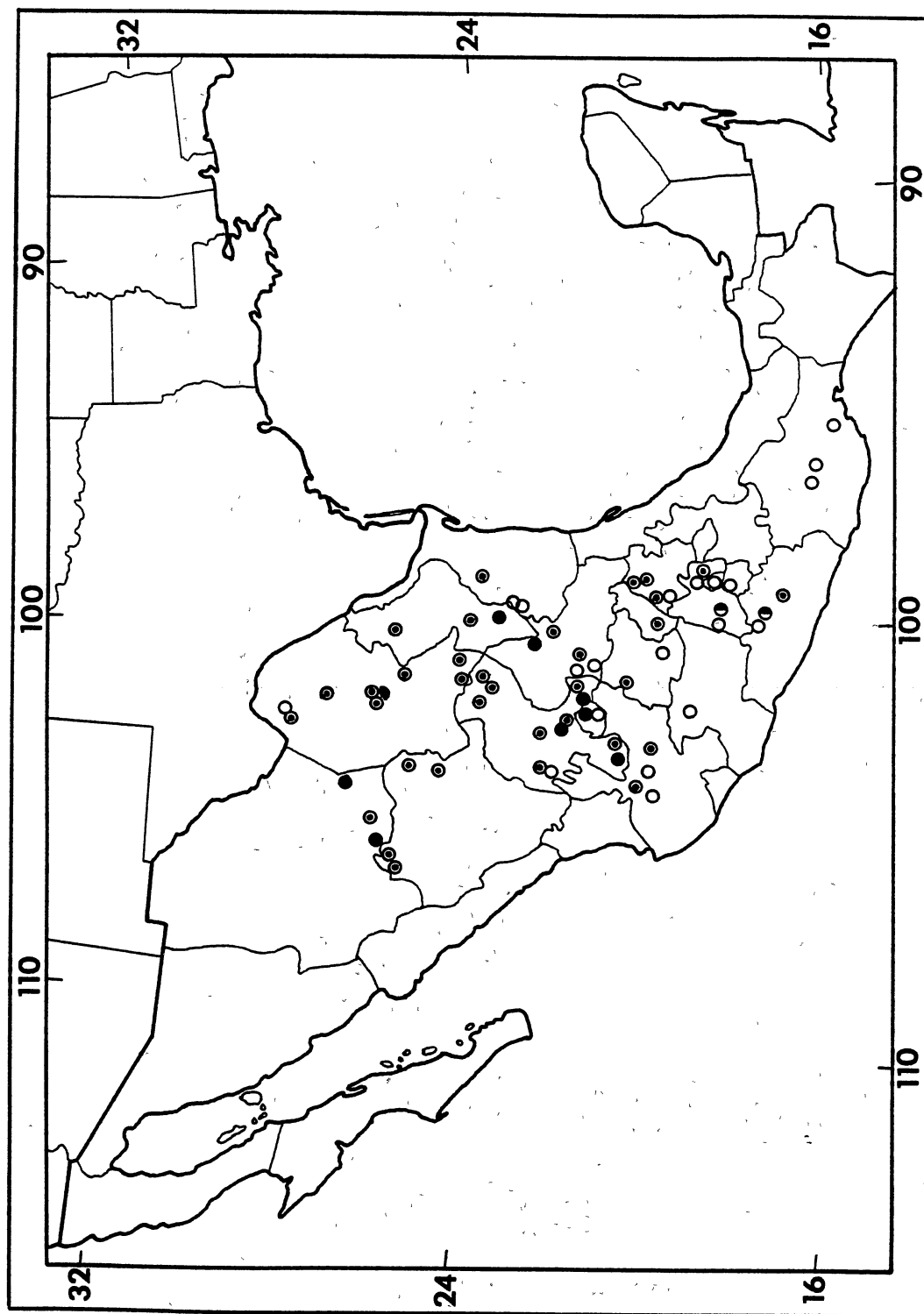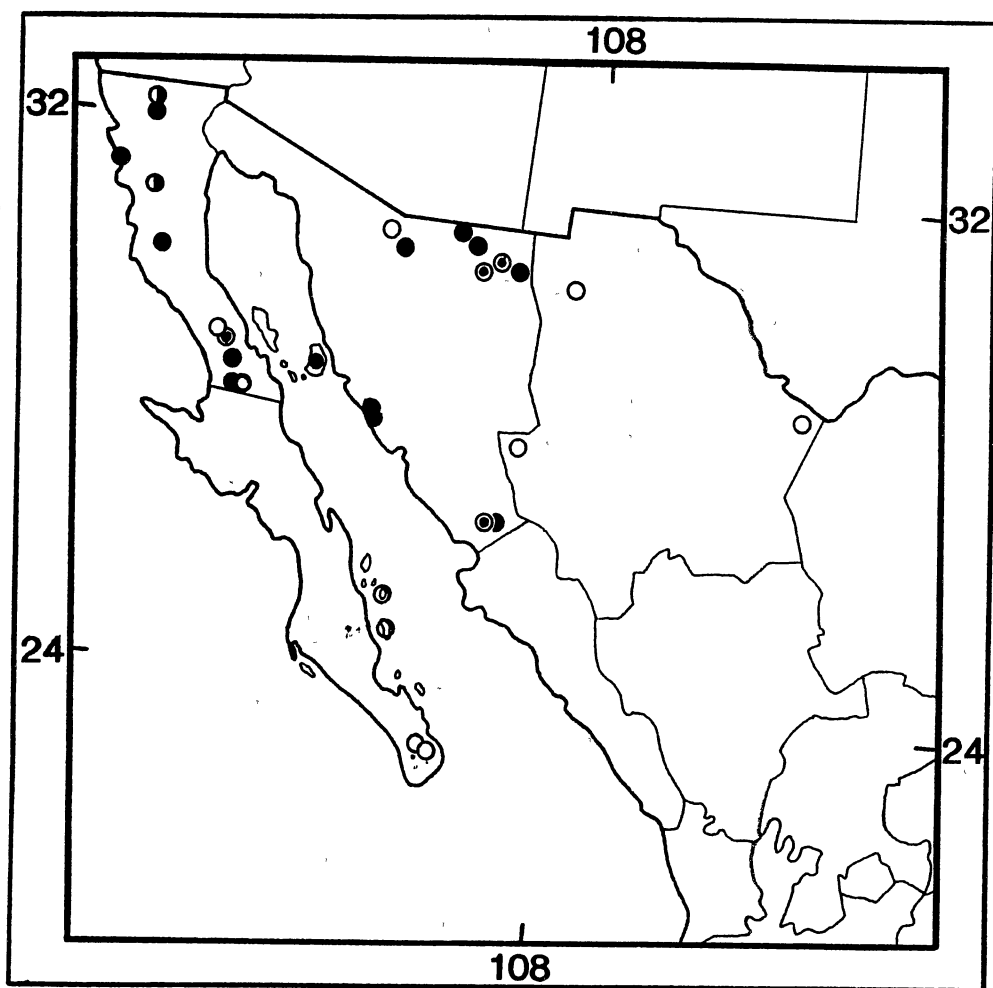
CHAPTER III

GEOGRAPHIC VARIATION IN THE MEXICAN BIG-EARED BAT,
IDIONYCTERIS PHYLLOTIS, WITH DESCRIPTIONS
OF SUBSPECIES

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ABSTRACT.--Geographic variation in 17 cranial characters
of 145 specimens of Idionycteris phyllotis was examined
using univariate and multivariate techniques. Three
populations, identified by size, are given subspecific
status. Larger individuals occur in the central portion of
the range and smaller individuals in northern and southern
populations. Idionycteris phyllotis phyllotis occurs in
Mexico, I. p. mogollonensis in New Mexico and southern
Arizona, and I. p. hualapaiensis in northern Arizona,
Nevada, and Utah.

The Mexican big-eared bat, Idionycteris phyllotis, was
described from a specimen collected in San Luis Potosí,

Mexico (Allen, 1916). Only three specimens had been collected when Cockrum (1956) reported the first record of the species from the United States, a specimen from Cochise County, Arizona. Commissaris (1961) reported distribution and forest habitat associations of 32 additional specimens from southeastern Arizona and predicted occurrence of this bat as far north as Flagstaff, Arizona, a prediction borne out by Hayward and Johnson (1961) and Findley and Jones (1961). Jones (1961) also reported the species from forest habitat at four locations in Catron County, New Mexico. Populations from presumably atypical habitat (desert) in Mohave Co., Arizona, were reported by Cockrum and Musgrove (1964), and additional material from Mexico was reported by Genoways and Jones (1967).

Present knowledge of the distribution of I. phyllotis indicates an elongate range from southern Utah and Nevada through mountainous regions of central and southern Mexico (Czaplewski, 1983). Handley (1959) examined the three specimens available to him and considered the species to be monotypic. However, from a sample of 25 specimens together with data from the literature, Genoways and Jones (1967) noted a slight increase in size from south to north, the only exceptions being five smaller individuals from Mohave County, Arizona, at the northern limit of the known distribution. Since that study, the known northern limit had been extended to Nevada (O'Farrell and Bradley, 1969) and Utah (Black, 1970; Armstrong, 1974; Poche, 1975), but

lack of sufficient study material has precluded examination
of geographic variation until recently.

MATERIALS AND METHODS

I examined 145 museum specimens representing the entire
known range of _Idionycteris_ _phyllotis_. Seventeen cranial
characters (Fig. 1) were measured with a Lasico digitizer
(to 0.1 mm) for each undamaged skull: total length (TL),
zygomatic breadth (ZB), cranial breadth (CB), mastoid
breadth (MB), width of interorbital constriction (IOC),
length of maxillary toothrow (MT), palatal length (PL),
basicranial length (BL), auditory bulla length (ABL),
intercanine width (ICW), palatal breadth across the third
molars (PBM3), cranial depth (CD), dentary length (DL),
moment arm of the temporal (MAT), moment arm of the masseter
(MAM), coronoid to angle distance (CA), and mandibular fossa
to condyle distance (FC). Data were collected on adult
specimens only, adults being recognized by fused epiphyses
in wing bones. Measurements of some characters (e.g., total
length) differed from literature reports for the same
specimens. I believe this is a result of the perception of
reference points in hand-held caliper-measured versus
stage-mounted, cross-hair reticle measured specimens. Thus,
measurements are consistent within this study but in some
cases may not compare directly with literature measurements.
Typically, my measurements are slightly smaller. Sex and
external measurements including total length (ETL), length

of tail (TAIL), length of hind foot (FOOT), and length of
ear (EAR) were recorded from specimen labels; see
acknowledgements for list of museums providing specimens.
Multivariate analyses excluded external measurements because
of the high variability these characters exhibited due to
measurement by many individuals.

Specimens were coalesced into 16 geographic samples:
NEVADA: Clark County (CLAR); ARIZONA: Mohave Co. (MOHA),
Coconino Co. north of the Colorado River (COCO-N), Coconino
Co. south of the Colorado River (COCO-S), Yavapai Co.
(YAVA), Gila Co. (GILA), Graham Co. (GRAH), Cochise Co.
(COCH); NEW MEXICO: Catron Co. (CATR), Grant Co. (GRAN),
Socorro Co. (SOCO); UTAH: San Juan Co. (SANJ); MEXICO:
Coahuila (COAH), Durango (DURA), Jalisco (JALI), and Nuevo
Leon (NUEV). A specimen from extreme northwestern
Chihuahua, Mexico, was grouped with specimens from Cochise
Co., Arizona, and a specimen from Queretaro, Mexico, was
grouped with specimens from Jalisco (due to similar
latitude). Specimens from Mexico represented a greater
geographic area than did U.S. specimens, yet the limited
sample size required treatment as a group for some analyses.
Specimens from Coconino County, Arizona were separated into
two groups based on the natural barrier of the Grand Canyon.

I used a two-way univariate (ANOVA) and multivariate
(MANOVA using Wilk's Criterion) analysis of variance to
evaluate the contributions of sex and geographic location to

total variance in the raw variables. A cluster analysis
(procedure UPGMA of NT-SYS, Rohlf et al., 1972) subsequently
was performed on a matrix of taxonomic distances between
species derived from raw data. Craniometric data were then
transformed to base 10 logarithms to help linearize the size
component of the data (Owen, 1988) and because it
legitimizes linear statistics (Humphries et al., 1981) and
functions much as standardization of characters (Schnell,
1970). Principal components (PCs) were extracted from the
variance-covariance matrix of transformed data. Scores for
individuals were plotted on the plane of the first two PC
vectors to explore the data for possible groupings of
localities. Centroids for each geographic location were
calculated from the scores of individuals on the first two
PC axes. A minimum spanning tree (Sneath and Sokal,
1973:255) connecting centroids of geographic locations was
calculated using NT-SYS based on all 17 PC vectors. The
tree was superimposed on the centroids of the plot of the
first two PC's to evaluate distortion in the reduced vector
space. Canonical discriminant analysis (CDA) was used to
define differences among groups. Significance of
Mahalanobis distances between CDA group centroids was tested
with F-statistics. The DISCRIM procedure of the Statistical
Analysis System (SAS, 1985) was used to determine closest
affinities of individuals. Following assignment of
individuals and locations into operational taxonomic units
(OTU's; Sneath and Sokal, 1973:68), pairwise comparisons

were made using Tukey-Kramer tests for unequal sample sizes
(Sokal and Rohlf, 1981:245) on untransformed variables to
document the nature of geographic variation per variable.

RESULTS

Analysis of variance indicated that all 17 variables,
with the exceptions of width of the interorbital
constriction and cranial depth, differed geographically
($P<0.0275$ for moment arm of the masseter and $P<0.0001$ for
all others). Differences due to sex were noted in mastoid
breadth, auditory bulla length, and dentary length
($P<0.004$). Significant interactions ($p<0.05$) were observed
in dentary length and moment arm of the masseter.
Significance was found by MANOVA in geographic ($p<0.0001$)
and sexual ($p<0.0011$) variation, and also in their
interaction ($p<0.0402$). Further analyses were conducted
both including and excluding sexually dimorphic characters.
Because results reflecting geographic variation were the
same in both sets of analyses, sexes were combined and
analyses based on the full data set are reported here.
Characters which provided apparent discrimination in CDA
analysis were scrutinized for effects of sexual dimorphism
prior to interpretation.

The UPGMA cluster of locations generally grouped samples
within geographically logical regions. Samples from the
Arizona-New Mexico area formed a tight group (cluster 1,
Fig. 2), and another cluster joined samples from the

northern and southern ends of the range. Within the latter cluster, the four locations in Mexico grouped together (cluster 2) but samples from the northern end of the range did not (clusters 3 and 4). Specimens from Utah and northern Coconino Co., Arizona clustered more closely with material from Mexico than they did with material from northwestern Arizona.

Principal components analysis (Fig. 3) also indicated coherent regional grouping. The generally uniform character loadings (Table 1) indicated that PC I, which provided the only separation of groups, is a general size vector. The first axis separates smaller specimens from Nevada, northern Arizona, and Utah from larger specimens from Arizona below the Grand Canyon, New Mexico, and extreme northwestern Chihuahua, Mexico. Individuals from most of Mexico had intermediate scores on PC I. The minimum spanning tree (Fig. 3) indicated relatively little distortion in the two-dimensional space. Some locations were farther apart than they appeared but relationships between locations reflected the results of cluster analysis.

The canonical discriminant analysis of locations, like the PC analysis, showed that the northern and central geographic populations could be completely separated on the first axis; the southern (Mexican) population was moderately distinguished on the second axis. Vectors of canonical coefficients (Table 1) indicate that populations on the

first axis were distinguished most by mastoid breadth, and palatal, basicranial, and dentary lengths. The second axis provided limited separation based on lengths of the maxillary toothrow and auditory bullae. Mahalanobis distances between the northern and both of the other populations were significantly different (p<0.0001), but the distance between the central and southern population was not. All three characters shown to be sexually dimorphic in the ANOVA were important characters in discrimination by CDA. However, the contribution of sexual to total variation was small, and the characters proved useful in discrimination of populations.

Discriminant analysis based on 132 intact skulls indicated misidentification of only two specimens. Specimens from the northernmost (small) population and the geographically intermediate (large) population, as defined by cluster and principal component analyses, were accurately discriminated by the function in all cases. One specimen from Coahuila, Mexico was associated with the population of larger individuals and a specimen from Durango, Mexico was identified with the northern small population.

DISCUSSION

The first specimen of I. phyllotis was collected in 1878 and described in 1916, but the species was not found in the United States until 1955. In 1961 (see earlier citations), several papers suddenly documented the occurrence of this

bat at several locations in the U.S. It is curious why this
bat had remained so elusive to science. Morphological
variation in the species suggests that it did not recently
disperse into the United States, because two distinct
populations can be identified - both different from
populations in Mexico.

My results are in good agreement with the pattern of
geographic variation noted in the more limited study by
Genoways and Jones (1967). Specimens from Nevada, Utah, and
Arizona north of the Grand Canyon through Mohave Co. are
consistently small in body size. Specimens from near
Flagstaff (Coconino Co.) south of the Grand Canyon through
southeastern Arizona and west-central New Mexico are
uniformly larger. Specimens from Mexico are typically
intermediate in size, making them more difficult to
distinguish in the principal component analysis. Knowledge
of the geographic origin of a specimen prevents
misidentification of specimens from the two smaller
populations, but discriminant analysis suggested that the
material from Mexico is more variable.

Sample sizes were small from Mexico (n=15) and from the
northern population (n=18), and some counties (or states of
Mexico) were represented by only one or two specimens. As a
result, corresponding populations are not as accurately
represented on the PC axes as are those populations
represented by centroids for clusters of several specimens.

However, if distinct groups exist, variation within groups should be less than variation between groups, thus a single specimen from a different location should fall within the variation of its group of proper membership. This approach is discussed by Sneath and Sokal (1973:183) as the "exemplar method". For example, a single specimen from Clark Co., Nevada was most similar to specimens from neighboring Mohave Co., Arizona, and a specimen from Yavapai Co., Arizona was most like specimens from other locations in its geographic range. Yet, material from Coconino Co., Arizona (north of the Grand Canyon) and San Juan Co., Utah appeared most similar to material from Mexico. Conclusions about these specimens must remain tentative due to sample size (n=4), but they are larger than individuals from Mohave Co., Arizona; size explains their similarity to material from Mexico. Discriminant analysis assigned these four specimens to the group including material from Mohave County.

Both sample size and the lack of continuity of sampling locations make difficult the interpretation of clinal variation. A specimen from extreme northwestern Chihuahua was as large as specimens from the U.S., but a specimen from Nueva Casas Grandes, Chihuahua, was as small as specimens from farther south in central Mexico. The latter specimen was a subadult (Bogan and Williams, 1970) and may not provide useful metric information. There exists a gap in records from Chihuahuan samples to those from northern Durango. Thus gradation in size between Arizona-New Mexico

samples and those of central Mexico is open to speculation.
Geographic separation of samples north versus south of the
Grand Canyon spans less distance; specimens were available
from the North Rim and from near Flagstaff. Further,
Barbour and Davis (1969:186) recorded field observations
which were believed to be of _Idionycteris_ _phyllotis_ from the
South Rim of the Grand Canyon. The two populations in this
area may represent a step cline, reflected in the lack of
overlap of specimens on the PC plot.

Differences in habitat may provide explanations for size
differences seen in U.S. populations. Most specimens are
reported from pine or pine-oak woodlands (Commissaris, 1961;
Jones, 1965; Findley et al., 1975). Hoffmeister (1986:106)
noted that specimens taken near Portal (Cochise Co.),
Arizona below woodland "may represent areas where drinking
water was available rather than being preferred habitat."
Habitat in the Lower Sonoran biotic zone in Mohave Co.,
Arizona, was considered at the time to be atypical for I.
phyllotis (Cockrum and Musgrove, 1964), but Lower Sonoran
habitat was also noted in the Grand Canyon region (Ruffner
and Carothers, 1975). However, elevation alone does not
appear to explain size differences. Elevation of nine
capture sites in the desert related populations averaged
4602 ft. (range 2600-8100), while forest related samples in
southern Arizona and New Mexico (23 sites) were caught at a
mean elevation of 6367 ft. (range 3550-8600). Mean
elevation at seven Mexican sites was 6929 ft. (range

4500-9800), and most were in forested habitat (Genoways and Jones, 1967). In addition, Jones (1965) noted that Idionycteris phyllotis from the Mogollon Mountains region of New Mexico and Arizona was active in a narrow range of temperature (9-17°C) and was more limited in geographic distribution than species of bats active in a wider range of temperatures.

Conclusions regarding taxonomy are limited by lack of data from karyological or electrophoretic analyses. However, such data are probably not forthcoming, particularly from the Mexican and northernmost populations, considering that less than 20 museum specimens could be located for either of these groups. Except in certain locations, these bats are encountered only sporadically and even colonies may not occur in the same locations in successive years (Barbour and Davis, 1969:185). Carter et al. (1966) suggested the possibility of subspecies based on fur color, shape of the tragus, and size. Lidicker (1962) noted that most authors would recognize populations having "their own evolutionary tendencies" as distinct subspecies. My morphological analyses clearly indicated independent groups in the north and middle of the range. Skull characteristics provided less discrimination of Mexican specimens, but color and tragus characteristics add to the distinction of material from Mexico (see below). Thus, I recognize the Mexican populations as a third subspecies.

Idionycteris phyllotis hualapaiensis, subsp. n.

Holotype.--Adult female, skin and skull no. 26478, University of Illinois Museum of Natural History; obtained on 10 July 1962 by B. Musgrove and L. Ross, original no. 1027; type locality 1 mi. SW Union Pass, 2600 ft., Mohave Co., Arizona.

Distribution.--At least extreme southern Nevada (Clark Co.), northern Arizona (Mohave Co. and Coconino Co. north of the Grand Canyon) and southern Utah, typically in lower Sonoran habitat (Fig. 4).

Diagnosis.--Size small for the species (Table 1). Rostrum short, dentary small, mastoid breadth and length of the maxillary toothrow particularly small.

Measurements.--External and cranial measurements of specimens from Nevada, Arizona, and Utah are given in Table 2. Measurements (in mm) of the holotype and means of the holotype and three paratypes (UIMNH 26479-26481) are: TL, 16.5 (16.4); ZB, 9.3 (9.3); CB, 8.5 (8.7); MB, 9.4 (9.4); IOC, 4.1 (4.1); MT, 5.3 (5.4); PL, 6.5 (6.4); BL, 13.7 (13.6); ABL, 4.4 (4.4); ICW, 2.1 (2.1); PBM3, 6.1 (6.1); CD, 5.3 (5.2); DL, 10.6 (10.3); MAT, 2.8 (2.9); MAM, 2.4 (2.4); CA, 4.2 (4.2); FC, 3.6 (3.4). External measurements are: total length 114 (114), tail length 49 (48),hind foot length 10 (11), ear length 38 (38).

Comparisons--From I. p. mogollonensis (see below), I. p. hualapaiensis differs in being conspicuously smaller in most measurements. From I. p. phyllotis, (see below), I. p. hualapaiensis differs in being smaller, particularly in length of the maxillary toothrow.

Etymology--The subspecific name honors the Hualapai Indians who occupied the Mohave County, Arizona, area and for whom a local valley and mountain range are named.

Remarks.--Literature indicates that individuals are most common in the vicinity of Union Pass, Mohave Co., Arizona (Cockrum and Musgrove, 1964).

Idionycteris phyllotis mogollonensis, subsp. n.

Holotype.--Adult female, skin and skull no. 14835, University of New Mexico, Museum of Southwestern Biology; obtained on 7 July 1962 by C. J. Jones, original no. 3098; type locality Mogollon Mountains, 9 mi. E Mogollon, Catron County, New Mexico.

Distribution.--Arizona south of the Grand Canyon through yellow pine forest and oak woodland (Commissaris, 1961; Jones, 1965), to southeastern Arizona and west central New Mexico, and extreme northwestern Chihuahua, Mexico (Fig. 4).

Diagnosis.--Size largest for the species; mastoid breadth, rostrum, and dentary especially large. Tragus more rounded, fur paler and longer.

Measurements.--External and cranial measurements of specimens from Arizona, New Mexico, and Chihuahua, Mexico are given in Table 2. Measurements (in mm) of the holotype and means of the holotype and six paratypes (MSB 14830-14834, 14836) are: TL, 17.5 (17.4); ZB, 9.5 (9.6); CB, 8.8 (8.8); MB, 9.8 (9.9); IOC, 3.9 (4.2); MT, 5.6 (5.6); PL, 6.6 (6.8); BL, 14.5 (14.6); ABL, 4.5 (4.5); ICW, 2.3 (2.3); PBM3, 6.4 (6.3); CD, 5.2 (5.4); DL, 11.0 (10.9); MAT, 3.0 (3.1); MAM, 2.6 (2.5); CA, 4.4 (4.5); FC, 3.7 (3.6). External measurements are: total length, 115 (113); tail length, 49 (49); hind foot length, 9 (10); ear length, 38 (38).

Comparisons.--From I. p. hualapaiensis (see above), I. p. mogollonensis differs in being conspicuously larger and having a stronger rostrum and dentary and greater width across the mastoid region. From I. p. phyllotis, I. p. mogollonensis differs in being larger, having proportionately longer auditory bullae, having paler and longer fur, and having a more rounded tragus.

Etymology.--The subspecific name refers to the mountain range from which most specimens of this subspecies have been collected.

Remarks.--Most specimens have been collected in Catron Co., New Mexico and Coshise Co., Arizona, but it is not clear whether this is due to sampling intensity or population density.

<u>Idionycteris</u> <u>phyllotis</u> <u>phyllotis</u> (Allen, 1916)

<u>Holotype</u>.--Adult (sex unknown), skin and skull no. 5943, Harvard University, Museum of Comparative Zoology; obtained on 24 March 1878 by E. Palmer; type locality San Luis Potosí, probably near the city of the same name, México (Handley, 1959:130).

<u>Distribution</u>.--Northern Durango, México south to Jalisco and Distrito Federal in the Sierra Madre Oriental, Sierra Madre Occidental, and transverse volcanic belt (Fig. 4).

<u>Diagnosis</u>.--Size slightly larger than <u>I</u>. <u>p</u>. <u>hualapaiensis</u> but smaller than <u>I</u>. <u>p</u>. <u>mogollonensis</u>. Tragus more acutely pointed, fur darker and shorter than in other forms.

<u>Measurements</u>.--External and cranial measurements of specimens from Mexico are given in Table 2. Measurements (in mm) of the holotype given by Allen (1916) are: greatest length, 17.5; basal length, 14.9; palatal length, 8.5; zygomatic breadth, 10.0; interorbital constriction, 4.8; mastoid breadth, 10.0; width of braincase, 9.6; upper tooth row, 7.0. External measurements are: hind foot length, 10; ear length, 31 (measurements for total length and tail length were not given).

<u>Comparisons</u>.--See comparisons previously given for <u>I</u>. <u>p</u>. <u>phyllotis</u> with other taxa.

Etymology.--The subspecific name represents the nominate subspecies.

Remarks.--The type specimen was not examined, but measurements provided by Allen (1916) are larger than those recorded from specimens from Mexico in this study. Some of this variation is likely due to use of different reference points, and additional variation may be due to different instrumentation used in measurement. Of note, the same contrast between our measurements was seen for Plecotus mexicanus.

Specimens examined
Idionycteris phyllotis hualapaiensis, subsp. n.

ARIZONA: Mohave Co.: 1 mi. S Union Pass, 2800 ft., 1 (TTU), 3 (UI); 2 mi. W Union Pass, Black Mts., Chalk Peak, 2800 ft., 2 (UA), 1 (UI); 1 mi. SW Union Pass, 2600 ft., 4 (UI); 1 mi. N Littlefield, Beaver Dam Creek at Beaver Dam Resort, 1 (MNA), 1 (LACM); 1 mi. S Utah border, Beaver Dam Wash, 1 (UMHN); Coconino Co.: Grand Canyon National Park, Shiva Temple, 7600 ft., 1 (MNA); Grand Canyon National Park, 4 mi. NW North Rim headquarters, 8100 ft., 1 (MNA).

NEVADA: Clark Co.: White Rock Spring, ca. 15 mi. W Las Vegas, 1 (NSM).

UTAH: San Juan Co.: T30S, R20E, NW 1/4 NE 1/4 Sec. 29, 5015 ft., 1 (TTU); 5 mi. N Blanding, 6000 ft., 1 (MSB).

Additional records.

ARIZONA: Mohave Co.: vic. Pipe Springs National
Monument, 5000 ft. (Genoways and Jones, 1967); OK Mine, 68
mi. N Kingman, 3000 ft. (Cockrum and Musgrove, 1964);
Kingman, 3500 ft. (Cockrum and Musgrove, 1964).

NEVADA: Clark Co.: Calico Spring, Red Rock Canyon,
Spring Mts. (O'Farrell and Bradley, 1969); Mesquite (Poche,
1975).

UTAH: San Juan Co.: Squaw Spring, T30S, R19E, SE 1/4 SW
1/4 Sec. 25, Canyonlands National Park, ca. 20 mi. N and 30
mi. W Monticello (Armstrong, 1974); Washington Co.: Gould
Wash, T42S, R12W, NW 1/4 SW 1/4 Sec. 19, ca. 7 km SE
Hurricane (Poche, 1975).

Idionycteris phyllotis mogollonensis, subsp. n.

ARIZONA: Cochise Co.: S fork Cave Creek, 3 1/2 mi. SW
Portal, 5400 ft., 1 (OSU) 1 (MSU) 1 (MWSU) 1 (KU) 1 (UMNH);
Chiricahua Mts., ca. 1 1/4 mi. E, 1 1/2 mi. S Raspberry
Peak, Rucker Canyon, 2 (MVZ); Southwest Research Station,
5400 ft., 1 (LACM) 2 (AMNH); 1 mi. WNW Portal, 4900 ft., 1
(UA) 1 (KU) 1 (USNM); 1.8 mi. W, 2.0 mi. S Portal, 5100
ft., 1 (LSUS); 1.5 mi. W, 1.6 mi. S Portal, 5040 ft., 1
(LSUS). Coconino Co.: 28 mi. S, 9 mi. E Flagstaff, 2 (MSB);
3 mi. N Flagstaff, pond at mouth of Rio del Flag, 7100 ft.,
5 (MNA); 3 mi. NW Flagstaff, Ramada of Museum of Northern
Arizona, 1 (MNA); 4 mi. N Flagstaff, stock pond near Hwy

180, 7100 ft., 1 (TCWC); 3 mi. N Flagstaff, Northern Arizona Museum grounds, 7100 ft., 2 (MNA) 2 (NAU); SW base Mt. Elden, E Flagstaff, 2 (UI) 1 (NAU). Gila Co.: Sierra Ancha, Wilbank's Ranch, 7200 ft., 1 (FMNH) 4 (KU) 1 (AMNH) 7 (UI). Graham Co.: 1 mi. N, 6 1/2mi. W Klondyke, Oak Grove Canyon, 3550 ft., 1 (TCWC) 1 (TTU) 1(MWSU) 1 (UA) 1 (MVZ) 1 (USNM). Yavapai Co.: Dry Beaver Creek, 12 mi. SE Sedona, 2 (NAU).

NEW MEXICO: Catron Co.: 19 mi. E Mogollon, 1 (OSU); Black Range, Taylor Creek, 2 mi. NE Wall Lake, 8 (MSB); Glenwood, State Fish Hatchery, 3 (MSB); Mogollon Mts., 10 mi. E Mogollon, Willow Creek, 2 (MSB); Mogollon Mts., 9 mi. E Mogollon, 8400 ft., 14 (MSB) 1 (MVZ) 1 (LSUMZ) 1 (UA) 5 (MHP); 2 mi. N, 1 mi. W Mogollon, Mineral Creek, T10S, R19W, Sec. 20, 6000 ft., 1 (NMSU); 10 mi. E Gila Cliff dwellings, T12S, R11W, Sec. 36, 7500 ft., 1 (WNMU); Gila Wilderness, McKenna Park, 8600 ft., 1 (WNMU); 14 mi. E Mogollon near Willow Creek Forest Camp, 8200 ft., 1 (WNMU); Woodland Park, T11S, R15W, Sec. 35, 7300 ft., 1 (WNMU); head of McKenna Creek, T12S, R15W, Sec. 30, 7650 ft., 2 (WNMU); Iron Creek, Spruce Canyon, T11S, R17W, Sec. 2, 7900 ft., 2 (WNMU); Little Creek, T12S, R15W, SW 1/4 Sec. 33, 7300 ft., 2 (WNMU); Little Turkey Park, T13S, R14W, Sec. 20, 1 (WNMU); West Fork Corral, T11S, R16W, Sec. 20, 1 (WNMU). Grant Co.: Mimbres River, 17 mi. NNE San Lorenzo, T14S, R11W, Sec. 33, 6800 ft., 1 (WNMU); 8 mi. SSE Gila, Cora Miller Mine, 4700 ft., 2 (WNMU); 7 mi. S Cliff, Davis Canyon, T16S, R17W, Sec. 33, 4500 ft., 1 (WNMU); 5 mi. NW Silver City, Little Bear

Mt., 1 (WNMU). Socorro Co.:, 32 mi. S, 28 mi. W Socorro, Nogal Canyon, 1 (LSUMZ) 1 (TTU); Weir Tank, 1.5 mi. E Springtime Campground, 7200 ft., 1 (MSB); San Mateo Mts., Nogal Canyon, T9S, R5W, NE 1/4 Sec. 6, 7000 ft., 1 (MSB).

MEXICO: Chihuahua: 2 mi. S, 5 mi. W San Francisco, 5500 ft., 1 (KU).

Additional records:

ARIZONA: Gila Co.: Aztec Peak (Johnson and Johnson, 1964).

Idionycteris phyllotis phyllotis

MEXICO: Chihuahua: 11.1 mi. SE Nueva Casas Grandes, 1 (MSB). Coahuila: 5 mi. S, 4 mi. E Bella Unión, 2 (USNM). Durango: Navarro, ca. 72 km W (by road) from Hidalgo del Parral, Chihuahua, 6100 ft., 4 (LACM) 1 (UA); Presa de Ojito, ca. 50 km W (by road) from Hidalgo del Parral, Chihuahua, 7600 ft., 1 (LACM). Jalisco: 5 mi. W Atenquique, 7700 ft., 1 (KU); Volcán de Fuego, 9800 ft., 2 (KU). Nuevo León: 17 mi. SW Monterrey, Huasteca Canyon, 4500 ft., 1 (TCWC); 3 mi. SW La Escondida, 6300 ft., 2 (KU). Queretaro: 2 mi. W San Joaquin, 1 (TCWC).

Additional records.

MEXICO: Distrito Federal: Ciudad Universitaria, 2250 m (Villa, 1967:427). San Luis Potosí: near San Luis Potosí (Handley, 1959:131). Tamaulipas: Miquihuana (Handley,

1959:131).

ACKNOWLEDGMENTS

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Table 1. Character loadings on the first three principal
components (PCs) and standardized canonical
coefficients for 17 cranial measurements (codes
identified in text) of *Idionycteris* *phyllotis*.

	PC I	PC II	PC III	CAN 1	CAN 2
Eigenvalue	0.0016	0.0005	0.0003		
% total variance	43.52	13.28	8.41		
Cumulative % variance	43.52	56.80	65.21		
Characters:					
TL	0.234	0.104	-0.036	0.359	-0.472
ZB	0.187	0.028	-0.088	0.057	0.125
CB	0.135	0.044	-0.092	-0.144	0.269
MB	0.214	0.072	-0.082	0.968	0.226
IOC	0.037	-0.113	0.007	-0.116	0.255
MT	0.237	0.090	-0.101	0.311	0.718
PL	0.283	0.211	-0.053	0.515	-0.071
BL	0.266	0.133	-0.029	0.499	-0.149
ABL	0.217	0.103	0.032	-0.195	-1.039
ICW	0.351	0.167	-0.365	0.311	0.336
PBM3	0.198	0.066	-0.159	-0.041	-0.310
CD	0.071	0.032	-0.053	-0.064	-0.202
DL	0.253	0.090	0.064	-0.532	-0.060
MAT	0.344	0.118	0.283	0.344	0.135

Table 1. Continued.

	PC I	PC II	PC III	CAN 1	CAN 2
MAM	0.298	-0.902	-0.157	-0.082	-0.220
CA	0.321	-0.112	0.020	-0.026	0.436
FC	0.221	-0.081	0.831	0.349	-0.071

Table 2. Means and standard deviations () by subspecies for
17 skull and 4 external measurements of <u>Idionycteris</u>
<u>phyllotis</u>. Means with different letters (A, B, or C)
are significantly different (Tukey-Kramer, $P < 0.05$).
The second line is the range for the character.
Character codes are identified in text.

	IPH (n=18)	IPM (n=105)	IPP (n=15)
TL	16.44 (0.34)A	17.34 (0.26)B	16.75 (0.23)C
	15.8-16.9	16.5-18.0	16.2-17.0
ZB	9.25 (0.18)A	9.66 (0.17)B	9.55 (0.21)B
	8.8-9.6	9.3-10.1	9.2-9.9
CB	8.57 (0.18)A	8.85 (0.16)B	8.78 (0.12)B
	8.2-8.9	8.5-9.3	8.6-9.1
MB	9.32 (0.14)A	9.85 (0.16)B	9.64 (0.13)C
	9.1-9.5	9.3-10.2	9.5-9.9
IOC	4.08 (0.11)A	4.11 (0.14)A	4.17 (0.12)A
	3.9-4.3	3.7-4.4	3.9-4.4
MT	5.30 (0.13)A	5.61 (0.11)B	5.49 (0.11)C
	5.1-5.5	5.3-5.8	5.3-5.7
PL	6.36 (0.22)A	6.81 (0.19)B	6.53 (0.17)C
	6.0-6.8	6.1-7.2	6.2-6.8
BL	13.67 (0.29)A	14.54 (0.25)B	14.01 (0.23)C
	13.1-14.1	13.7-15.2	13.7-14.6
ABL	4.36 (0.09)A	4.53 (0.11)B	4.33 (0.09)A
	4.2-4.5	4.3-4.8	4.2-4.5

Table 2. Continued.

	IPH (n=18)	IPM (n=105)	IPP (n=15)
ICW	2.13 (0.09)A	2.31 (0.07)B	2.25 (0.09)C
	2.0-2.3	2.1-2.5	2.1-2.4
PBM3	6.08 (0.12)A	6.35 (0.14)B	6.25 (0.12)C
	5.9-6.3	6.0-6.7	6.0-6.4
CD	5.21 (0.11)A	5.28 (0.16)A	5.24 (0.15)A
	5.0-5.4	5.0-5.7	4.9-5.4
DL	10.30 (0.21)A	10.82 (0.27)B	10.49 (0.15)A
	9.9-10.6	10.0-11.3	10.1-10.7
MAT	2.86 (0.05)A	3.09 (0.10)B	3.01 (0.15)C
	2.8-2.9	2.8-3.3	2.7-3.3
MAM	2.42 (0.13)A	2.51 (0.13)B	2.47 (0.15)AB
	2.2-2.7	2.2-2.9	2.2-2.8
CA	4.19 (0.13)A	4.47 (0.14)B	4.39 (0.16)B
	4.0-4.5	4.1-4.8	4.2-4.8
FC	3.47 (0.16)A	3.62 (0.14)B	3.51 (0.12)A
	3.2-3.8	3.3-3.9	3.3-3.7
ETL	109.4 (4.10)A	113.4 (4.16)B	110.7 (2.81)A
	102-116	103-135	104-116
TAIL	48.1 (2.49)A	50.3 (3.01)B	47.3 (3.85)A
	43-52	40-57	40-53
FOOT	9.9 (0.83)A	9.9 (1.08)A	9.3 (1.03)A
	9-11	7-12	8-11

Table 2. Continued.

	IPH (n=18)	IPM (n=105)	IPP (n=15)
EAR	37.2 (2.43)A	39.2 (2.35)B	38.9 (1.16)AB
	31-40	33-45	37-41

Fig. 1. Skull measurements used in the analysis of
Idionycteris phyllotis. Refer to text for description
of character codes.

Fig. 2. Cluster analysis (UPGMA) of 16 samples of
Idionycteris phyllotis generated from the distance
matrix. The coefficient of cophenetic correlation is
0.796. Symbols indicate locality groupings: N =
northern, C = Central, S = southern portions of the
range.

Fig. 3. Scatter diagram of principal components I and II
generated from the variance-covariance matrix of 17
cranial measurements using 16 samples of Idionycteris
phyllotis from the entire species range (location codes
identified in text). Filled circles are centroids for
specimens from most of Arizona and New Mexico, open
circles represent locations in Mexico, and triangles
represent locations in Nevada, Utah, and northwestern
Arizona. Polygons indicate the total scatter of
individuals within the three groups. A minimum
spanning tree is superimposed on the centroids.
Symbols N, C, and S as in Fig. 2.

Fig. 4. Distribution of subspecies of Idionycteris
phyllotis. Circles = I. p. hualapaiensis, squares = I.

p. <u>mogollonensis</u>, and triangles = <u>I</u>. <u>p</u>. <u>phyllotis</u>.
Filled symbols are specimens examined, open symbols are
additional records believed to belong to the taxa
indicated. Circled dot indicates type locality for the
species. Question marks indicate locations of
uncertain subspecific identification (no specimen in
Arizona and subadult specimen in Chihuahua).

r = 0.796

Distance
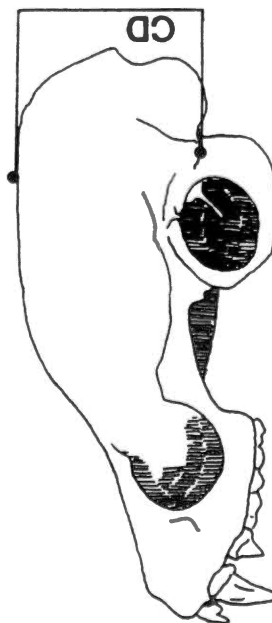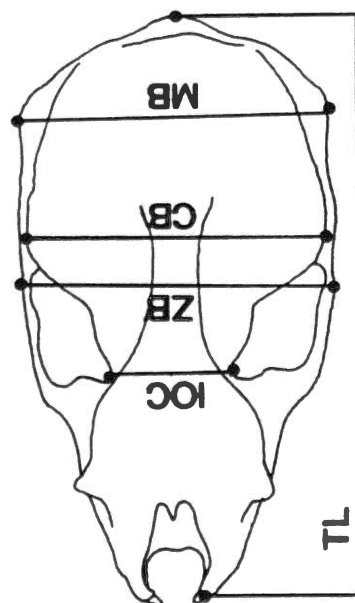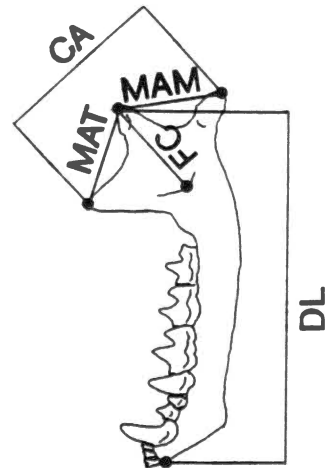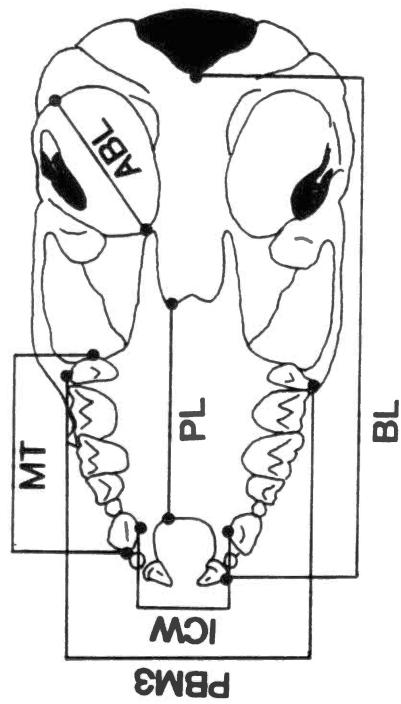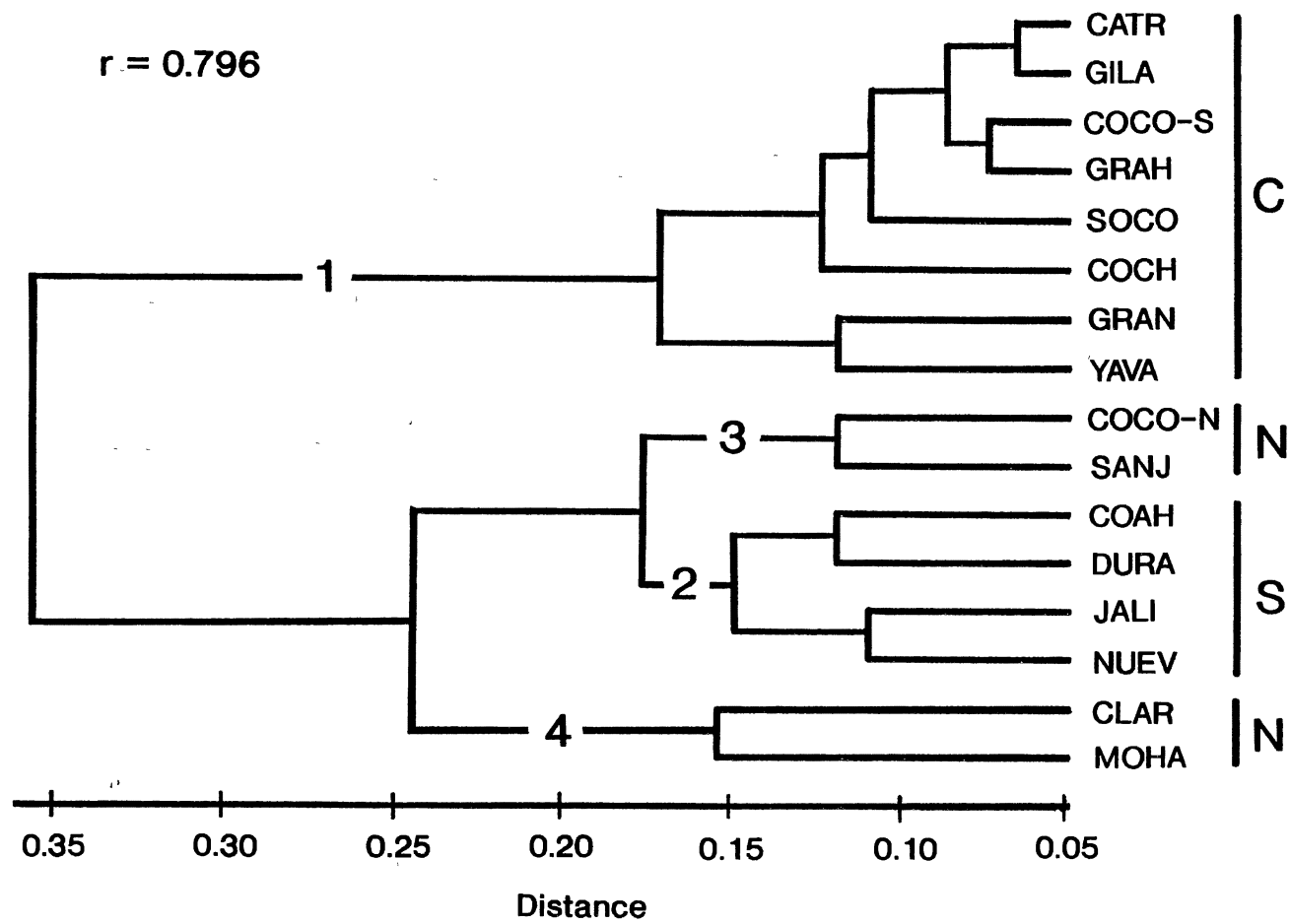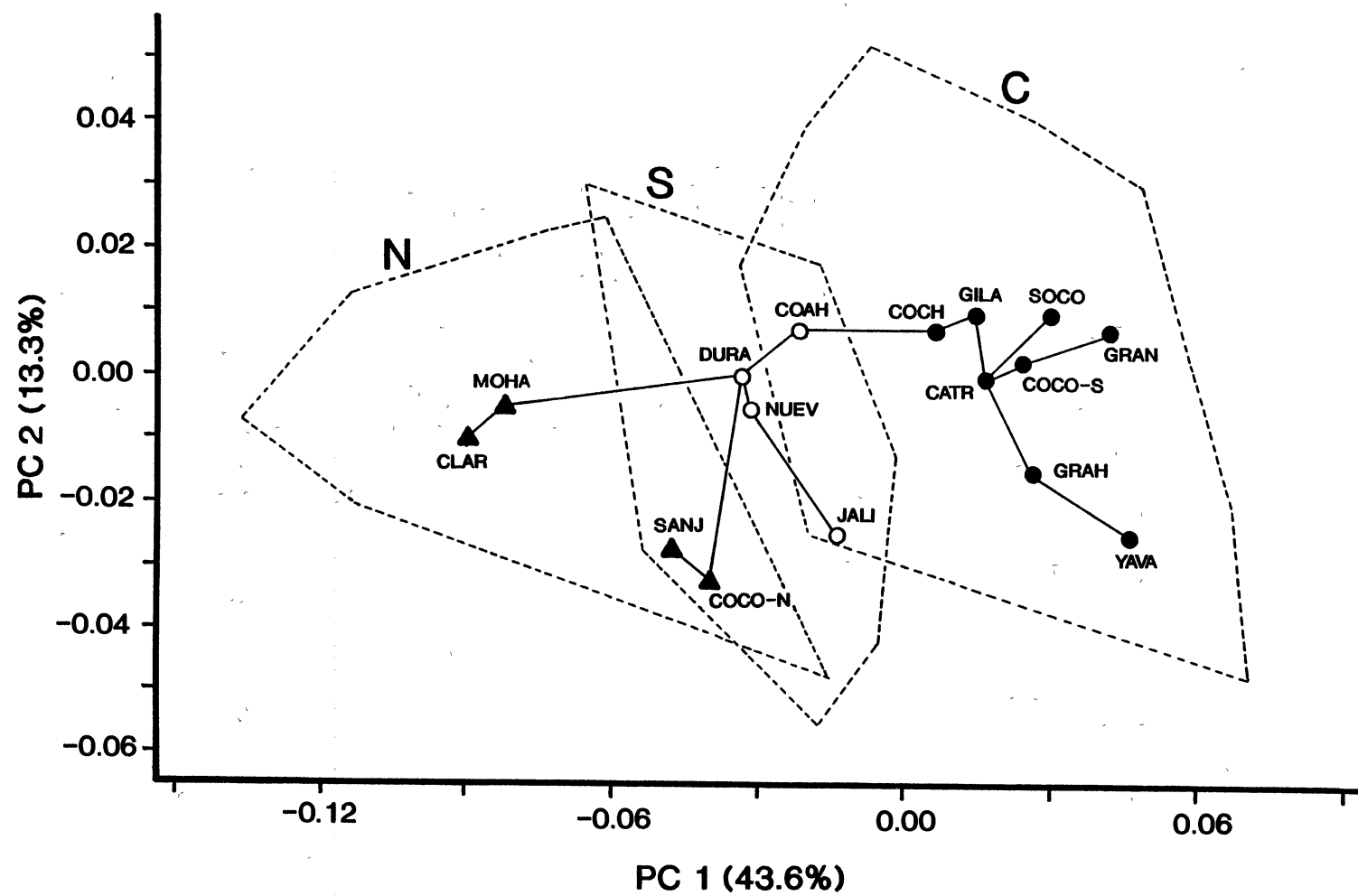
CHAPTER IV

PARSIMONY ANALYSIS AND THE PHYLOGENY OF THE PLECOTINE
BATS (CHIROPTERA: VESPERTILIONIDAE)

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ABSTRACT.--Phylogenetic relationships among the plecotine
bat taxa Plecotus, Idionycteris, Barbastella, Euderma, and
Corynorhinus were examined using 33 characters of the skin
and skull. Character states for the hypothetical ancestor
were defined by evaluation of outgroup taxa including 11
species of Myotis, two species of Pipistrellus, and
Lasionycteris noctivagans (chromosomally similar taxa).
Character states shared by all outgroup taxa were considered
to be primitive, allowing identification of derived states
for ingroup taxa. Cladistic analysis performed using the
branch-and-bound algorithm of PAUP yielded a single most
parsimonious tree. Interpretation of the cladogram
indicates that each of the taxa is to be regarded as a
genus. This supports the contention that Idionycteris is a
distinct genus, and argues against the previously accepted

subgeneric designation of <u>Corynorhinus</u>. I thus elevate <u>Corynorhinus</u> to full generic status and limit <u>Plecotus</u> to species of the Palearctic.

Relationships within the Vespertilionid bat tribe Plecotini (<u>sensu</u> Koopman and Jones, 1970) were first examined in detail by Handley (1959). His taxonomic arrangement included the genera <u>Barbastella</u>, <u>Euderma</u>, and <u>Plecotus</u>, with the latter containing three subgenera (<u>Plecotus</u> of the Old World, <u>Corynorhinus</u> and <u>Idionycteris</u> of the New World). <u>Idionycteris</u> was considered a generally primitive form while <u>Euderma</u> was the most specialized, particularly in auditory and dental characteristics. Williams <u>et</u> <u>al</u>. (1970) suggested generic recognition of <u>Idionycteris</u> based on the distinctiveness of the standard karyotype and its greater similarity to that of <u>Euderma</u>. However, Baker <u>et</u> <u>al</u>. (1974) noted that distinction should be based not on magnitude of karyological divergence, but rather on origin of the <u>Idionycteris</u> karyotype coupled with additional morphological data. Bickham (1979) reported the nature of G- and C-banded chromosomes in <u>Idionycteris</u> and <u>Corynorhinus</u> and concluded that the origin of the karyotype was more complex than the single centric fusion previously hypothesized. Cladistic analysis of additional G- and C-band data (Stock, 1983) indicated even greater complexity.

The model of karyotypic evolution proposed by Stock (1983) was accepted by Leniec et al. (1987) "broadening its scope to include palearctic species". Exactly how Barbastella and Plecotus fit with nearctic Corynorhinus was not made clear. Two characters distinguish the subgenera Corynorhinus and Plecotus (Volleth, 1985) - notably only two karyotypic characters distinguish Euderma from Idionycteris (Stock, 1983). Karyotypes of Barbastella and palearctic Plecotus are considered to be identical (Fedyk and Ruprecht, 1983; Leniec et al., 1987), thus analysis of karyotypes provides little information concerning the relative phylogenetic position of these morphologically very different taxa, except in their relation to Corynorhinus.

Nader and Hoffmeister (1983) compared bacular morphology of Plecotus, Corynorhinus, and Idionycteris, and concluded that the distinctive size and shape of the baculum justified placing Idionycteris in a separate genus. Comparisons of Corynorhinus and literature descriptions of Plecotus bacula indicated considerable differences, but generic status of Corynorhinus was not suggested. Subgeneric status of Corynorhinus has been generally accepted since Handley (1959) revised the group.

MATERIALS AND METHODS

Specimens (skins and skulls) of each described species of five plecotine taxa (genera or subgenera, i.e., Barbastella, Euderma, Idionycteris, Plecotus, Corynorhinus) were borrowed

from museums (see acknowledgments), and states for each of 33 characters (listed below) were determined for each taxon. Polarization of character states was achieved using outgroup methodology (Watrous and Wheeler, 1981; Maddison et al., 1984). Ancestral charater states were inferred from examination of several outgroup species: Myotis (11 species) Pipistrellus (2 species), and Lasionycteris noctivagans. Bickham's (1979) chromosomal analysis suggested a close relationship among these taxa and the plecotines. Use of several species of Myotis reduced the probability of treating as ancestral a condition actually derived in some arbitrarily selected outgroup species. Similarly, use of other genera helped detect characters derived in all Myotis species. I used only those characters for which primitive states could be inferred decisively from the out-group taxa (Maddison et al., 1984).

The following characters of skulls and skins were used to assess phylogenetic relationships among the Plecotini. Zero states correspond to primitive (plesiomorphic) conditions, numbered states represent derived (apomorphic) conditions. Multistate characters were unordered in the analysis.

> Character 1. Position of hamulus of the pterygoids: 0 = curves medially, 1 = straight and parallel with longitudinal axis of skull.
>
> Character 2. Relation of lateral borders of pterygoids to longitudinal axis of skull: 0 = angled medially, 1 = vertical.

Character 3. Position of third upper premolar: 0 = in
line with toothrow, 1 = offset from toothrow.

Character 4. Shape of anterior border of auditory
bullae: 0 = pointed, 1 = rounded.

Character 5. Location of greatest cranial depth: 0 =
posterior of cranium, 1 = anterior of cranium.

Character 6. Location of greatest cranial breadth: 0 =
middle of cranium, 1 = posterior of cranium.

Character 7. Spine at anterior tip of nasals: 0 =
absent, 1 = present.

Character 8. Shape of coronoid process of dentary
(lateral view): 0 = rounded, 1 = with a hook-like
process.

Character 9. Angle of dentary (lateral view): 0 =
curved, 1 = straight.

Character 10. Tubercle on anterior surface of angular
process of dentary (dorsal view): 0 = absent,
1 = present.

Character 11. Supraorbital region: 0 = smooth or weakly
ridged, 1 = strongly ridged.

Character 12. Bone connection between coronoid and
condyle of dentary: 0 = straight, 1 = moderately
decurved, 2 = strongly decurved.

Character 13. Postorbital expansion of zygomatic arch:
0 = absent, 1 = located on middle third of arch,
2 = located on posterior third of arch.

Character 14. Medial aspect of auditory bullae: 0 = smooth, 1 = emarginated.

Character 15. Auditory bullae: 0 = round, 1 = elliptical.

Character 16. Basial pits: 0 = present, 1 = absent.

Character 17. Shelf-like process on lateral wall of pterygoids: 0 = absent, 1 = present.

Character 18. Sagittal crest: 0 = present, 1 = absent.

Character 19. First and second upper incisors: 0 = both large, 1 = second incisor much smaller, 2 = both small.

Character 20. Hamulus of pterygoid (lateral view): 0 = extending as a process, 1 = broadly connected to pterygoid.

Character 21. Fourth lower premolar: 0 = double rooted, 1 = single rooted.

Character 22. External narial vacuities (dorsal view): 0 = as wide as long, 1 = longer than wide.

Character 23. Ventral emargination in anterior palate: 0 = extends to canines, 1 = extends past canines.

Character 24. Size of infraorbital foramen: 0 = small, 1 = large.

Character 25. Infraorbital plate: 0 = not twisted to produce a process, 1 = twisted, resulting in a process located dorsoposterior to infraorbital foramen.

Character 26. Upper canine: 0 = longer than fourth
upper premolar, 1 = shorter than fourth upper
premolar.

Character 27. Shape of premaxilla (lateral view): 0 =
sloping, triangular, 1 = truncated, rectangular.

Character 28. Posterior parapterygoid foramen: 0 =
behind or even with posterior extent of hamulus of
pterygoid, 1 = anterior to hamulus.

Character 29. Fourth upper premolar: 0 = wider than
long, 1 = longer than wide.

Character 30. Posterior nares opens: 0 = in middle
third of pterygoids, 1 = in anterior third, 2 =
in posterior third.

Character 31. Auricle: 0 = small, 1 = large.

Character 32. Second phalanx of third digit: 0 =
shorter than first phalanx, 1 = longer than first
phalanx.

Character 33. Posterior basal lobe of auricle: 0 = not
attached to base of the tragus, 1 = attached
to base of tragus.

The purpose of cladistic analysis is to find the shortest
possible path of all variables in terms of the order and
polarity of their states, thus a single decision is made
based on total relationships within and among the states of
all characters (Pimentel and Riggins, 1987). Analysis was
performed with version 2.4.0 of Swofford's (1985) program
PAUP (Phylogenetic Analysis Using Parsimony) using the

branch-and-bound (BANDB), option which is guaranteed to find the most parsimonious tree (Hendy and Penny, 1982).

RESULTS

The single shortest length tree (Table 1) had a consistency index of 0.822 and required 45 steps (Fig. 1). Synapomorphies that identify the Plecotini include (character numbers in parentheses): greatest depth of skull toward front of cranium (5), absence of basial pits (16), reduction in size of second upper incisors (19), and second phalanx of third digit longer than first phalanx (32). Two characters (location of cranial depth and loss of basial pits) were reversed in some taxa, but they are most parsimoniously interpreted as synapomorphies at this level. The major features of the tree are: (1) all taxa belong to successive monophyletic groups, and each taxon is a plesiomorphic sister group to all taxa to its right in the cladogram, and (2) Idionycteris and Euderma form the most apomorphic group.

Corynorhinus, Plecotus, Idionycteris, and Euderma are linked as a monophyletic group by eight synapomorphies: hamulus straight (1), pterygoid walls vertical (2), anterior of auditory bullae rounded (4), angle of dentary straight (9), postorbital expansion of zygomatic arch present (13), fourth lower premolar single rooted (21), parapterygoid foramen anterior to hamulus (28), and auricle large (31). Characters 2, 21, and 28 were reversed in some terminal

taxa. Plecotus, Idionycteris, and Euderma share four
derived features: greatest cranial breadth posterior (6),
supraorbital region strongly ridged (11), a shelf-like
process present on lateral wall of the pterygoids (17), and
external narial vacuities longer than wide (22). Sister
group relationship of Idionycteris and Euderma is indicated
by a reversal in location of greatest cranial depth, being
posterior rather than anterior (5), strong decurvation of
the bony bridge between the coronoid and angle of the
dentary (12), elliptically shaped auditory bullae (15), loss
of the sagittal crest (18), twisting of the infraorbital
plate (25), and a rectangular premaxilla (27).

DISCUSSION

The phylogenetic relationship predicted by synapomorphous
features of morphological characters could be most
rigorously evaluated by testing for congruence with
karyological or biochemical data sets (Hood and Smith,
1982). Unfortunately, no complete studies are available for
comparison. Stock (1983) provided a cladistic treatment of
G-banded chromosomal homologies of Euderma, Idionycteris,
and Corynorhinus (Plecotus in his paper), which corroborates
my conclusions from morphology: Corynorhinus formed the
sister group to a clade comprising Idionycteris and Euderma.
Because Idionycteris was more closely related to Euderma
than to Corynorhinus based on karyotypes, it could be
inferred that Idionycteris does not belong to a taxonomic

category exclusive of <u>Euderma</u>, i.e., the treatment of <u>Corynorhinus</u> and <u>Idionycteris</u> as subgenera and of <u>Euderma</u> as a genus as suggested by Handley (1959) is not supported. In general, karyotypic and morphologic data appear to be rather congruent with the exception of karyotypic imprecision concerning relationships among <u>Barbastella</u>, <u>Plecotus</u>, and <u>Corynorhinus</u>.

A classification of the Plecotini based on the cladogram is possible using criteria developed by Nelson (1972, 1973) and elaborated by Cracraft (1974), who termed the process "phyletic sequencing". Cracraft noted that monophyletic taxa of equal rank can be sequenced with the convention that each taxon is the sister group of all taxa listed below it in the classification. When none of the lineages below the terminal dichotomy are themselves dichotomous, the relationships are precisely represented by phyletic sequencing only (the procedure of subordination is not required). Thus, I propose the following classification for the Plecotini, modified from Koopman and Jones (1970):

Family: Vespertilionidae

Subfamily: Vespertilioninae

Tribe: Plecotini

<u>Barbastella</u>

<u>Corynorhinus</u>

<u>Plecotus</u>

<u>Idionycteris</u>

<u>Euderma</u>

The cladistics-based classification supports the generic distinction of Idionycteris proposed by Williams et al., (1970) and Nader and Hoffmeister (1983). Further, it indicates that Corynorhinus is a valid generic designation.

Handley (1959:104-106) summarized the nomenclatoral history of the group, then presented an evaluation of their taxonomy. He inferred character states (p. 109) for the hypothetical ancestor for his subgenera Idionycteris, Corynorhinus, and Plecotus based on a study of recent and fossil material. The value of fossil material in assigning character state polarity is questionable when direct lineage relationship between fossil and recent material cannot be demonstrated. Certain of Handley's "primitive" characters were included in the present analysis (numbers 11, 13, 16, 18, 19, 31), and examination of characters states among the taxa suggest that a "common-is-primitive" approach might have been used by Handley to infer some ancestral conditions. Based on outgroup comparisons, however, characters 11, 13, and 18 are treated here as derived states. Further, parsimony analysis as performed here treats all characters equally, while intuition of an investigator often gives differential weighting to characters based on perceived taxonomic value. Thus, inferences about phylogenetic relationships are not in agreement with those of Handley, who (p. 106) considered Idionycteris as a relict while Plecotus and Corynorhinus represented more advanced or later evolutionary stages.

Cladistic analysis indicates the reverse to be more likely.

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Table 1. Distibution of states for 33 characters of bats of
the tribe Plecotini (Vespertilionidae): <u>Barbastella</u>
(BARB), <u>Corynorhinus</u> (CORY), <u>Plecotus</u> (PLEC),
<u>Idionycteris</u> (IDIO), and <u>Euderma</u> (EUD). Ancestral
states are indicated by ANC, refer to text for
character descriptions.

<u>Character</u>	<u>ANC</u>	<u>BARB</u>	<u>CORY</u>	<u>PLEC</u>	<u>IDIO</u>	<u>EUD</u>
1	0	0	1	1	1	1
2	0	0	1	1	0	1
3	0	1	0	0	0	0
4	0	0	1	1	1	1
5	0	1	1	1	0	0
6	0	0	0	1	1	1
7	0	0	0	0	1	0
8	0	0	0	0	0	1
9	0	0	1	1	1	1
10	0	0	1	0	0	0
11	0	0	0	1	1	1
12	0	0	0	1	2	2
13	0	0	2	1	1	1
14	0	0	0	0	0	1
15	0	0	0	0	1	1
16	0	1	0	1	1	1
17	0	0	0	1	1	1
18	0	0	0	0	1	1
19	0	1	1	1	1	2

Table 1. Continued.

Character	ANC	BARB	CORY	PLEC	IDIO	EUD
20	0	0	0	0	1	0
21	0	0	1	0	1	1
22	0	0	0	1	1	0
23	0	0	1	0	0	0
24	0	0	0	0	1	0
25	0	0	0	0	1	1
26	0	0	0	0	0	1
27	0	0	0	0	1	1
28	0	0	1	1	1	0
29	0	0	0	1	0	0
30	0	1	0	2	2	0
31	0	0	1	1	1	1
32	0	1	1	0	1	1
33	0	0	0	0	0	1

Fig. 1. Cladogram of morphological characters for Plecotine
bats. Bars = synapomorphies, crosses = reversals, and
parallel lines = parallelisms. Character state changes
are 0-1 unless indicated otherwise.
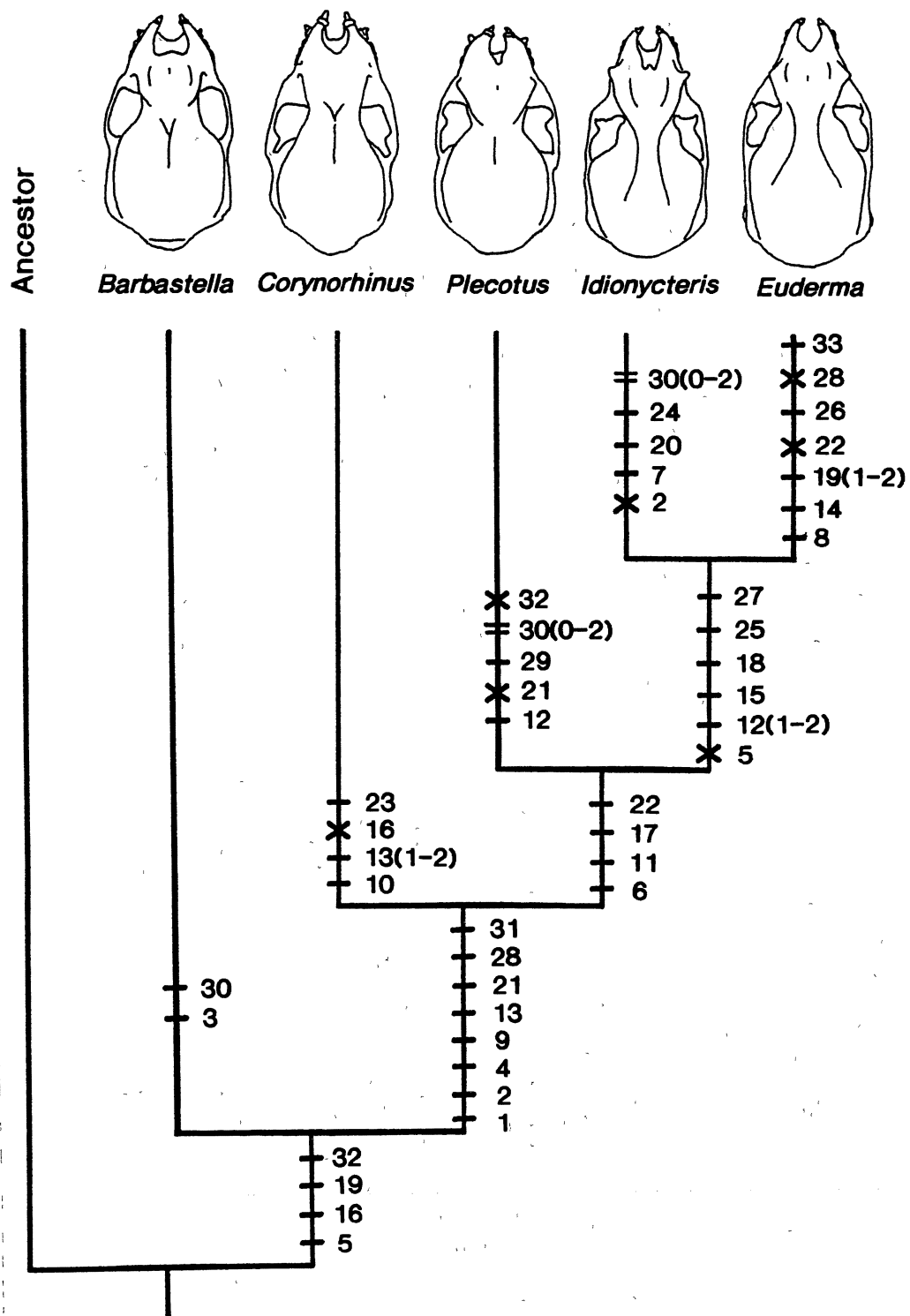
Barbastella   Corynorhinus   Plecotus   Idionycteris   Euderma

CHAPTER V

TOWARD OPTIMUM WING SIZE IN PLECOTINE BATS: ONTOGENETIC
ADJUSTMENTS IN SIZE OF BONY ELEMENTS

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ABSTRACT.--Aerodynamic requirements for flight in bats
suggest the importance of a wing large enough to provide
lift but small enough to reduce energy drains due to drag.
Balance between these needs could be maintained by
compensated growth which allows later-developing bony
elements to adjust for variance in earlier growth. This
hypothesis was evaluated using measurements of wing bones
from several taxa of plecotine bats. Forearms, metacarpals,
and first phalanxes were measured, standardized for size,
and each bone was classified as small, average, or large in
comparison to the mean. Comparisons were then made between
serial elements of the wing to determine the frequency of
each possible set of size combinations, and Chi-square tests
were used to identify significant comparisons. Results
indicated that the forearm and digits tend to compensate for
one another. For example, if the forearm is large, the

digit (metacarpal plus first phalanx) will tend to be small. Analysis of coefficients of variation further supported the hypothesis of compensation. Apparently, developmental plasiticity is the selected mechanism of development in wings of some species of bats.

Morphological structures composed of sequentially developing bony elements can provide insight into an ontogenetic question that apparently has been largely ignored: Is there growth compensation in later development that adjusts for variance (environmental or genetic) in earlier growth? If so, then the size of later-developing bony elements should be negatively correlated with the size of earlier-developing elements. A corollary of the growth-compensation hypothesis is that the variance in size of the component elements will be greater than that of the overall structure. In this paper, I evaluate these expectations in a study of bony elements comprising the wings of several species of plecotine bats.

Several attributes of the bat wing make it ideal for a study of growth compensation in sequentially developing elements. Pearson et al. (1952) and Jones (1967) showed that the proximal bony elements of the forelimb develop and mature earlier than more distal elements, which would provide the opportunity for compensation to occur. Further, the bony elements comprise a simple system for analysis

because the elements are discrete, relatively few in number, and primarily one-dimensional (length) in growth. Finally, it is likely that overall wing shape and size are more susceptible as a unit to natural selection than are the individual bony elements. In other words, within limits, the elements are free to vary, so long as overall size and shape of the wing remains near the optimum. Growth compensation in later developing elements might be predicted in such a system.

Precise wing size as an evolutionary necessity can be inferred from studies of flight speed in bats. The flight speed required to remain airborne is reflected by wing loading (ratio of body weight to wing area). Increased wing loading requires greater speed to achieve lift. Consequently, fast fliers have higher wing loadings than slow fliers. Animals that fly slowly must therefore reduce wing loading by either decreasing body weight or increasing wing area (Findley et al., 1972).

Hayward and Davis (1964) noted a positive correlation between forearm length and flight speed in 15 species of bats in the western United States. Struhsaker (1961) inferred that the shape of the flight membrane was the greatest single factor determining the mode of flight: shorter, wider wings produce slower and more maneuverable flight while longer, narrower wings result in faster but less maneuverable flight. Wing outlines and calculated wing

loadings of 23 species of bats (Farney and Fleharty, 1969) accentuate the adaptive variation found in wings of different species.

The evolutionary forces that shape chiropteran wings should provide adaptations that particularly suit each species to an available niche. For example, those species of bats that have wider wings are more maneuverable (and often can hover), thus allowing insects to be gleaned from foliage. It is possible that "extra" wing area has evolved in response to aerodynamic requirements necessary for feeding habits characteristic of the species, to allow occasional transport of young, or to compensate for holes or tears in the flight membranes (Davis, 1969). The need for such "extra" wing area, however, must be balanced against the excessive aerodynamic drag and concomitant increase in energy required for operation of larger flight surfaces (Davis, 1969).

METHODS

Skins of _Plecotus townsendii_ (n = 1288), _P. rafinesquii_ (n = 101), _P. mexicanus_ (n = 74) and _Idionycteris phyllotis_ (n = 110) were borrowed from museums (see acknowledgments). Seven length variables (Fig. 1) were measured with calipers (to 0.1 mm): forearm (ARM), third metacarpal (X3), first phalanx on third digit (X31), fourth metacarpal (X4), first phalanx on fourth digit (X41), fifth metacarpal (X5), and first phalanx on fifth digit (X51). Measurements of other

phalanxes were not taken due to the difficulty in locating the tapering end of these bones, the inability to measure homologs on all phalanges, and the variability due to flexibility at the tip of terminal wing bones.

Measurements were log-transformed and subjected to principal components analysis. This approach makes no a priori assumptions regarding structure in the data, thus it could be used to gain preliminary insight relative to the hypothesis. Structure which could be interpreted as compensation would indicate that further investigation was warranted.

If data structure is partially due to compensation between bony elements of the wing, a bone (or combination of bones) which is "larger than expected" should be compensated by a bone or bones "smaller than expected". A preliminary size standardization was necessary because all bones of a generally larger bat would be larger than expected and size would obscure other sources of variation. Length of digit 4 (ARM+X4+X41) for each individual in each of 15 samples was standardized to the average length of the wing along digit 4 for the sample. Thus, each bone of a small bat was enlarged and each bone of a large bat was reduced based on the degree of enlargement or reduction required to make digit 4 length equal among bats in each sample. The procedure essentially removes variation due to general size, but has no effect on variation reflecting allometric relationships between bones

(Bookstein <u>et</u> <u>al</u>., 1985: p.145).

Standardization disqualified digit 4 from analysis
because the comparison of arm to hand length (X4+X41) <u>must</u>
indicate compensation (if the arm is long, the hand is short
because these bones always sum to the mean size). Digit 4
was used for standardization because: (1) wing length (digit
3) and width (digit 5) were of primary interest and (2) low
residual correlations from the size factor of a preliminary
factor analysis indicated X4 variation was the best
indicator of size.

Means and standard deviations for size-standardized
variables were calculated and used to classify each bone of
an individual bat as large, normal, or small compared to
mean bone length. A bone was considered large if its length
was in the upper 40% of the normal distribution, small if in
the lower 40%, and normal within the middle 20%. Normality
of distributions was verified prior to this analysis using
program 2D of the BMDP package (Dixon, 1981). Relationships
among bones of the arm and digits 3 and 5, respectively,
were evaluated by determination of the frequency of
occurrence of different pairwise combinations (e.g.,
large-small, small-small). Combinations including normal
sizes were treated as random variation and excluded from
analysis because, from the point of view of compensation,
greater error variation occurs near the middle of the
distribution. For this reason, 10% of the variation on

either side of the mean was arbitrarily dropped to increase the power of the analysis to detect compensation.

Statistical significance of frequencies was determined by Chi-square tests using a correction for sample sizes less than 200 (Sokal and Rohlf, 1981). Digits 3 and 5 were examined in five pairwise combinations to reveal most significant patterns. For example, comparisons on digit 3 were: ARM - hand (X3+X31), ARM - X3, ARM - X31, X3 - X31, and ARM+X3 - X31. For each comparison I determined the number of times each wing bone (or combination of bones) was small, normal, or large, and obtained frequencies of size comparisons (large-small, large-large, small-large, small-small). Evidence of compensation was indicated when the frequency of large-small plus small-large comparisons was significantly greater than large-large plus small-small comparisons.

To evaluate compensation between taxa and geographically within taxa, I examined several samples based on taxa and distributions given by Handley (1959). Sample size was sufficient in the widely distributed Plecotus townsendii pallescens to examine three locations: Northeast (PTP-NE) including Montana, South Dakota, Colorado, Utah, and Wyoming, Southwest (PTP-SW) including Texas and New Mexico, and West (PTP-W) including Arizona and southern California. Samples from the Pacific Northwest were referable to P. t. townsendii (PTT). A geographically isolated population from

western Oklahoma and adjacent areas of Kansas and Texas (PTP-OK), considered by Handley (1959) to be subspecies intergrades, was considered independently. In each of these cases, sexes were treated separately due to sexual dimorphism in size (Handley, 1959). Type-I error rate for tests on these 12 subsamples of P. townsendii was controlled using a sequential Bonferroni approach (Rice, 1989).

Small sample sizes from other taxa and locations precluded separate study of sexes. These taxa were examined by reducing sexual dimorphism via the "zwitter" technique of Schnell et al. (1985). Means by sex were calculated and the difference between sexes per variable was determined (females were always larger). Half the difference per variable was subtracted from females and added to males to simulate a sexless data set. This approach was applied to P. t. australis (PTA) from Mexico, P. t. virginianus (PTV) from Virginia, West Virginia, Kentucky, and North Carolina, P. rafinesquii macrotis (PRM) from the southeastern United States, P. mexicanus (PMX) from Mexico, and Idionycteris phyllotis (IPH), from central and southern Arizona and adjacent areas of New Mexico.

If results indicating compensation in the preceding analysis are valid, a negative correlation is expected between any elements demonstrating compensation. Further, the coefficient of variation (CV) for compensating sets of elements should be significantly less than the CVs of the

individual bones involved. This corollary to the growth compensation hypothesis was evaluated by comparing the mean CV for individual elements comprising the compensating bones with the CV of the bones evaluated as a unit. In other words, I obtained the mean CV based on individual bones involved in compensating sets and compared it to the CV calculated for the set taken as a whole, using a test of homogeneity of CVs (Sokal and Braumann, 1980). This test was also used to compare CVs of individual bones to insure homogeneity prior to calculation of mean CVs. Type-I error rate was controlled using the sequential Bonferroni approach. Compensation was interpreted when variation in the set was less than mean variation in individual elements.

RESULTS

The first eigenvector of principal components analysis (PC1) for all samples was interpreted as size due to positive and approximately equal coefficients for all variables. The second vector (PC2) represented a contrast between the arm and metacarpals and the first phalanxes in samples except for Idionycteris phyllotis (Table 1).

Analyses of bones along the length of the wing provided evidence of compensation in all examined pairs of bony elements except for the comparison of metacarpals (X3) and first phalanxes (X31), although not all populations exhibited compensation (Table 2). The most apparent trend was demonstrated in comparisons of the forearm with combined

bones of the digit (ARM-3). Chi-square values were generally larger for the ARM-3 comparison than for ARM-X3 (comparison of forearm and metacarpal). Relative size of chi-square values generally indicate that compensation by metacarpals merely contributes to greater compensation by the digit. The same observation can be made for the comparison of forearm and first phalanx length (ARM-X31), but compensation appeared to be represented best by the combination of metacarpal and phalanx against forearm length. Three populations indicated compensated growth when the combined forearm and metacarpal was compared to the phalanx, but these appeared to be less important than ARM-3 due to fewer significant cases and lower chi-square values.

Comparisons of ARM-3 by sex in Plecotus townsendii indicated that females were more likely to show compensated growth (4 of 5 cases for females, 2 of 5 for males). Geographic comparisons indicated no compensation in the northeast (PTP-NE), compensation by females only in the southwest (PTP-SW) and northwest (PTT), and compensation by both sexes in the west (PTP-W) and midwest (PTP-OK). All three species of Plecotus exhibited compensation, but a closely related genus (Idionycteris) did not.

Patterns of compensation among bony elements of digit 5 (wing width) followed the same trends described for digit 3, except that compensation was observed in all samples except Idionycteris phyllotis.

Correlation coefficients comparing the arm with digits 3 and 5 ranged between -0.20 and -0.67, and all were significant at P < 0.05 (most at P < 0.0001), supporting the compensation hypothesis. Coefficients of variation diminished in size when based on the sum of elements indicated by the initial analysis to compensate (Table 4). Tests of CVs for ARM - DIGIT3 and ARM - DIGIT5 indicated homogeneity, thus the mean CV was taken as the best estimate of the CV of bones independent of effects of compensation. Comparison of the mean CV with the CV for the bones taken as a unit indicated that variation was significantly reduced in all samples (P < 0.0001).

DISCUSSION

Compensation was interpreted from results of PCA because all phalanxes on PC2 had negative loadings while all metacarpals and the forearm were positive. This suggested that comparison of the combined forearm and metacarpal with the phalanx (N3-X31 and N5-X51) would most likely show compensation during further analyses. However, results indicated comparisons of forearm and digits to best indicate compensated growth. This result is probably due to the use of modified data: PC analyses were based on log-transformed data and compensation analyses were based on size-standardized data.

The hypothesis of compensation between elements of the wing in Plecotus is supported in this study. When forearms

are relatively large or small, compensation is found in the digits such that the wing itself is not too large or small. Width of the wing may be subjected to more selective pressure, judging from number of significant cases and size of chi-square values. But it appears that both length and width must be within an optimal range, and that compensation by the bony elements of the wing is the mechanism by which this occurs.

The greater tendency of females to exhibit compensation along digit 3 may be due to changing aerodynamic requirements during pregnancy. At this critical time, a female must still forage efficiently while carrying the additional weight of offspring, which results in increased wing loading. Animals can reduce wing loading by decreasing body weight or increasing wing area (Findley et al., 1972), but because prepartum individuals cannot do either, they may have to fly faster to maintain lift while foraging. Females may be under greater selective pressure because inefficient foragers likely have reduced fitness. Females must have wings adaptively suited for adept flight during most of the year (like males), but also large enough to support additional weight of young. Males do not experience seasonal weight variation as do females, thus males are apparently under less selective pressure and their fitness is less affected.

The propensity of females to demonstrate compensated growth along digit 3 appeared to have a geographic component. Females showed compensated growth in all locations except the northeast (Montana, South Dakota, Colorado, Utah, and Wyoming), while males compensated only in the west (Arizona and southern California) and midwest (Oklahoma, Kansas, and Texas). Lack of compensation by females in the northeastern samples might be related to habitat or climatic phenomena, but explanation of a trend based on a sample of five locations is tenuous.

The consistent indication of compensation along digit 5, regardless of sex, suggests the need for precise wing width. The flight pattern of these bats includes hovering (Handley, 1959), which requires a wider wing but which increases drag during normal flight. Wing width is important because the proximal portion of the wing (plagiopatagium and propatagium) produces most of the lift developed by the wing-beat cycle (Vaughan, 1970). Wing width is expressed by the aspect ratio (the ratio of forearm and wing tip lengths to length of the fifth digit): high aspect ratios characterize narrower wings. Increasing aspect ratio decreases drag and permits greater speed, but reduces lift, while low aspect ratio wings generate considerable drag at high speeds but provide maximal lift at low speeds (Findley et al., 1972; Findley and Wilson, 1982). The plecotine bats have relatively low aspect ratios (Findley et al., 1972). Compensatory growth in digit 5 underscores an evolutionary

balance between the benefit of hovering flight and the loss of speed and energy due to aerodynamic drag.

Idionycteris phyllotis demonstrated no compensatory growth along digits 3 or 5. This result was anticipated by principal components analysis, where PC2 appeared to reflect a contrast between X41 and X51 rather than between linear sets of bones. Sample size limits my interpretation of these observations because certain populations of P. townsendii were also insignificant for digit 3. However, a conservative interpretation is that compensatory growth may not occur in all groups of bats. Perhaps bats that hover, such as *Pipistrellus*, are more likely to demonstrate this phenomenon than are those species which fly much faster.

The significant negative correlation between the forearm and digits 3 and 5 indicated that larger forearms would be succeeded by smaller digits, and vice versa. Results of analysis of CVs strengthened this conclusion. Sokal and Braumann (1980) noted that if homogeneity of all coefficients of variation from a single population sample was indicated, in effect the CVs would represent a horizontal line at the level of the average CV for all variables. Thus, when added variables produce a CV of significantly less size than the mean of individual variables in the homogeneous set, the reduced variation can be attributed to compensation. Notably, evidence of compensation was found in all samples using this approach,

even though Type-I error rate had been controlled. The
first approach to analysis was conservative in this respect.

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Table 1. Eigenvectors for PC 2 for 15 populations of bats.
Variable and sample names given in text.

	PTP-NE		PTP-SW	
	Male	Female	Male	Female
ARM	0.1165	0.2294	0.2452	0.4830
X3	0.5043	0.4808	0.4785	0.3620
X31	-0.4255	-0.3084	-0.1978	-0.4463
X4	0.4548	0.4589	0.4707	0.4137
X41	-0.3672	-0.2807	-0.3313	-0.1604
X5	0.4185	0.4335	0.4328	0.3957
X51	-0.1850	-0.3791	-0.3914	-0.2880

	PTP-W		PTP-OK	
	Male	Female	Male	Female
ARM	0.3447	0.2962	0.2417	0.3050
X3	0.3903	0.4443	0.4194	0.4787
X31	-0.0930	-0.2600	-0.3557	-0.1551
X4	0.4353	0.4315	0.4902	0.4897
X41	-0.4495	-0.3241	-0.3861	-0.3633
X5	0.3625	0.3906	0.4182	0.4456
X51	-0.4440	-0.4510	-0.2738	-0.2887

Table 1. Continued.

	PTT		PTA	PTV
	Male	Female		
ARM	0.2426	0.2849	0.1972	0.3312
X3	0.4648	0.5047	0.4711	0.4197
X31	-0.1969	-0.0938	-0.1169	-0.3388
X4	0.4724	0.4169	0.5504	0.4188
X41	-0.3170	-0.2856	-0.3220	-0.1117
X5	0.4358	0.3523	0.5056	0.4004
X51	-0.4156	-0.5252	-0.2515	-0.5013

	PMX	PRM	IPH
ARM	0.2471	0.4861	-0.0006
X3	0.2765	0.3124	0.0604
X31	-0.7867	-0.3355	0.1270
X4	0.3032	0.3584	0.1020
X41	-0.0975	-0.4279	0.5552
X5	0.3606	0.3392	0.0606
X51	-0.1103	-0.3564	-0.8111

Table 2. Chi-square values for comparisons along the arm
and hand at digit 3. Sample names are described
in methods, comparisons relate to symbols in Fig. 1.
The 3 represents X3+X31, and N3 is ARM+X3. Asterisk
indicates significant comparisons based on p < 0.05,
sequential Bonferroni approach used on P. townsendii.

Comparison

Sample	N	Sex	ARM-3	ARM-X3	ARM-X31	N3-X31	X3-X31
PTP-NE	115	F	4.985	5.641	0.016	2.215	2.561
	56	M	4.321	7.259	0.552	0.036	0.000
PTP-SW	107	F	7.018*	2.286	2.618	2.526	0.000
	98	M	0.590	2.241	0.000	0.015	0.403
PTP-W	157	F	9.091*	3.360	8.253*	7.924*	0.000
	116	M	24.014*	12.444*	4.661	10.721*	0.955
PTP-OK	126	F	11.362*	7.890*	3.507	9.446*	1.013
	101	M	6.017*	3.698	0.000	1.333	0.721
PTT	133	F	8.862*	6.782	5.803	1.176	0.184
	114	M	5.309	9.763*	0.907	5.823	0.000
PTA	88	-	9.796*	4.688	9.188*	7.547	0.000
PTV	77	-	16.488*	10.256*	7.225	3.200	0.000
PMX	74	-	12.852*	3.380	2.041	0.000	0.327
PRM	101	-	23.881*	23.045*	2.526	5.352	0.907
IPH	110	-	2.726	2.441	4.513	2.361	0.014

Table 3. Chi-square values for comparisons along the arm
and hand at digit 5.   Sample names are described
in methods, comparisons relate to symbols in Fig. 1.
The 5 represents X5+X51, and N5 is ARM+X5. Asterisk
indicates significant comparisons based on p < 0.05,
sequential Bonferroni approach used on P. townsendii.

Comparison

Sample	N	Sex	ARM-5	ARM-X5	ARM-X51	N5-X51	X5-X51
PTP-NE	115	F	6.349*	10.081*	4.438	0.628	0.507
	56	M	14.815*	13.793*	1.026	0.214	0.372
PTP-SW	107	F	6.349*	3.879	0.357	1.038	0.213
	98	M	19.593*	15.018*	2.161	1.085	0.016
PTP-W	157	F	8.911*	5.628	0.935	0.577	0.250
	116	M	13.433*	10.081*	7.224	6.125	0.062
PTP-OK	126	F	13.653*	10.740*	1.013	7.440	0.557
	101	M	7.843*	7.018*	0.262	0.062	0.014
PTT	133	F	21.333*	11.688*	9.346*	2.500	0.719
	114	M	10.400*	18.349*	0.014	0.013	0.047
PTA	88	-	19.321*	15.022*	1.208	8.491*	1.397
PTV	77	-	6.881*	1.761	0.800	0.000	0.985
PMX	74	-	4.500*	6.283*	1.620	0.735	0.022
PRM	101	-	11.758*	14.017*	2.841	2.925	0.246
IPH	110	-	1.125	2.286	1.333	0.736	0.662

Table 4. Coefficients of variation (CV) for the ARM,
DIGIT3 (X3+X31), total length along digit 3 (W3=ARM+
X3+X31), DIGIT5 (X5+X51), and total length along
digit 5 (W5=ARM+X5+X51). The reduced CV for W3 and
W5 was significant in all cases (P < 0.0001).

Sample	N	Sex	ARM	Digit3	W3	Digit5	W5
					Comparison		
PTP-NE	115	F	1.052	1.382	0.771	1.251	0.610
	56	M	1.185	1.908	1.005	1.230	0.592
PTP-SW	107	F	1.217	1.589	0.759	1.351	0.639
	98	M	1.152	1.387	0.804	1.403	0.704
PTP-W	157	F	1.085	1.310	0.680	1.286	0.663
	116	M	1.096	1.375	0.635	1.252	0.634
PTP-OK	126	F	1.065	1.597	0.853	1.232	0.631
	101	M	1.167	1.383	0.831	1.224	0.669
PTT	133	F	1.242	1.611	0.858	1.326	0.684
	114	M	0.999	1.456	0.764	1.458	0.741
PTA	88	–	1.271	1.291	0.656	1.278	0.543
PTV	77	–	0.950	1.122	0.521	1.071	0.570
PMX	74	–	1.153	1.528	0.864	1.331	0.667
PRM	101	–	1.463	1.574	0.648	1.501	0.614
IPH	110	–	1.009	1.153	0.638	1.244	0.730

Figure 1. Variables used for analysis of growth patterns in wings of plecotine bats, based on log transformed raw data. See text for descriptions of characters.
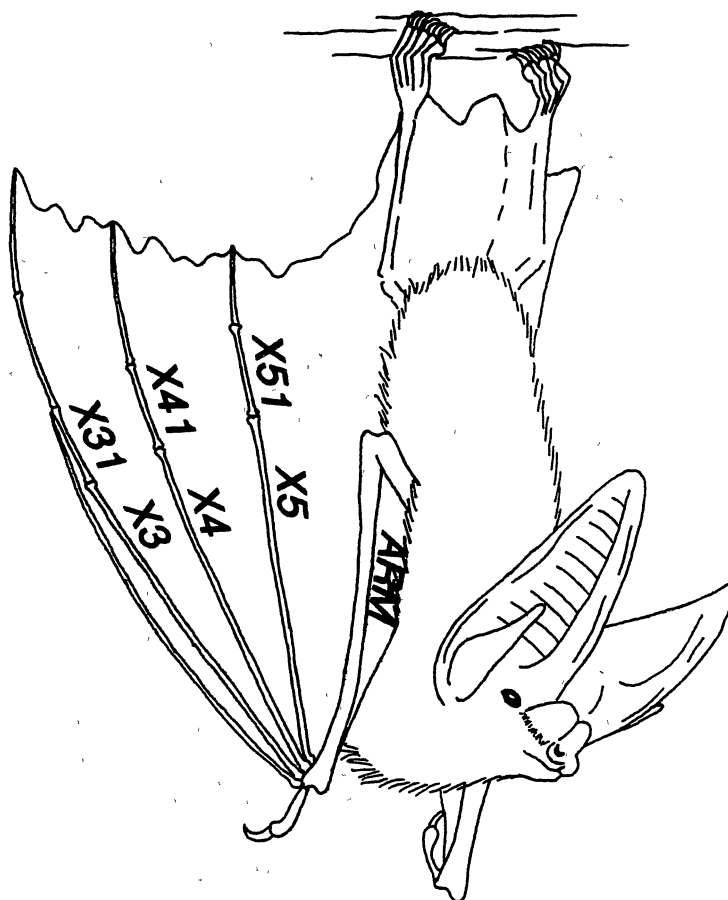
CHAPTER VI

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