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Edited by
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INTRODUCTION

Because of their adaptive diversity and, in many instances, unique morphological attributes, bats of the family Phyllostomatidae long have fascinated biologists. Known only from the New World, most species of phyllostomatids are limited distributionally to tropical environments, but some representatives occur as far north as the southwestern United States and others southward to the northern parts of Argentina and Chile; some species also are distributed on the Bahamas and islands of the Greater and Lesser Antilles. With the advent in recent years of improved methods of collecting bats, a tremendous wealth of information on phyllostomatids has accumulated, and it is the purpose of this three-part publication, which contains a total of 27 individual chapters, to bring these data together in order to assess what now is known about the family and to provide a departure point for future studies.

Owing to the large number of contributions, all of which were solicited by us from persons we felt to be knowledgeable of the subject matter, and the fact that several contributions are necessarily lengthy, the decision was made to group chapters into three volumes, each separately numbered as a Special Publication of The Museum at Texas Tech University. In order to establish a workable approach by which reference could be made consistently to taxa throughout the series, an annotated checklist by Jones and Carter (published in the first part of the trilogy) was circulated to all authors. Each was asked to follow the nomenclature and systematic arrangement in the checklist or, alternatively, to document departures therefrom. This system, it is hoped, will allow readers to relate information from one chapter to another and from one volume to the next without the handicap of conflicting names for the same organism.

Manuscripts first were requested from contributors in 1973 and most had been received by the end of 1974. Part I of the series was published in 1976 and Part II in 1977. As editorial work progressed, some authors provided up-dated information and all authors had the opportunity to insert limited materials at the time they received galley proofs. Therefore, content is as current as reasonably could be anticipated for a project of this kind. Organization and editorial style follow that established for the Special Publications of The Museum at Texas Tech University. Otherwise, authors were allowed broad latitude concerning material to be included in their chapters. Accordingly, and for obvious other reasons, some chapters overlap others in content.

Even though some redundancy has resulted, we thought it best to have a section on the cited literature with each contribution. Citations to manuscripts in Part III are carried in text as "this volume."

For the convenience of readers who may not have seen Part I of the series (Spec. Publ. Mus., Texas Tech Univ., 10:1-218, 1976), the titles, authors, and pagination of its contents are as follows: Introduction (Baker, Jones, and Carter), p. 5; Annotated checklist, with keys to subfamilies and genera (Jones and Carter),

pp. 7-38; Zoogeography (Koopman), pp. 39-47; Chiropteran evolution (Smith), pp. 49-69; Collecting techniques (Tuttle), pp. 71-88; Care in captivity (Greenhall), pp. 89-131; Economics and conservation (C. Jones), pp. 133-145; Brain anatomy (McDaniel), pp. 147-200; and Lactation and milk (Jenness and Studier), pp. 201-218.

Following a two-page introduction by the editors, Part II (Spec. Publ. Mus., Texas Tech Univ., 13:1-364, 1977) includes: Endoparasites (Ubelaker, Specian, and Duszynski), pp. 7-56; Ectoparasites (Webb and Loomis), pp. 57-119; Oral biology (Phillips, Grimes, and Forman), pp. 121-246; Echolocation and communication (Gould), pp. 247-279; Thermoregulation (McManus), pp. 281-292; Feeding habits (Gardner), pp. 293-350; and Movements and behavior (Fenton and Kunz), pp. 351-364.

February 1978

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SYSTEMATIC AND DISTRIBUTIONAL NOTES

J. KNOX JONES, JR., AND DILFORD C. CARTER

Since completion of the manuscript for an annotated checklist of phyllostomatid bats, which appeared in the first part of this trilogy (Jones and Carter, 1976), several publications have come to our attention that alter the systematic arrangement originally presented or extend the known distribution of included species. These papers are summarized here for the convenience of those who may not have all the recent literature available to them and also in order to make the three-volume set on the biology of the Phyllostomatidae more useful as a source of references. Some of this new information also is incorporated in an annotated checklist of the bats of México and Central America by Jones *et al.* (1977).

Systematics

In a recent appraisal of the taxonomy and zoogeography of *Macrotus waterhousii* in the West Indies, Buden (1975) reached the conclusion that only two subspecies should be recognized there: *waterhousii* (*jamaicensis* a synonym) on Jamaica, Hispaniola, and Puerto Rico, and in the southern Bahamas; *minor* (*compressus* a synonym) on Cuba, Grand Cayman, and in the northern Bahamas. Anderson and Nelson (1965) had recognized four subspecies in the Antillean segment of the distribution of *M. waterhousii*.

Greenbaum *et al.* (1975) convincingly argued, on the basis of karyotypes, that *Mesophylla* is generically distinct from *Ectophylla*, a conclusion earlier reached on the basis of morphologic comparisons by Starrett and Casebeer (1968).

We earlier listed the subgenus *Xenoctenes* to include *Micronycteris hirsuta*. Davis (1976) provided evidence for abandoning *Xenoctenes* as valid and returned *M. hirsuta* to the nominate subgenus.

Distributional records listed for Perú by Gardner (1976) were taken into account in preparation of our checklist, but the publication arrived too late to insert remarks relating to systematics. Among these, Gardner suggested that all species of small *Tonatia* (*brasiliensis*, *venezuelae*, and *minuta*) probably are conspecific and that *Lichonycteris degener* may be synonymous with *L. obscura*. He also questioned the report of *Lonchophylla concava* from Perú.

Buden (1976) studied the genus *Erophylla* systematically and reduced the then-recognized two species, including a total of six subspecies, to two subspecies of a single species, *E. sezekorni*, as follows: *sezekorni* (*mariguanensis*, *planifrons*, and *syops* synonyms) from the Bahamas, Cuba, Jamaica, and the Cayman Islands; *bombifrons* (*santacristobalensis* a synonym) from Hispaniola and Puerto Rico.

Buden (1977) also reviewed morphological variation in *Brachyphylla* and concluded that all extant populations should be referred to the one species *B.*

cavernarum. Subspecies recognized by Buden were: *cavernarum* (Puerto Rico, Virgin Islands, Lesser Antilles south to St. Vincent); *minor* (Barbados); *nana* (Cuba and Grand Cayman); and *pumila* (Hispaniola and the Caicos Islands in the southern Bahamas). Verona (1974) earlier arranged all named taxa of *Brachyphylla* as subspecies of the single species *cavernarum,* but gave no reasons for having done so.

In a paper on activity patterns of bats taken near Iquitos, Perú, Davis and Dixon (1976) used the names "*Artibeus planirostris*" and "*Artibeus fuliginosus,*" evidently based at least in part on information contained in the unpublished doctoral dissertation of Donald R. Patten. They also listed *Artibeus pumilio* as a distinct species; we referred to *pumilio* as a subspecies of *A. cinereus.* Similarly, Smith and Genoways (1974) used the name combination "*Artibeus planirostris trinitatis*" in reference to a population on Margarita Island, Venezuela. They cited Patten's unpublished dissertation as the basis for recognition of specific status for *planirostris* (which we listed as a subspecies of *jamaicensis*). We have read Patten's dissertation and do not believe he intended to apply the specific name *planirostris* to *jamaicensis*-like bats from the Caribbean coastal area of northern South America and adjacent islands; nevertheless, we deplore the use of manuscript names and strongly suggest that such information not be incorporated into the published literature without appropriate documentation.

Handley (1976) provided a valuable annotated checklist of Venezuelan bats in which there are several departures from the systematic scheme we employed. Unfortunately, none of these departures is documented with evidence or other explanation; rather, it is indicated that the author will describe new taxa and discuss nomenclatural changes in another paper that was "in press" but which, to our knowledge, has not yet appeared.

Finally, Jones (1978) described a new subspecies of the *Artibeus jamaicensis* complex from the Antillean island of St. Vincent (*schwartzi*), and Davis and Carter (1978) named as new *Tonatia evotis,* which occupies a distribution from Chiapas southeastward in the Caribbean versant of Central America to Honduras within the range earlier ascribed to *T. silvicola* (note change in spelling). They also described a new subspecies of the latter (*T. s. centralis*) from Honduras, Nicaragua, and Costa Rica, and a second new subspecies (*T. s. occidentalis*) from western Ecuador and Perú, while restricting the distribution of the nominate subspecies to the region from Panamá into South America as far as Amazonian Brazil, Bolivia, and Perú.

[Koopman's (1978) important contribution on systematics and zoogeography of Peruvian bats was received after our report was in galley proof. It contains accounts for 71 species of phyllostomatids. Among the important systematic comments are the following: *Mimon koepckeae* was regarded as a subspecies of *M. crenulatum*; *Choeroniscus inca* was synonomized with *C. minor*; *Vampyrops nigellus* was placed as a subspecies of *V. lineatus*; *Enchisthenes* was reduced to subgeneric status under *Artibeus,* as has been done by several other authors; *Artibeus glaucus* and *A. watsoni* were regarded as conspecific with *A.*

cinereus, but *A. anderseni* was recognized as a distinct species; *Diaemus* was considered congeneric with *Desmodus*. Additionally, Koopman recognized and defined the species *Artibeus fraterculus*, *A. fuliginosus*, and *A. planirostris* as distinct from *A. jamaicensis*—we listed *fraterculus* and *planirostris* as subspecies of *A. jamaicensis*, and *fuliginosus* represents the "underscribed species" mentioned in the same account.]

[After this paper was in paged proof, we became aware of a review of the genus *Lonchorina* by Hernandez-Camacho and Cadena-G. (Caldesia, 13:199-251, 1978), which included description of a new species, *Lonchorhina marinkellei* (p. 229), with type locality at Durania, near Mitú, Colombia.]

Faunistics

Starrett (1976) and LaVal (1977) recorded species of bats, including phyllostomatids, new to the fauna of Costa Rica. The latter paper contains the first reported specimen of *Micronycteris daviesi* from North America under the generic (instead of subgeneric) designation *Barticonycteris*. Koopman (1975) summarized the bat fauna of the Virgin Islands and its zoogeographic relationships. In a report on bats from southern Haiti, Klingener *et al.* (1978) recorded the first whole specimens of *Phyllonycteris poeyi obtusa*, previously known only from skeletal remains.

Greenbaum and Jones (1978) reported new records of phyllostomatids from several Middle American countries and Carter and Jones (1978) recorded several new species for the Mexican state of Hidalgo, including the northeastern-most record of *Chiroderma villosum*. Furthermore, Baker and Genoways (1978) summarized in a useful way the zoogeography of Antillean bats, and Baker *et al.* (1978) reported on bats from the island of Guadeloupe.

In our checklist, we indicated that *Vampyrops dorsalis* was known from Costa Rica eastward into South America. Our inclusion of Costa Rica within the known distribution of this bat evidently was in error as we now can find no published accounts of this species to the north of Panamá. Regarding new distributional records, Belize and Costa Rica can be added to the countries previously listed as within the known distribution of *Phylloderma stenops*, Michoacán included within the known distribution of *Musonycteris harrisoni*, and Oaxaca added to that of *Uroderma magnirostrum*. Also, *Centurio senex* now is known on the mainland of South America from Venezuela.

Readers should be aware of the Mammalian Species series, published by the American Society of Mammalogists, in which useful summaries of the biology of individual species of mammals are published. More than 100 accounts thus far have been distributed or are in press, of which eight of those previously published deal with phyllostomatids: *Ardops nichollsi* (Jones and Genoways, 1973), *Hylonycteris underwoodi* (Jones and Homan, 1974), *Macrophyllum macrophyllum* (Harrison, 1975), *Macrotus waterhousii* (Anderson, 1969), *Monophyllus redmani* (Homan and Jones, 1975*a*), *M. plethodon* (Homan and Jones, 1975*b*), *Stenoderma rufum* (Genoways and Baker, 1972), and *Sturnira*

thomasi (Jones and Genoways, 1975). Also of interest is a catalogue of type specimens of bats in European museums that was compiled by Carter and Dolan (1978). In this work, evidence was presented to establish the correct spelling of *Vampyrodes caraccioli* (spelled *caraccioloi* in our checklist).

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MORPHOMETRICS

PIERRE SWANEPOEL AND HUGH H. GENOWAYS

In this paper, we have attempted to cite all relevant literature in which mensural data pertaining to phyllostomatid bats has appeared. We are not so naïve as to believe this goal was reached, but we do believe most pertinent publications are listed, including all major works relating to each species. This information serves as a summary of what currently is known concerning morphometrics of phyllostomatids and hopefully provides a basis for future morphometric studies of members of the family.

Early descriptive accounts of phyllostomatids were based mostly on material preserved in fluid and generally lacked mensural data; most measurements that were included were of external dimensions only. In the late 1800s and 1900s, cranial measurements began to appear in the literature as did the first systematic reviews of phyllostomatid groups, notably those dealing with *Micronycteris* (Andersen, 1906*a*), *Carollia* (Hahn, 1907), *Uroderma* and *Artibeus* (Andersen, 1908), and *Glossophaga* (Miller, 1913*b*). Through the years, systematic studies have become more and more sophisticated, involving substantial mensural data and complex methods of analysis, culminating in multivariate analyses such as those of Davis and Baker (1974), Baker *et al.* (1972*a*), and Power and Tamsitt (1973).

In the following accounts, papers in which measurements have appeared are listed for each species. Additionally, when appropriate information is available in the published record one or more of the following kinds of variation are discussed: age, individual, secondary sexual, and geographic. Accounts are included for all species listed by Jones and Carter (1976). Within each subfamily, genera and species are listed alphabetically. A standard set of measurements for specimens of all species of phyllostomatids is given in Appendix 1. One external (length of forearm) and seven cranial measurements (greatest length of skull, condylobasal length, zygomatic breadth, postorbital constriction, breadth of braincase, length of maxillary toothrow, breadth across upper molars) were taken with dial calipers from each specimen. Four males and four females were measured for each species except in those instances when fewer specimens were available to us.

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Subfamily Phyllostomatinae

Chrotopterus auritus (Peters, 1857)

Measurements of *Chrotopterus auritus* have been recorded as follows: Peters (1857), external measurements of the holotype of *Chrotopterus auritus*; Dobson (1878*a*), external measurements of one specimen; Elliot (1904), and Goodwin (1942*a*), external and cranial measurements of one specimen; Elliot (1917), external measurements of one specimen; Anthony (1920), external and cranial measurements of holotype of *C. colombianus* (sex unknown) from Colombia; Lima (1926), external measurements of a male from Brazil; Cunha Vieira (1942), external measurements of four males and a female and cranial measurements of a male and female from Brazil; Goodwin (1946), external and cranial measurements of a male from Brazil; Hall and Kelson (1959), cranial measurements of a male and female from Veracruz; Burt and Stirton (1961), external and cranial measurements of a specimen from El Salvador; Villa-R. (1967), external and cranial measurements of a male from México; Rick (1968), forearm and cranial measurements of three males and a female from Costa Rica; Goodwin (1969), forearm and cranial measurements of two males (one subadult) from Chiapas; Villa-R. and Villa Cornejo (1969), external and cranial measurements of a male and two females from Argentina; Taddei (1975*a*), external measurements of six specimens and cranial measurements of seven specimens (mean, SE, range) of males and females combined from Brazil.

Individual variation.—Coefficients of variation for external ($N=6$, males and females combined) and cranial measurements ($N=7$, males and females combined) of specimens from Brazil ranged from 1.89 to 5.37 in external measurements and from 0.84 to 4.08 in cranial measurements (Taddei, 1975*a*).

Lonchorhina aurita Tomes, 1863

Measurements for *Lonchorhina aurita* have been recorded as follows: Tomes (1863), external and cranial measurements of the holotype of *L. aurita*; Peters (1866*b*), external measurements of one specimen; Dobson (1878*a*), external measurements of the holotype from Trinidad; Elliot (1904), external and cranial measurements of one specimen; Miller (1912), external and cranial measurements of a male and female from Panamá; Anthony (1923), external and cranial measurements of the male holotype of *L. aurita occidentalis* from Ecuador, and forearm measurements of three specimens and cranial measurements of one specimen of *L. aurita aurita* from Venezuela; Cunha Vieira (1942), external measurements of three males and cranial measurements of two males from Brazil; Goodwin (1942*a*), external measurements of a specimen from Honduras; Goodwin (1946), external and cranial measurements of a male and female from Panamá; Goodwin (1953), external and cranial measurements of the holotype of *L. a. occidentalis* as given by Anthony (1923); Felten (1956*a*), external measurements of two males and cranial measurements of a male from El Salvador; Hall and Kelson (1959), external and cranial measurements of a male and female from Panamá; Burt and Stirton (1961), external measurements of two males

and cranial measurements of a male from El Salvador; Goodwin and Greenhall (1961), forearm and cranial measurements of two females and a juvenile male from Trinidad; Pirlot (1967), external measurements of one specimen; Villa-R. (1967), external measurements of 22 and cranial measurements of 21 males and females combined (mean, SD, and range) from México; Goodwin (1969), forearm and cranial measurements of four females from Oaxaca; Tuttle (1970), external measurements of a male and two females from Perú; Linares and Ojasti (1971), external and cranial measurements of 26 specimens from Trinidad and Venezuela.

Lonchorhina orinocensis Linares and Ojasti, 1971

Linares and Ojasti (1971) gave external and cranial measurements (mean, SD, range) of five specimens from Venezuela, including the female holotype.

Macrophyllum macrophyllum (Schinz, 1821)

Measurements for *Macrophyllum macrophyllum* have been recorded as follows: Dobson (1878*a*), external measurements of a specimen from Brazil; Cunha Vieira (1942) external measurements of two females and cranial measurements of one female from Brazil; Goodwin (1946), external and cranial measurements of a male from Guyana; Felton (1956*a*), external measurements (mean, range) of five males and cranial measurements of three males from El Salvador; Hall and Kelson (1959), external and cranial measurements of a male from Guyana; Hill and Bown (1963), external and cranial measurements of a male and female from Ecuador; Davis *et al.* (1964), external measurements of two males from Nicaragua; Hill (1964), forearm and cranial measurements of a male from Guyana; Starrett and Casebeer (1968), forearm and cranial measurements of a male and female from Costa Rica; Harrison and Pendleton (1974), external and cranial measurements of nine males and three females from El Salvador; Harrison (1975), forearm and cranial measurements (range) for the species; Taddei (1975*a*), external and cranial measurements (mean, SD, range) of eight males from Brazil.

Individual variation.—Taddei (1975*a*) gave coefficients of variation for external (0.48-8.03) and cranial measurements (0.27-3.51) for eight males from Brazil.

Macrotus californicus Baird, 1858

Measurements of *Macrotus californicus* have been recorded as follows: Baird (1858), external measurements of a specimen from California in the original description of *M. californicus;* H. Allen (1864), external measurements of eight specimens; H. Allen (1894*a*, 1894*b*), mean external and cranial measurements of four individuals and external measurements of another eight specimens; Elliot (1901), external measurements of one specimen; Elliot (1904), external and cranial measurements of one specimen; Rehn (1904), external measurements (mean, range) of five topotypes (Imperial Company, California), and cranial measurements (mean, range) of six specimens; Stephens (1906), external measurements of one specimen; Grinnell (1918), external and cranial measurements of 18 females from California; Hall (1946), external measurements of two males and mean and range of nine females and cranial measurements of a male and a female from Nevada; Anderson and Nelson (1965), external and cranial measurements (mean, SD, range) of four samples from throughout the geographic range of the species; Villa-R. (1967), external measurements (mean, SE, range) of five males and eight females and cranial measurements (mean, SE, range) of five males and four females from México; Anderson (1972), external measurements of a large sample and cranial measurements of one individual from Chihuahua.

Secondary sexual variation.—Anderson and Nelson (1965) reported no secondary sexual dimorphism in 28 males and 30 females from California.

Geographic variation.—According to Anderson and Nelson (1965), there is a geographic uniformity in characters of populations from the southern end of Baja California north to California, Nevada, and Arizona and then southward through Sonora. Consequently, they recognized no geographic races within the area that is now considered to constitute the distribution of *M. californicus.*

Macrotus waterhousii Gray, 1843

Measurements of *Macrotus waterhousii* have been recorded as follows: Saussure (1860*c*), external measurements of one specimen; Gundlach (1872, 1877), external measurements of a Cuban specimen; Dobson (1876), external measurements of the holotype of *M. bocourtianus* from Guatemala; Dobson (1878*a*), external measurements of two specimens; H. Allen (1890*a*), external measurements of one specimen in the original description of *M. w. bulleri* from Jalisco; H. Allen (1894*a*), external measurements of one specimen probably from Jalisco; J. A. Allen (1904), external measurements (mean) of seven specimens from Tehuantepec, Oaxaca, compared to those of one specimen from Yautepec, Morelos; Elliot (1904), external and cranial measurements of four specimens; Rehn (1904), external and cranial measurements of the various subspecies (revision of the genus); Elliot (1905), range of external and cranial measurements of the different subspecies; Shamel (1931), external and cranial measurements of the male holotype of *M. w. herberfolium* from Providencialis Island and the measurement range of five specimens (= *M. w. waterhousii*) Hispaniola; Martinez and Villa-R. (1938), external measurements of three specimens and cranial measurements of two from Morelos; Martinez and Villa-R. (1940), external and cranial measurements (mean, SD) of samples of males and females from the Guerrero; Goodwin (1942*a*), external and cranial measurements of one specimen; Anderson and Nelson (1965), external and cranial measurements (mean, SD, range) of 12 samples from throughout the geographic range of the species; Choate and Birney (1968), cranial measurements of subfossil specimens from Puerto Rico; Anderson (1969), external measurements for the genus as the two species are treated conspecifically under *M. waterhousii*; Goodwin (1969), forearm and cranial measurements of three males and two females from Oaxaca; Alvarez and Ramirez-Pulido (1972), external and cranial measurements (mean, range) of 11 specimens from Tamaulipas and San Luis Potosí; Silva-Taboada (1974), measurements of fossil mandibles from Cuba; Buden (1975*b*), external and cranial measurements (mean, SD, range) of large samples from northern Bahamas, southern Bahamas, Cuba, Hispaniola, Jamaica, and means of smaller samples from Isle of Pines, Grand Cayman, and Navassa for sexes combined.

Individual variation.—In specimens from Guerrero, coefficients of variation (CV) for external measurements varied in males from 1.93 to 11.16 and in females from 1.67 to 8.09; for cranial measurements, in males from 1.36 to 3.08 and in females from 0.65 to 3.90 (Martinez and Villa-R., 1940).

According to Anderson and Nelson (1965), length of skull proved to be the least variable character, and then in order of increasing variability were the breadth of braincase, length of bulla, interorbital breadth, and breadth at canines. External measurements were generally more variable than cranial measurements. The coefficient of variation for total length, however, was usually no greater than that of the more variable cranial measurements.

Buden (1975*b*) showed in West Indian specimens that cranial (except breadth at canines) and forearm measurements were the least variable measurements, whereas tail length generally showed extremely high CVs. Forearm and cranial CV values, other than that of breadth at canines, ranged from 1.03 to 3.58; values for breadth at canines varied from 2.78 to 4.63. The coefficient of variation values observed in tail length ranged from 6.19 to 9.13.

Geographic variation.—Anderson and Nelson (1965) noted an increase in size from northwest to southeast through the range of *Macrotus waterhousii*. This held true for all measurements except length of bulla, which increased in size from southeast to northwest. Specimens from eastern Cuba were larger than those from the western end of the island. However, samples from different parts of western Cuba and the Isle of Pines did not differ significantly in size (Anderson and Nelson, 1965). Geographic variation was found within Hispaniolan samples—those from Haiti averaged larger than those from the Dominican Republic. Populations on Hispaniola were larger in size than those on Cuba and the southern Bahamas. Specimens from several northern Bahaman islands were not significantly different in size but averaged larger than those from Cuba (Anderson and Nelson, 1965) and smaller than those from the southern Bahamas and Hispaniola. Bats from Jamaica, according to Anderson and Nelson (1965), were larger than those from Cuba, and intermediate in size between Cuban and southern Bahaman and Hispaniolan populations (Anderson and Nelson, 1965:21). Specimens from Oaxaca averaged significantly larger than those from Morelos (region of the type locality) but were not as large as specimens from Hispaniola and the southern Bahamas. Specimens from Oaxaca averaged larger than the western Cuban specimens. A sample from Morelos, Guerrero, and Puebla were only slightly larger in cranial size than a sample from Jalisco.

Buden (1975*b*) stated that the statistical data he used were comparable to those of Anderson and Nelson (1965) but concluded that a dendrogram, based on levels of morphological differences, placed the northern Bahaman specimens with the Cuban ones. An increase in specimen size from southwest to northeast throughout the West Indies (western to eastern Cuba to northern Bahamas; and Jamaica, Hispaniola, to southern Bahamas) was found. Ear length, however, did not show this pattern (Buden, 1975*b*). Buden (1975*b*) also described an increase in size from western Cuba to eastern Cuba as did Anderson and Nelson (1965). However, in contrast to Anderson and Nelson, Buden did not find intra-island variation on Hispaniola.

Davis and Baker (1974) reported a general trend of size increase on the mainland from north to south in all measurements. Their multivariate analyses showed that the groups were nonclinally tied one to another with respect to geography.

Micronycteris behni (Peters, 1865)

Measurements of *Micronycteris behni* have been recorded as follows: Peters (1865*b*), external measurements of the holotype from Brazil; Dobson (1878*a*), external measurements of a specimen; Andersen (1906*a*), external measurements of two specimens and cranial measurements of one specimen from Perú; Sanborn (1949*a*), range of forearm length in the species.

Micronycteris brachyotis (Dobson, 1878)

Measurements of *Micronycteris brachyotis* have been recorded as follows: Dobson (1878*b*), external measurements of the male holotype of *M. brachyotis* from Cayenne; Miller (1900*c*), forearm length for *M. brachyotis*; Andersen (1906*a*), external and cranial measurements of the holotype of *M. brachyotis* (after Dobson 1878*b*); Sanborn (1949*a*), external and cranial measurements of the holotype and two topotypes of *M. platyceps* (= *M. brachyotis*) and external measurements of four additional specimens from Trinidad; Hall and Kelson (1959), external and cranial measurements of the holotype of *M. platyceps*, two topotypes, and one female; Goodwin and Greenhall (1961), forearm measurements (range) of 16 specimens from Trinidad, cranial measurements of one male and two females including the holotype of *M. platyceps*, and a comparison of external and cranial measurements of a large adult male from Trinidad and the holotype of *M. brachyotis* from Cayenne; Davis *et al.* (1964), external and cranial measurements of a female from Chiapas; Jones (1966), forearm and cranial measurements of a male from Guatemala; Villa-R. (1967),

external measurements of one specimen from Oaxaca; Rick (1968), external and cranial measurements of eight males and one female from Guatemala; Goodwin (1969), forearm and cranial measurements of a male from Oaxaca; Marinkelle and Cadena (1972), forearm measurement of one male from Colombia, and external and cranial measurements of one female from Colombia; Starrett (1976), forearm measurements of a female, male, and juvenile male from Costa Rica.

Geographic variation.—The holotype of *M. brachyotis* from Cayenne, an old male with worn teeth, was larger than a series of specimens from Trinidad but not larger than a speciment of *M. platyceps* from Nicaragua (Goodwin and Greenhall, 1961).

Micronycteris (= Barticonycteris) daviesi (Hill, 1964)

Measurements of *Micronycteris daviesi* have been recorded as follows: Hill (1964), external and cranial measurements of the female holotype from Guyana; Tuttle (1970), external measurements of two males and one female from Perú.

Micronycteris hirsuta (Peters, 1869)

Measurements of *Micronycteris hirsuta* have been recorded as follows: Peters (1869), external measurements of the holotype; Dobson (1878*a*), external measurements of one specimen; Elliot (1904), external measurements of one specimen from Costa Rica; Andersen (1906*a*), external measurements of two specimens and cranial measurements of one from Costa Rica; Sanborn (1932), external and cranial measurements of a female from Colombia; Goodwin (1946), external and cranial measurements of a male and female from Costa Rica; Hershkovitz (1949), external and cranial measurements of two males and one female from northern Colombia; Sanborn (1949*a*), range of forearm and greatest length of skull for the species; Hall and Kelson (1959), external and cranial measurements of a male and female from Costa Rica; Goodwin and Greenhall (1961), forearm length (range) of 12 specimens, and cranial measurements of three males and two females from Trinidad; Hill (1964), forearm and cranial measurements of one female from Guyana; LaVal (1969), external and cranial measurements of a male and female from Honduras; Gardner *et al.* (1970), external and cranial measurements of one male from Costa Rica; Valdez and LaVal (1971), external and cranial measurements of two males from Nicaragua; Baker *et al.* (1973), forearm and cranial measurements (mean, SE, range, CV) of two samples, one from Trinidad (four specimens) and the other from Honduras (one specimen) and Nicaragua (four specimens).

Individual variation.—Coefficients of variation in forearm and cranial measurements obtained from four specimens from Trinidad revealed little variation (CV, 0.8-2.3), whereas one specimen from Honduras and four from Nicaragua combined showed higher values than those from Trinidad (CV, 1.2-4.1) (Baker *et al.*, 1973).

Geographic variation.—Valdez and LaVal (1971) recorded this species for the first time from Nicaragua and showed that the two specimens obtained were smaller than those from Costa Rica and other countries recorded by Goodwin (1946), Sanborn (1949*a*), Goodwin and Greenhall (1961), and Gardner *et al.* (1970). However, these Nicaraguan specimens proved to differ little from Honduran specimens (LaVal, 1969). Forearm and cranial measurements of specimens from Trinidad averaged larger than those for specimens from Honduras and Nicaragua, but only forearm and greatest length of skull proved to be significantly different (Baker *et al.*, 1973).

Micronycteris megalotis (Gray, 1842)

Measurements of *Micronycteris megalotis* have been recorded as follows: Dobson (1878*a*), external and cranial measurements of one specimen; Miller (1898), external measurements for specimens from Nicaragua (including the male holotype of *M. m.*

microtis), Trinidad (one male), Margarita (one male and female), Colombia (two males and females), Honduras (two males), Colima (four males and three females), Jalisco (two males and three females), and Oaxaca (one female); Miller (1900*c*), forearm length for *M. m. microtis*; Robinson and Lyon (1901), external measurements of five males and six females from Venezuela; Elliot (1904), external and cranial measurements of one specimen and external measurements of the holotype of *M. m. microtis*; Rehn (1904), external and cranial measurements of the holotype of *Macrotus pygmaeus* (= *Micronycteris megalotis*) and one male from Yucatán; Andersen (1906*a*), external measurements of the holotype of *M. m. microtis* (after Miller 1898), external and cranial measurements (range) of 30 (18 cranial) specimens from Brazil, Perú, Guyana, Venezuela, Trinidad and Tobago, and of 10 (nine cranial) specimens from Colombia, Guatemala, Honduras and México; Lyon (1906), ear measurements of the holotype of *M. m. microtis* and a specimen from Venezuela; Lima (1926), external measurements of a male from Brazil; Goodwin (1934), external measurements of one specimen from Guatemala; Martinez and Villa-R. (1938), external measurements of one specimen from Morelos; Cunha Vieira (1942), external measurements of four males and cranial measurements of two males from Brazil; Goodwin (1942*a*), forearm and cranial measurements of two specimens of unknown sex from Honduras; Goodwin (1946), external and cranial measurements of two males from Costa Rica; Sanborn (1949*a*), range of forearm length of three subspecies; Hershkovitz (1949), forearm measurement of one specimen and skull measurements of another, both from Trinidad; Dalquest (1953*a*), external measurements of eight males and 10 females, and cranial measurements of seven males and nine females from San Luis Potosí; Goodwin (1953), external and cranial measurements of the holotype *Macrotus pygmaeus* from Yucatán; Goodwin (1954), external measurements of a specimen from Tamaulipas; Felten (1956*a*), external and cranial measurements of two males from El Salvador; Felten (1956*d*), external measurements (mean, range) of specimens from El Salvador; Goodwin and Greenhall (1961), forearm measurements of three specimens from Trinidad and three from Tobago (unsexed), and cranial measurements of a male from Trinidad; Burt and Stirton (1961), range of forearm and cranial measurements of eight males and five females combined from El Salvador; Husson (1962), external and cranial measurements of six males and three females from Surinam; Tamsitt and Valdivieso (1963*a*), mean and range of external and cranial measurements of three males and four females combined from Colombia; Valdivieso (1964), mean and range of external and cranial measurements of specimens from Colombia; Brosset (1965), external and cranial measurements of two males from Ecuador; Villa-R. (1967), external measurements of six males and 10 females, and cranial measurements of eight males and seven females from México; Pirlot (1968), forearm measurement of a male from Perú; Goodwin (1969), forearm and cranial measurements of four males and five females from Oaxaca; Gardner *et al.* (1970), wing and cranial measurements (mean, range) of six males and one female combined from Costa Rica; Jones *et al.* (1971*b*), mean and range of forearm and cranial measurements of three males and five females from westcentral Nicaragua, of three males and three females from Isla del Maiz Grande, and of three males and three females from Río Coco, and forearm and cranial measurements of one male from Bonanza, Nicaragua, and cranial measurements of the *M. m. microtis* holotype (male) from Greytown, Nicaragua; Watkins *et al.* (1972), forearm and cranial measurements of two males and females from Jalisco; Jones *et al.* (1973), forearm and cranial measurements of three males from the Yucatan Peninsula; Birney *et al.* (1974), forearm and cranial measurements of a female from Yucatán; Smith and Genoways (1974), forearm and cranial measurements of a male and female from Margarita Island, Venezuela; Taddei (1975*a*), external and cranial measurements (mean, SE, range, CV) of males and females combined ($N = 10$) from Brazil.

Individual variation.—Coefficients of variation for 10 specimens (sexes combined) from Brazil were given for external and cranial measurements by Taddei (1975*a*). Cranial

measurements showed little variation (CV, 0.66 to 3.18), whereas those for external measurements were more variable (CV, 1.77 to 5.48).

Geographic variation.—Variation in size in *M. megalotis* between two localities in Costa Rica (Fila la Maquina, Cordillera Talamaca, 6600 to 8700 feet; Rincon and Tilaran, below 700 feet) were discussed by Gardner *et al.* (1970). Those from the higher altitude proved to be larger than those from the lower. Size differences were particularly evident in wing dimensions; no difference in ear length was observable (see also Jones *et al.*, 1971*b*). Although cranial measurements seemed to be more or less equal, specimens from the higher altitude tended to be larger.

Jones *et al.* (1971*b*) concluded that specimens from westcentral Nicaragua and Isla del Maíz Grande were, on the average, considerably larger in skull and forearm measurements than the holotype of *M. m. microtis* from Greytown, eastern Nicaragua. Specimens from Río Coco were intermediate between the two morphological types leading these authors to suggest that intergradation occurred between them. No difference in ear length was found. In the original description, Miller (1898) claimed that *M. m. microtis* was characterized by much smaller ears. Lyon (1906) presented evidence that the ears of the holotype were small and not damaged. Forearm measurements of four specimens previously obtained from Isla del Maíz Grande (G. M. Allen, 1929) were also relatively big according to Jones *et al.* (1971*b*).

Micronycteris minuta (Gervais, 1856)

Measurements of *Micronycteris minuta* have been recorded as follows: Dobson (1878*a*), external measurements of one specimen from Brazil; Thomas (1901*c*), forearm measurements of the holotype as given by both Gervais and Dobson; Andersen (1906*a*), external measurements of eight specimens (range) and cranial measurements of six specimens (range) from Brazil; G. M. Allen (1908), external and cranial measurements of one female from Brazil; Cunha Vieira (1942), external measurements of a male from Brazil; Sanborn (1949*a*), range of forearm length in the species, forearm and cranial measurements of one specimen from Colombia; Goodwin (1953), external measurements of the female holotype of *M. hypoleuca* (= *M. minuta*) from Colombia; Goodwin and Greenhall (1961), range of forearm length of 12 specimens and cranial measurements of one male and two females from Trinidad; Linares (1969), external and cranial measurements of a male and female from Venezuela; Gardner *et al.* (1970), mean and range of external and cranial measurements of four specimens (three males, one female) from Costa Rica; Valdez and LaVal (1971), external and cranial measurements of one male from Nicaragua and the range of measurements of three males and one female from Costa Rica.

Geographic variation.—According to Sanborn (1949*a*), specimens from Brazil appeared to be larger than specimens from Colombia.

Micronycteris nicefori Sanborn, 1949

Measurements of *Micronycteris nicefori* have been recorded as follows: Sanborn (1949*a*), external and cranial measurements of the male holotype and the range of measurements of four paratypes from Colombia; Goodwin and Greenhall (1961), forearm length of the holotype, the range of this measurement in five specimens from Trinidad, and cranial measurements of the holotype (male) and a male and female from Trinidad; Hill (1964), forearm (two males) and cranial measurements of one specimen from Guyana; Baker and Jones (1975), external and cranial measurements of a female from Nicaragua; Starrett (1976), external and cranial measurements of five males and cranial measurements of one male from Costa Rica; LaVal (1977), forearm length, greatest length of skull, and weight of a male from Costa Rica.

Geographic variation.—According to Starrett (1976), his specimens from Costa Rica agreed closely in most measurements with those given by Sanborn (1949*a*) for specimens from Colombia.

Micronycteris pusilla Sanborn, 1949

Measurements of *Micronycteris pusilla* have been recorded as follows: Sanborn (1949*a*), external and cranial measurements of the male holotype from Brazil; Goodwin (1953), forearm and cranial measurements of the holotype.

Micronycteris schmidtorum Sanborn, 1935

Measurements of *Micronycteris schmidtorum* have been recorded as follows: Sanborn (1935), external and cranial measurements of the holotype and paratype (both males) from Guatemala; Goodwin (1942*a*), external and cranial measurements of the holotype from Guatemala; Sanborn (1949*a*), range of forearm measurements in the species; Hall and Kelson (1959), external and cranial measurements of the holotype from Guatemala and one male; Davis *et al.* (1964), external and cranial measurements of a male from Nicaragua; Villa-R. (1967), external and cranial measurements of two specimens from Yucatán; Starrett and Casebeer (1968), forearm (two males, mean and range of five females) and cranial measurements (two males, two females) from Guanacaste, Costa Rica; Jones *et al.* (1973), forearm and cranial measurements of one juvenile female from the Yucatan Peninsula; Baker and Jones (1975), external and cranial measurements of a male from Nicaragua.

Micronycteris sylvestris (Thomas, 1896)

Measurements of *Micronycteris sylvestris* have been recorded as follows: Thomas (1896), external and cranial measurements of the male holotype from Costa Rica; Elliot (1904*a*), external and cranial measurements of one specimen; Andersen (1906*a*), external and cranial measurements of the male holotype from Costa Rica; Goodwin (1946), external and cranial measurements of the male holotype from Costa Rica; Hall and Kelson (1959), cranial measurements of the holotype of *M. sylvestris* and one male; Goodwin and Greenhall (1961), forearm and cranial measurements (range) of four males from Trinidad and four males from Veracruz; Villa-R. (1967), external measurements (mean, range) of nine specimens and cranial measurements (mean, range) of five specimens from Colima and Jalisco; Goodwin (1969), forearm and cranial measurements of two females from Veracruz; Linares (1969), external and cranial measurements of a female from Venezuela.

Geographic variation.—Specimens from Trinidad were similar to Mexican and Central American specimens; however, skulls of the material from Trinidad were relatively shorter than those from México (Goodwin and Greenhall, 1961).

Mimon bennettii (Gray, 1838)

Measurements of *Mimon bennettii* have been recorded as follows: Saussure (1860*c*), external measurements of one specimen of *Vampirus auriculus* (= *M. bennettii*); Peters (1866*b*), external measurements of a specimen from Brazil; Dobson (1878*a*), external measurements of one specimen; Lima (1926), external measurement of a specimen from Brazil; Cunha Vieira (1942), external and cranial measurements of a female from Brazil; Dalquest (1957), external and cranial measurements of one specimen from Brazil; Husson (1962), external and cranial measurements of two females from Surinam; Hill (1964), forearm and cranial measurements of a male from Brazil.

Mimon cozumelae Goldman, 1914

Measurements of *Mimon cozumelae* have been recorded as follows: Goldman (1914*b*), external and cranial measurements of the holotype from Cozumel Island off the east coast of Yucatán; Elliot (1917), external and cranial measurements of the holotype; Sanborn (1941), external measurements of two specimens from Yucatán; Goodwin (1942*a*, 1946), external measurements of a male and female from Yucatán; Dalquest (1957), external and cranial measurement (mean) of 10 specimens from Veracruz; Hall and Kelson (1959),

forearm and cranial measurements of the holotype of *M. cozumelae*; Carter *et al.* (1966), forearm measurements of a male and female from Chiapas; Villa-R. (1967), external measurements of one male and one female from Yucatán and one male from Oaxaca, and cranial measurements of the male and female from Yucatán; Goodwin (1969), forearm and cranial measurements of five males and five females from Oaxaca; Gardner *et al.* (1970), external and cranial measurements of one male from Costa Rica; Valdez and LaVal (1971), external and cranial measurements of one female and the mean of two males from Honduras; Marinkelle and Cadena (1972), forearm measurements of one male from Colombia.

Geographic variation.—According to Gardner *et al.* (1970), their male from Costa Rica closely resembled a male from Chiapas in cranial measurements.

Mimon crenulatum (É. Geoffroy St.-Hilaire, 1810)

Measurements of *Mimon crenulatum* have been recorded as follows: Peters (1866*a*), external measurements of a specimen from Brazil; Dobson (1878*a*), external measurements of one (*M. longifolium*) from Brazil, and a specimen from an unknown locality; Thomas (1903*c*), external and cranial measurements of the male holotype of *M. c. picatum* from Brazil; Cunha Vieira (1942), external and cranial measurements of two specimens from Brazil; Sanborn (1949*b*), forearm and cranial measurements of two males from Perú; Handley (1960), external and cranial measurements of five males and four females from Brazil, Trinidad, Venezuela, Panamá, and Ecuador (including the holotype of *M. c. keenani*); Goodwin and Greenhall (1961), external and cranial measurements of a male from Trinidad; Husson (1962), external and cranial measurements of two males from Surinam; Hill (1964), forearm of two males and females and cranial measurements of one male from Guyana; Jones (1964), external and cranial measurements of a female from Campeche and measurements available from the holotype of *M. c. keenani* from Panamá; Gardner *et al.* (1970), external and cranial measurements (mean, range) of four specimens (two males and females) from Costa Rica; Gardner and Patton (1972), forearm and cranial measurements (mean, range) of four males and three females from Perú.

Mimon koepckeae Gardner and Patton, 1972

Gardner and Patton (1972) recorded external and cranial measurements (mean, range) of two males and one female and the measurements of the female holotype from Perú.

Phylloderma stenops Peters, 1865

Measurements of *Phylloderma stenops* have been recorded as follows: Peters (1866*b*), external measurements of one specimen from Cayenne; Dobson (1878*a*), external measurements of *Guandira cayanensis* from Cayenne; Goodwin (1940, 1946, 1953), external and cranial measurements of the female holotype of *P. stenops septentrionalis* from Honduras; Goodwin (1942*a*), external and cranial measurements of two specimens from Honduras; Hall and Kelson (1959), external and cranial measurements of the *P. septentrionalis* holotype and one female; Husson (1962), external and cranial measurements of the male holotype from Cayenne; Hill (1964), external and cranial measurements of three females from Guyana, one male from Brazil, and of the holotype of *Guandira cayanensis* (= *P. stenops*); Carter *et al.* (1966), external and cranial measurements of a male from Chiapas; Gardner (1976), external and cranial measurements of a female from Perú; LaVal (1977), forearm length and weight of a female from Costa Rica.

Phyllostomus discolor (Wagner, 1843)

Measurements of *Phyllostomus discolor* have been recorded as follows: Peters (1865*b*) external measurements of one specimen from Brazil; Dobson (1878*a*), external measure-

ments of one specimen; Elliot (1905*b*; 1917), external and cranial measurements of the holotype of *P. verrucossum* from Oaxaca; Miller (1932), forearm (range of five specimens) and cranial measurements of a specimen from Barro Colorado Island, Canal Zone; Sanborn (1936), forearm and condylobasal length of skull measurements (range) of specimens from Brazil (*discolor*), and from Oaxaca, Veracruz, and Guatemala (*verruscosus*); Cunha Vieira (1942), external measurements of a male from Brazil and female from an unknown locality; Goodwin (1942*a*), external and cranial measurements of two males from Honduras; Goodwin (1946), cranial measurements of two males from Honduras; Dalquest (1951), external and cranial measurements of two males and one female from Trinidad; Felten (1956*a*), external measurements (mean, range) of 185 males and 217 females, and cranial measurements (mean, range) of 35 males and 39 females from El Salvador; Burt and Stirton (1961), forearm and cranial measurements (range) of 15 males and 12 females from El Salvador; Goodwin and Greenhall (1961), forearm measurements (range) of four specimens (two males and females) and cranial measurements of one female from Trinidad; Davis and Carter (1962*a*), forearm and cranial measurements of one male from Costa Rica; Husson (1962), external and cranial measurements of eight males and two females from Surinam; Valdivieso and Tamsitt (1962), external measurements (range) of five males and three females and cranial measurements of two specimens from Colombia; Tamsitt and Valdivieso (1963*a*), external measurements (mean, range) of 11 specimens (seven males, four females) and cranial measurements of one male and female from Colombia; Pirlot (1967), external measurements of two specimens; Villa-R. (1967), external measurements of 13 specimens (mean, SD, range) and cranial measurements (mean, SD, range) of 14 specimens from México; Goodwin (1969), forearm and cranial measurements of six males and three females from Oaxaca; Power and Tamsitt (1973), forearm and cranial measurements (means) of males and females from various localities in southern México to South America; Smith and Genoways (1974), external and cranial measurements of four females (mean, range) and two males (means) from Margarita Island, Venezuela; Taddei (1975*a*), external (30 males, 30 females) and cranial measurements (mean, SD, range) of 15 males and females from Brazil; Gardner (1976), external and cranial measurements of a male from Perú.

Individual variation.—Taddei (1975*a*) reported coefficient of variation values for external measurements of Brazilian specimens to vary from 2.38 to 6.51, whereas CVs for cranial measurements varied from 0.96 to 4.45.

Secondary sexual variation.—Taddei (1975*a*) found females averaged larger than males in 17 external measurements and significantly so in three of these, length of ear, digit III-phalanx 2, digit V-phalanx 2. Males averaged larger than females in 15 cranial measurements and significantly so in five of these, breadth across canines, breadth across molars, zygomatic width, mastoid breadth, cranial depth. Power and Tamsitt (1973), performing a MANOVA, showed that males were significantly bigger than females, and a subsequent discriminant function analysis revealed that mastoid width and zygomatic width contributed greatly to the separation of the sexes.

Geographic variation.—In forearm and condylobasal length of skull, specimens from Barro Colorado Island, Canal Zone, were somewhat greater in size than three topotypes of *P. discolor* from southern México (Miller, 1932). Dalquest (1951), comparing cranial measurements of Trinidad specimens with those from Venezuela, found no difference, whereas forearm length appeared to be slightly less than in specimens from the mainland. Davis and Carter (1962*a*) stated that the measurements considered to that time as an expression of geographic variation were in reality due to individual variation. According to Husson (1962), external and cranial measurements of Surinam specimens agree well with those given by Sanborn (1936), Dalquest (1951), and Goodwin and Greenhall (1961) for specimens from Trinidad and Venezuela. When comparing these data with those from El Salvador (Felten, 1956*a*), Husson (1962) concluded that the cranial measurements were larger in the specimens from El Salvador. Power and Tamsitt (1973) stated that populations

west of the Andes in southwestern Ecuador, those near or within the Andes mountains in central Colombia, and those east of the Andes in eastern Colombia were quite similar and did not warrant subspecific recognition. Smith and Genoways (1974) found external and cranial measurements of specimens from Margarita Island, Venezuela, comparable to those given by Sanborn (1936) for specimens from Brazil, Venezuela, and French Guiana, and by Goodwin and Greenhall (1961) for material from Trinidad.

Phyllostomus elongatus (É. Geoffroy St.-Hilaire, 1810)

Measurements for *Phyllostomus elongatus* have been recorded as follows: Peters (1865*b*), external measurements of a specimen from Brazil; Dobson (1878*a*), external measurements of one specimen; Sanborn (1936), forearm and cranial measurements of a female from Ecuador; Cunha Vieira (1942), external measurements of three males and one female and cranial measurements of one male from Brazil; Husson (1962), external and cranial measurements of four males and two females from Surinam; Butterworth and Starrett (1964), external and cranial measurements of a male from Venezuela; Hill (1964), forearm measurements of a male and female and cranial measurements of a female from Guyana.

Geographic variation.—Measurements of six specimens from Surinam correspond well to those given by Sanborn (1951) for specimens from Perú, and by Husson (1962) for material from Guyana.

Phyllostomus hastatus (Pallas, 1767)

Measurements for *Phyllostomus hastatus* have been recorded as follows: Dobson (1878*a*), external measurements of one specimen; Flower and Lydekker (1891), forearm length of the species; Jentink (1893), forearm length of a male from Guyana; Robinson and Lyon (1901), external measurements of five males and eight females from Venezuela; J. A. Allen (1904), external and cranial measurements (range) of two males and four females (including the female holotype of *P. h. panamensis*) from Chiriquí, Panamá, external and cranial measurements of the male holotype of *P. h. caurae* from Colombia, and cranial measurements (mean, range) of two specimens from Trinidad and four from eastern Venezuela; Elliot (1904), external and cranial measurements of one specimen; G. M. Allen (1908), external measurements of three and cranial measurements of one specimen from Brazil, and external measurements of five specimens from Costa Rica; Miller (1912), external and cranial measurements of a male from Panamá; Cabrera (1917), external and cranial measurements of the male holotype of *P. h. curaca* and the range of some of these measurements in three females from Ecuador; Lima (1926), external measurements of a male from Brazil; Cunha Vieira (1942), external measurements of eight males and three females and cranial measurements of three males from Brazil; Dalquest (1951), forearm and cranial measurements (mean) of four specimens from Trinidad; Goodwin (1953), forearm and cranial measurements of the female holotype of *P. h. panamensis* from Panamá and of the holotype of *P. h. caucae* from Colombia; Hall and Kelson (1959), external and cranial measurements of a male and female from Costa Rica; Goodwin and Greenhall (1961), forearm measurements (range) of five specimens (two males, three females) and cranial measurements of one female from Trinidad; Husson (1962), external and cranial measurements of eight males and two females from Surinam; Taddei (1975*a*), external measurements (mean, SD, range) of 20 males and 20 females and cranial measurements (mean, SD, range) of 15 males and 15 females from Brazil.

Individual variation.—Taddei (1975*a*) gave CV values for external measurements from 1.28 to 6.04 and for cranial measurements from 1.06 to 2.84.

Secondary sexual variation.—In all of the 15 cranial measurements taken by Taddei (1975*a*), males proved to be significantly larger than females, this was also the case in eight of the 17 external measurements.

Geographic variation.—According to J. A. Allen (1904), specimens from Chiriquí, Panamá, were much larger than those from Trinidad and eastern Venezuela. Specimens from Costa Rica seemed to correspond fairly well with the holotype of *P. h. panamensis* from Chiriquí (G. M. Allen, 1908).

Phyllostomus latifolius Thomas, 1901

Measurements for *Phyllostomus latifolius* have been recorded as follows: Thomas (1901*b*), forearm and cranial measurements of the male holotype and external measurements of a second male from Guyana; Husson (1962), external and cranial measurements of six paratypes (four males, two females) from Guyana; Marinkelle and Cadena (1972), forearm and cranial measurements (means) of five females from Colombia.

Tonatia bidens (Spix, 1823)

Measurements for *Tonatia bidens* have been recorded as follows: Dobson (1878*a*), external measurements of one specimen from Brazil; Lima (1926), external measurements of a specimen from Brazil; Sanborn (1936), external measurements (range) of three males and cranial measurements of two males from Brazil; Cunha Vieira (1942), external and cranial measurements of a female from Brazil; Goodwin (1942*b*), external and cranial measurements (range) of one male and five females from the Amazon basin, one male from Venezuela, and two males and six females from Costa Rica; Goodwin (1946); forearm and cranial measurements of a male and female from Costa Rica; Koopman and Williams (1951), cranial measurements of the holotype and paratype of *Tonatia bidens saurophila* from Jamaica and of one specimen of *T. b. bidens* from Costa Rica and another from Guyana; Goodwin (1953), one cranial measurement of the holotype of *T. b. saurophila* from Jamaica; Hall and Kelson (1959), forearm and cranial measurements of a male and female from Costa Rica; Goodwin and Greenhall (1961), forearm and cranial measurements of one male and one female from Trinidad; Hill (1964), forearm measurements of one male and two females and cranial measurements of one female from Guyana; Carter *et al.* (1966), external and cranial measurements of a female from Guatemala; Pirlot (1967), external measurements of one specimen; Gardner *et al.* (1970), forearm and cranial measurements of a female from Costa Rica; Valdez and LaVal (1971), external and cranial measurements of one male and four females (mean, range) from Honduras; Gardner (1976), external and cranial measurements (mean, range) of seven specimens from Perú.

Tonatia brasiliense (Peters, 1866)

Measurements for *Tonatia brasiliense* have been recorded as follows: Peters (1866*b*), external measurements of the holotype from Brazil; Dobson (1878*a*), external measurements of the holotype from Brazil; Cunha Vieira (1942), external measurements based on Peters (1866*b*); Goodwin (1942*b*), external and cranial measurements of one male and one female from Brazil and Peters' measurements of the holotype; Goodwin and Greenhall (1961:236), forearm and cranial measurements of the holotype; Gardner (1976), external and cranial measurements of two males from Perú.

Tonatia carrikeri (J. A. Allen, 1910)

Measurements for *Tonatia carrikeri* have been recorded as follows: J. A. Allen (1910), external measurements for the male holotype and five females and cranial measurements of the holotype from Venezuela; Goodwin (1942*b*), external and cranial measurements of one male and one female from Venezuela; Goodwin (1953), external and cranial measurements of the holotype from Venezuela; Husson (1962), external and cranial measurements of a male from Surinam; Gardner (1976), external and cranial measurements of two females from Perú.

Geographic variation.—Husson (1962) noted that a male from Surinam was smaller than one reported by Goodwin (1942*b*) from Venezuela and that it compared more favorably with a female from Venezuela.

Tonatia minuta Goodwin, 1942

Measurements of *Tonatia minuta* have been recorded as follows: Goodwin (1942*b*), external and cranial measurements of the female holotype of *T. nicaraguae* from Nicaragua, and the male holotype of *T. minuta* and two females from Ecuador; Goodwin (1946), forearm and cranial measurements of the holotype of *T. nicaraguae*; Goodwin (1953), external and cranial measurements of the holotype of *T. minuta* and *T. nicaraguae*; Hall and Kelson (1959), forearm and cranial measurements of the holotype of *T. nicaraguae* and one female; Goodwin and Greenhall (1961), forearm and cranial measurements of a male, female, and juvenile from Trinidad and the holotype of *T. minuta*; Davis and Carter (1962*a*), external and cranial measurements of a male and the female holotype of *T. nicaraguae* from Nicaragua; Davis *et al.* (1964), external and cranial measurements of one female from Panamá; LaVal (1969), external and cranial measurements of one male and the mean of two females from Honduras; Gardner *et al.* (1970), forearm and cranial measurements of five males (mean, range) from Costa Rica; Jones *et al.* (1971*b*), external and cranial measurements of two males from Nicaragua; Ojasti and Naranjo (1974), external and cranial measurements of one male from Venezuela.

Geographic variation.—LaVal (1969) noted that the three specimens (one male, two females) he measured from Honduras were notably larger in some measurements (forearm, third metacarpal, length of skull) than those reported by Davis and Carter (1962*a*) and Davis *et al.* (1964). According to Gardner *et al.* (1970), specimens from Costa Rica were smaller than those reported from Honduras by LaVal (1969) but similar in size to those reported by Davis and Carter (1962*a*) and Davis *et al.* (1964) from Nicaragua and Panamá. Jones *et al.* (1971*b*) concluded that their specimens from Nicaragua resembled material reported from Nicaragua by LaVal (1969) and averaged larger than other published measurements (Goodwin, 1942*b*; Davis and Carter, 1962*a*; Davis *et al.*, 1964; Gardner *et al.*, 1970). A male collected in Venezuela was, according to Ojasti and Naranjo (1974), slightly larger than the average size reported from Eucador (Goodwin 1942*b*), Honduras (LaVal, 1969), Costa Rica (Gardner *et al.*, 1970), and Nicaragua (Jones *et al.*, 1971*b*).

Tonatia silvicola (D'Orbigny, 1836)

Measurements of *Tonatia silvicola* have been recorded as follows: Peters (1865*b*), external measurements of a specimen from Brazil; Dobson (1878*a*), external measurements of one specimen from Brazil; Elliot (1904), external and cranial measurements of one specimen; Thomas (1910), external and cranial measurements of the holotype of *T. s. laephotis*; Cabrera (1917), external measurements of a male and a female (*T. amblyotis*) from Ecuador; Sanborn (1936), external and cranial measurements (range) of specimens from Ecuador; Sanborn (1941), forearm and cranial measurements of one female from Perú, one specimen from British Honduras, four specimens from Bolivia, and the range of measurements of a series from Ecuador; Cunha Vieira (1942), external and cranial measurements of a male from Brazil; Goodwin (1942*a*), forearm and cranial measurements (range) of the species *T. amblyotis* (= *T. silvicola*); Goodwin (1942*b*), external and cranial measurements (range) of *T. amblyotis* from Bolivia, Ecuador, Colombia, and Panamá and cranial measurements of one specimen from British Honduras, and for *T. laephotis*, external measurements of one male and one female from the lower Amazon, and range of cranial measurements of 16 specimens from Brazil; Goodwin (1946), external and cranial measurements (range) of the species; Goodwin (1953), external and cranial measurements of the holotype of *Chrotopterus columbianus* (= *T. silvicola*) from Colombia; Husson (1962), external and cranial measurements of one male and two

females from Surinam; Hill (1964), forearm measurements of two males and females and cranial measurements of one female from Guyana; Jones (1964), external and cranial measurements of a male from Campeche; Carter *et al.* (1966), external and cranial measurements of a female from Guatemala; Villa-R. (1967), external and cranial measurements (range) of *T. s. silvicola* from México; Villa-R. and Villa Cornejo (1969), external measurements of one specimen from Argentina; Jones *et al.* (1973), forearm and cranial measurements of a male from Campeche.

Geographic variation.—According to Carter *et al.* (1966), measurements of a female from Guatemala approximated those given by Goodwin (1942*b*) for South American specimens but were slightly larger than those for a British Honduran specimen examined by Goodwin. Sanborn (1941) noted that forearm and total length of skull of a specimen from British Honduras were small for the species.

Tonatia venezuelae (Robinson and Lyon, 1901)

Measurements of *Tonatia venezuelae* have been recorded as follows: Robinson and Lyon (1901), external measurements for the male holotype and two additional males from Venezuela and cranial measurements of the holotype; Sanborn (1941), forearm measurements (range) in the original series; Goodwin (1942*b*), external and cranial measurements of a male and female from Venezuela (including cranial measurements of the holotype from Venezuela); Goodwin and Greenhall (1961:236), forearm and cranial measurements of a paratype; Ojasti and Naranjo (1974), external and cranial measurements of one specimen from Venezuela.

Trachops cirrhosus (Spix, 1823)

Measurements of *Trachops cirrhosus* have been recorded as follows: Saussure (1860*c*), external measurements of one specimen of *Tylostoma mexicana* (= *T. cirrhosus*); Peters (1865*c*), external measurements of a specimen from Brazil; Dobson (1878*a*), external measurements of one female from Bermuda; Elliot (1904), external measurements of one specimen; Goldman (1925), external and cranial measurements of the female holotype of *T. cirrhosus coffini* from Guatemala; Lima (1926), external measurements of a male from Brazil; Cunha Vieira (1942), external measurements of three males and three females and cranial measurements of two females from Brazil; Goodwin (1942*a*), external and cranial measurements of two females from Honduras and the holotype of *T. c. coffini* from Guatemala; Goodwin (1946), forearm and cranial measurements of one male from Colombia; Herskovitz (1949), external and cranial measurements (range) of 20 specimens (eight males, nine females, three unsexed) from northern Colombia; Felten (1956*a*), external and cranial measurements of a male from El Salvador; Felten (1956*b*), forearm and cranial measurements of the female holotype and two paratypes (a male and female) of *T. c. ehrhardti* from Brazil, and range of these measurements in two other subspecies, *coffini* (Guatemala, Honduras, El Salvador) and *cirrhosus* (Colombia); Burt and Stirton (1961), forearm and cranial measurements (range) of five males and 17 females from El Salvador; Goodwin and Greenhall (1961), forearm measurements (range) of two males and one female and cranial measurements of one male and one female from Trinidad; Davis and Carter (1962*a*), forearm and cranial measurements of a female from Costa Rica; Husson (1962), external and cranial measurements of one male from Surinam; Villa-R. (1967), external and cranial measurements of five specimens from México; Starrett and Casebeer (1968), forearm and cranial measurements of two females and means and ranges of four males from Costa Rica; Goodwin (1969), forearm and cranial measurements of four males and two females from Oaxaca.

Geographic variation.—Husson (1962), comparing external measurements of one male from Surinam with 20 specimens from Colombia (Hershkovitz, 1949), concluded that the Surinam specimen was large. The skull measurements, however, did not differ markedly.

Davis and Carter (1962*a*) found measurements of their one female from Costa Rica within the range of variation reported in this species from Colombia (Hershkovitz, 1949). These authors also concluded that other published measurements (Goldman, 1925; Felten, 1956*a*) fell within the range of the Colombian series (Hershkovitz, 1949).

Vampyrum spectrum (Linnaeus, 1758)

Measurements of *Vampyrum spectrum* have been recorded as follows: Dobson (1878*a*), external measurements of one specimen; Flower and Lydekker (1891), forearm length for the species; Elliot (1904), external and cranial measurements of a specimen; Goldman (1917) and Goodwin (1942*a*), external and cranial measurements of the male holotype of *V. s. nelsoni* from Veracruz; Sanborn (1941), external and cranial measurements of one female from Trinidad; Cunha Vieira (1942), external measurements from Dobson (1878*a*); Goodwin (1946), external and cranial measurements of one male from Nicaragua and of the holotype of *V. s. nelsoni*; Hall and Kelson (1959), forearm and cranial measurements of the holotype of *V. s. nelsoni*; Goodwin and Greenhall (1961), forearm measurements (one male, one female) and cranial measurements (one male) from Trinidad; Husson (1962), external and cranial measurements of three males, two females, and two unsexed specimens from Surinam, one male and one female from Cayenne, and one male from Guyana; Casebeer *et al.* (1963), external and cranial measurements of a male from Costa Rica; Hall and Dalquest (1963), external and cranial measurements of the holotype from Veracruz; Goodwin (1969), forearm and cranial measurements for two males, one from Veracruz the other from Nicaragua; Peterson and Kirmse (1969), external and cranial measurements of a female from Panamá; Gardner *et al.* (1970), external and cranial measurements of one female from Costa Rica.

Geographic variation.—Casebeer *et al.* (1963) stated that their measurements corresponded closely with those given by Goldman (1917) for the male holotype of *V. spectrum nelsoni* from Veracruz and were slightly smaller than measurements of specimens from Trinidad (Goodwin and Greenhall, 1961). Peterson and Kirmse (1969), comparing their female specimens from Panamá with those reported by Husson (1962) from the Guianas, found their specimen actually larger in most measurements than the mean of specimens from near the type locality (Surinam).

Subfamily Glossophaginae

Anoura brevirostrum Carter, 1968

Measurements of *Anoura brevirostrum* have been recorded as follows: Carter (1968), external and cranial measurements of the female holotype from Perú and (mean and range) of five specimens (one male, four females) from Perú; Gardner (1976), external and cranial measurements of a male from Perú.

Anoura caudifer (É. Geoffry St.-Hilaire, 1818)

Measurements of *Anoura caudifer* have been recorded as follows: Saussure (1860*c*), external measurements of one specimen of *A. ecaudata* (= *A. caudifer*); Peters (1869), external measurements of the holotype of *Anoura wiedii* from Brazil; Dobson (1878*a*), external measurements of one specimen; Lönnberg (1921), external and cranial measurements of a male from Ecuador in the original description of *A. c. aequatoris*; Lima (1926), external measurements of a specimen of *Lonchoglossa ecaudata* (*A. caudifer*) from Brazil; Sanborn (1933), forearm and cranial measurements (range) of 11 specimens from Brazil; Sanborn (1938), external measurements of two specimens and cranial measurements of one specimen from Venezuela; Sanborn (1941), forearm measurements (range) of two males from Venezuela and one male and four females from Brazil combined, and the forearm measurement of one male from Perú; Cunha Vieira (1942), external measurements of five

males and two females and cranial measurements of two males and two females from Brazil; Hershkovitz (1949), external and cranial measurements (range) of four males and one female combined, and these measurements for one young adult from Colombia; Husson (1962), external and cranial measurements of a female from Surinam; Tamsitt and Valdivieso (1966*b*), external measurements of a male and female, cranial measurements of a male from Colombia, and mean, SD, SE, and range in measurements of specimens from Andean and Amazonian populations; Taddei (1975*b*), external measurements of 40 males and 40 females and cranial measurements of 15 males and 15 females (mean, SE, range) from Brazil.

Individual variation.—In specimens from Brazil, coefficients of variation for external measurements varied in 40 males from 2.64 to 5.88 and in 40 females from 2.09 to 7.44; for cranial measurements in 15 males, CV values were from 1.37 to 4.27 and in 15 females from 1.22 to 3.17 (Taddei, 1975*b*).

Secondary sexual variation.—In material from Brazil, 17 external measurements showed no secondary sexual differences. However, in three (breadth across canines, zygomatic breadth, mastoid breadth) of 15 cranial measurements, males proved to be significantly larger than females (Taddei, 1975*b*).

Geographic variation.—Tamsitt and Valdivieso (1966*b*) found specimens from an Andean population to be generally larger in external measurements than those from an Amazonian population—forearm measurements proved to be significantly different. Cranial measurements were similar between the two populations and no geographic trend was obvious.

Anoura cultrata Handley, 1960

Measurements of *Anoura cultrata* have been recorded as follows: Handley (1960), external and cranial measurements of the female holotype from Panamá; Carter *et al.* (1966), external and cranial measurements of a male from Costa Rica; Carter (1968), external and cranial measurements (mean, range) of 15 specimens from Panamá and Costa Rica; Gardner *et al.* (1970), forearm and cranial measurements (mean, range) of five specimens (four males, one female) from Costa Rica; LaVal (1977), forearm length and weight of a specimen from Costa Rica.

Anoura geoffroyi Gray, 1838

Measurements of *Anoura geoffroyi* have been recorded as follows: Peters (1868), external measurements of the holotype of *A. g. lasiopyga* from México; Dobson (1878*a*), external measurements of the holotype of *Lonchoglossa wiedii* from Brazil, external measurements of the holotype of *A. geoffroyi*, and those of an immature specimen; Elliot (1904), external and cranial measurements of one specimen; Anthony (1921), external and cranial measurements of the female holotype of *A. g. antricola* from Ecuador; Lima (1926), external measurements of a male from Brazil; Sanborn (1933), external and cranial measurements (range) of specimens from Veracruz, Tlaxcala, Jalisco, and El Salvador; Goodwin (1934), external measurements of one specimen from Guatemala; Sanborn (1936), forearm and cranial measurements (range) of 11 males and two females from Guatemala; Cunha Vieira (1942), external measurements of a male and three females and cranial measurements of a male from Brazil; Goodwin (1942*a*), external and cranial measurements of one specimen; Goodwin (1953), external and cranial measurements of the female holotype of *A. g. antricola* and the holotype of *Glossophaga apolinari* from Colombia; Sanborn (1954), forearm measurements of one male and one female from Venezuela; Felten (1956*a*), external measurements of five males and eight females (mean and range), and cranial measurements of two males and one female from El Salvador; Anderson (1957), external and cranial measurements (mean, SD, range) of 58 males and 42 females from

Chiapas and of one specimen from Costa Rica; Baker (1960), external and cranial measurements of one male from Durango; Burt and Stirton (1961), forearm and cranial measurements of a specimen from El Salvador; Goodwin and Greenhall (1961), forearm measurements (range) of 15 males and cranial measurements of one male from Trinidad; Husson (1962), external and cranial measurements of six males from Surinam and one male from Cayenne; Valdivieso (1964), external measurements of a specimen from Colombia; Tamsitt and Valdivieso (1966*a*), forearm and cranial measurements of one female from Colombia; Villa-R. (1967), external measurements of 29 males and 10 females and cranial measurements of 28 males and 10 females (mean, SD, range) from México; Goodwin (1969), forearm and cranial measurements of three males and four females from Oaxaca; Spenrath and LaVal (1970), cranial measurements of two males from San Luis Potosí and of seven males (mean, range) from Chiapas; Matson and Patten (1975), forearm measurements of seven males (mean, range) and two females, and cranial measurements of five males (mean, range) and two females from Zacatecas.

Secondary sexual variation.—Anderson (1957) found no significant differences in both external and cranial measurements between 58 males and 42 females from Chiapas.

Geographic variation.—Anderson (1957) found a significant difference in forearm length and length of skull between specimens from South America and Chiapas.

Anoura werckleae Starrett, 1969

Starrett (1969) recorded external and cranial measurements of the male holotype and one female paratype from Costa Rica.

Choeroniscus godmani (Thomas, 1903)

Measurements of *Choeroniscus godmani* have been recorded as follows: Thomas (1903*a*), external and cranial measurements of the male holotype from Guatemala; Elliot (1904), external and cranial measurements of one specimen; Goodwin (1942*a*), external and cranial measurements of the holotype from Guatemala and a male from Honduras; Goodwin (1946), external and cranial measurements of one male and female from Costa Rica; Sanborn (1954), forearm and cranial measurements (range) of three males from Honduras, and two males, two females, and one unsexed specimen from Costa Rica combined; Hall and Kelson (1959), external and cranial measurements of one male and two females from Costa Rica; Burt and Stirton (1961), forearm and cranial measurements of one male and female from El Salvador; Gardner (1962*b*), external and cranial measurements of a female from Nayarit; Carter *et al.* (1966), external and cranial measurements of one female from Veracruz and one from Guatemala; Villa-R. (1967), external and cranial measurements of one female from Oaxaca; Goodwin (1969), forearm and cranial measurements of two males (subadult) and one female from Oaxaca; LaVal (1969), forearm and cranial measurements (mean, range) of six males and six females from scattered localities in México and Central America; Gardner *et al.* (1970), forearm and cranial measurements of one male and three females from Costa Rica.

Secondary sexual variation.—LaVal (1969), in a comparison of six males and six females from scattered localities in México and Central America, found females to be generally larger than males. He found no overlap in greatest skull length between the sexes. The rostrum was larger relative to the braincase in skulls from females.

Gardner *et al.* (1970) also noted in a collection of four specimens from Costa Rica, that the skull of the one male was considerably shorter than those of the three females from Costa Rica.

Sanborn (1954) stated, contrary to the above, that there is no great difference in size between the sexes.

Choeroniscus inca (Thomas, 1912)

Measurements of *Choeroniscus inca* have been recorded as follows: Thomas (1912*b*), external and cranial measurements of the male holotype from Perú; Sanborn (1954), forearm and cranial measurements of the holotype (after Thomas), external measurements of one male and two females, and cranial measurements of one male and three females from Venezuela.

Choeroniscus intermedius (J. A. Allen and Chapman, 1893)

Measurements of *Choeroniscus intermedius* have been recorded as follows: J. A. Allen and Chapman (1893), external measurements of the female holotype and two males from Trinidad; Goodwin (1953), forearm and cranial measurements of the female holotype from Trinidad; Sanborn (1954), forearm and cranial measurements of the holotype as given by Goodwin (1953), forearm measurement of the holotype as in the original description, and forearm length of an additional male from Trinidad; Goodwin and Greenhall (1961), external and cranial measurements of the female holotype, a male, and a female from Trinidad; Genoways *et al.* (1973), external and cranial measurements (mean, SE, range) of 10 males and 26 females from Trinidad.

Individual variation.—Coefficients of variation in external measurements ranged from 2.5 (total length for males) to 25.4 (length of tail vertebrae of females). CV values in cranial measurements ranged from 1.9 (mastoid breadth for females) to 6.9 (postorbital constriction for males). Females showed higher coefficients of variation than males in external measurements and lower values than males in cranial measurements (Genoways *et al.*, 1973).

Secondary sexual variation.—Females proved to be significantly larger than males in five (greatest length of skull, condylobasal length, mastoid breadth, breadth of braincase, length of maxillary toothrow) of 12 measurements tested. In two of the other seven measurements, males averaged larger than females and in one they were equal (Genoways *et al.*, 1973).

Choeroniscus minor (Peters, 1868)

Measurements of *Choeroniscus minor* have been recorded as follows: Peters (1868), external measurements of the male holotype from Surinam; Dobson (1878*a*), external measurements of one specimen from Surinam; J. A. Allen and Chapman (1893), external measurements as given by Dobson (1878*a*); Elliot (1904), external measurements of one specimen; Lima (1926), external measurements of a male from Brazil; Cunha Vieira (1942), external and cranial measurements of a female from Brazil; Sanborn (1954), forearm measurements of three specimens from Perú; Husson (1962), external and cranial measurements of the male holotype from Surinam; Valdivieso (1964), external and cranial measurements of one female from Colombia.

Choeroniscus periosus Handley, 1966

Handley (1966*a*) recorded external and cranial measurements of the female holotype from Colombia.

Choeronycteris mexicana Tschudi, 1844

Measurements of *Choeronycteris mexicana* have been recorded as follows: Peters (1868), external measurements of one specimen from México; Dobson (1878*a*), external measurements of a single specimen; J. A. Allen and Chapman (1893), external measurements as given by Dobson (1878*a*); Elliot (1904), external measurements of one specimen; Goodwin (1934, 1942*a*, 1946), external measurements of a specimen from Guatemala;

Dalquest (1953*a*), external and cranial measurements (mean) of four males from San Luis Potosí; Baker (1956), external and cranial measurements (mean, range) of three males and 10 females from Coahuila; Hall and Kelson (1959), external and cranial measurements of a male and female from Morelos; Schaldach and McLaughlin (1960), external and cranial measurements of two males and six females from Arizona, one female from Sonora, and four males and a female from Oaxaca (mean, range); Axtell (1962), external measurements of a male, female, and juvenile, and cranial measurements of the two adults from Coahuila; Baker and Greer (1962), external and cranial measurements (mean, range) of six males from Durango; Davis *et al.* (1964), external and cranial measurements of one female from Honduras; Villa-R. (1967), external measurements (mean, range) of seven males and females combined and cranial measurements (mean, range) of six males and females combined from México; Barbour and Davis (1969), range of forearm length of the species; Goodwin (1969), forearm and cranial measurements of three males from Oaxaca; Anderson (1972), external measurements of a specimen from Arizona and cranial measurements of one from Sinaloa; Findley *et al.* (1975), external measurements (mean, range) of 12 females from New Mexico.

Glossophaga alticola Davis, 1944

Measurements of *Glossophaga alticola* have been recorded as follows: Davis (1944), external and cranial measurements of the male holotype and a female from Tlaxcala; Davis and Russell (1952), external and cranial measurements (mean, range) of seven males and six females from Morelos; Gardner (1962*a*), a graphic representation (mean, SE, range) of variation in forearm and cranial measurements in the species; Villa-R. (1963), comparison of external and cranial measurements as in the original description of *Glossophaga morenoi, G. alticola,* and *G. commissarisi* and external measurements of 19 males and 18 females and cranial measurements of 19 males and 19 females of *G. morenoi* (mixed sample of *G. alticola* and *G. commissarisi*) from México; Villa-R. (1967), external measurements (19 males, 18 females) and cranial measurements (19 males, 19 females) of *G. morenoi* (mixed sample of *G. alticola* and *G. commissarisi* from México); Goodwin (1969), forearm and cranial measurements of five females and one subadult male from Oaxaca.

Glossophaga commissarisi Gardner, 1962

Measurements of *Glossophaga commissarisi* have been recorded as follows: Gardner (1962*a*), external and cranial measurements of the male holotype from Chiapas and a graphic representation (mean, SE, range) of variation in forearm and cranial measurements in the species; Villa-R. (1963), comparison of external and cranial measurements as in the original description of *Glossophaga morenoi, G. alticola,* and *G. commissarisi,* external measurements of 19 males and 18 females and cranial measurements of 19 males and 19 females of *G. morenoi* (mixed sample of *G. alticola* and *G. commissarisi*) from México; Villa-R. (1967), external measurements (18 males, 19 females) and cranial measurements (19 males, 19 females) of *G. morenoi* (mixed sample of *G. alticola* and *G. commissarisi*); Goodwin (1969), forearm and cranial measurements of a male, female, and three unsexed specimens from Oaxaca; Jones *et al.* (1972), forearm and cranial measurements of three females from Sinaloa.

Glossophaga longirostris Miller, 1898

Measurements of *Glossophaga longirostris* have been recorded as follows: Miller (1898), external and cranial measurements of the female holotype from Colombia; Robinson and Lyon (1901), external measurements and greatest length of skull for nine males and four females from Venezuela; G. M. Allen (1908), external measurements (range) of ten specimens from Carriacou, Lesser Antilles; Miller (1913*a*), external and cranial measure-

ments of the male holotype of *G. l. rostrata* from Grenada, Lesser Antilles; Miller (1913*b*), external and cranial measurements of nine males and one female from Venezuela, one male and one unsexed specimen from Colombia, nine males from Grenada, three males, two females, and three unsexed specimens from Carriacou, and ten males and ten females from Curaçao; Elliot (1917), external and cranial measurements of the holotype of *G. l. rostrum*; Hershkovitz (1949), external and cranial measurements (range) of five males and two females combined from Colombia; Husson (1960), forearm measurements (range) of 21 males and 42 females and cranial measurements (range) in 12 specimens from Aruba, Curaçao, and Bonaire islands; Goodwin and Greenhall (1961), forearm measurements of 10 females and cranial measurements of four females from Tobago, forearm measurements of 14 females and cranial measurements of 10 females from Trinidad; Tamsitt and Valdivieso (1963*a*) and Valdivieso (1964), external and cranial measurements of a male and two females from Girardot, Colombia; Smith and Genoways (1974), forearm and cranial measurements of specimens from Curaçao (20 from Miller, 1913*b*), Margarita Island (9), Venezuela (22), Trinidad (5), Grenada (9), and St. Vincent (10).

Geographic variation.—Smith and Genoways (1974) stated that a comparison of measurements obtained from specimens from Margarita Island with those of the mainland and Antillean islands showed that the material from Margarita Island is well within the range of variation of the mainland specimens and overlap those obtained from Antillean material.

Glossophaga soricina (Pallas, 1766)

Measurements of *Glossophaga soricina* have been recorded as follows: Dobson (1878*a*), external measurements of a female; H. Allen (1895), external measurements of the holotype of *Glossophaga truei*; Robinson and Lyon (1901), external measurements and greatest length of skull of one male and three females from Venezuela; Rehn (1902*a*), external and cranial measurements of the female holotype of *G. s. antillarum* from Jamaica and one specimen each from Guyana, Trinidad, and the Bahamas; Cabrera (1903), external measurements for the species in Chile; Elliot (1904), external measurements of one specimen from Tres Marias Islands and external and cranial measurements of two additional specimens; G. M. Allen (1908), forearm measurements of three specimens from Perú; G. M. Allen (1911), forearm and cranial measurements of a specimen from Jamaica; Miller (1913*b*), external and cranial measurements of nine individuals (eight females, one male) from Brazil, one female from Guyana, seven (five females, one male, one unsexed) from Venezuela, 10 (five females, five males) from Trinidad, five (two females, two males, one unsexed) from Colombia, eight (three females, five males) from Moyobamba, Perú, 11 (seven females, four males) from Paraguay, 20 specimens (nine females, 11 males) from the mainland of México, two (one female, one male) from Nicaragua, one male from Costa Rica, five (three females, two males) from Chiriquí, Panamá, 10 (five males, five females) from Panamá, 12 (six females, six males) from Tres Marias Islands, 14 (five females, nine males) from Balsas, Perú, three (two females, one male) from Charapex, Perú, and two females from Jamaica; Elliot (1917), external and cranial measurements (range) of specimens from Nayarit to Panamá; Lima (1926), external measurements of a male from Brazil; Goodwin (1934), external measurements (mean) of five specimens from Guatemala; Martinez and Villa-R. (1938), external measurements of one specimen and cranial measurements of four specimens of *G. morenoi* (= *G. soricina*) from Morelos; Martinez and Villa-R. (1941), external and cranial measurements (mean, variance, and correlation between measurements) of 52 males and 25 females from Guerrero; Cunha Vieira (1942), external measurements of nine males and one of unknown sex and cranial measurements of three males from Brazil; Goodwin (1942*a*), external and cranial measurements of two specimens from Honduras; Goodwin (1946), external and cranial measurements of two males from Costa Rica; Hershkovitz (1949), external and cranial measurements of three females from Colombia; Dalquest (1951), forearm and cranial measurements of one

specimen (sex unknown) from Trinidad; Davis and Russell (1952), external and cranial measurements (mean, range) of seven males and 12 females from Morelos (*G. s. leachi*); Dalquest (1953*a*), external measurements (means) of seven males and 15 females and cranial measurements (means) of nine males and seven females from San Luis Potosí; Villa-R. (1953), external and cranial measurements (mean, range) of specimens from Tlaxcala (1), Districto Federal (15), Morelos (12), and Guerrero (5); de la Torre (1954), external and cranial measurements of one female from Tamaulipas; de la Torre (1955), forearm measurements (mean, range) of nine specimens (six males, three females combined) from Guerrero; Felten (1956*a*), external measurements (mean, range) of 286 males and 200 females and cranial measurements of 27 males and 38 females from El Salvador; Ryan (1960), external measurements of two females from Guatemala; Burt and Stirton (1961), forearm and cranial measurements (range) of 43 males and 32 females from El Salvador; Goodwin and Greenhall (1961), forearm measurements (range) of 20 specimens and cranial measurements of three females from Trinidad; Husson (1962), external and cranial measurements of five males and five females from Surinam; Gardner (1962*a*), graphic representation (mean, range, SE) of variation in forearm and cranial measurements of the species; Tamsitt and Valdivieso (1963*a*), external measurements (mean, range) of 51 specimens from Colombia; Tamsitt and Valdivieso (1963*b*), external measurements of one male and one female from Colombia; Villa-R. (1963), comparison of external and cranial measurements as in the original description of *Glossophaga morenoi*, *G. alticola*, and *G. commissarisi*; Starrett and de la Torre (1964), forearm measurements of two males and 14 females (mean, range) from El Salvador, Honduras, Nicaragua, and Costa Rica; Valdivieso (1964), external measurements (mean, range) of 77 specimens from Colombia; Aellen (1965), external and cranial measurements of one male and one female from Perú; Villa-R. (1967), external measurements (mean, SE, range) of 70 males and 37 females and cranial measurements of 56 males and 25 females from México; Pirlot (1968), forearm measurements of a female from Perú; Goodwin (1969), forearm and cranial measurements of a female from Perú; Goodwin (1969), forearm and cranial measurements of two females, one subadult male, and three unsexed individuals from Oaxaca; Anderson (1972), external measurements of two specimens and cranial measurements of one from Chihuahua; Jones *et al.* (1972), forearm and cranial measurements (mean, range) of nine males and one female combined from Sinaloa; Taddei (1975*b*), external measurements (mean, SE, range) of 59 males and 47 females and cranial measurements of 20 males and 20 females from Brazil.

Individual variation.—In specimens from Brazil, coefficients of variation for external measurements varied in 59 males from 2.00 to 5.60 and in 47 females from 2.10 to 5.26; and for cranial measurements in 20 males, CVs ranged from 1.75 to 3.44 and in 20 females from 1.65 to 3.37 (Taddei, 1975*b*).

Secondary sexual variation.—Taddei (1975*b*) found females to be significantly larger than males in four (head and body length, forearm length, fourth and fifth metacarpal) of 17 external measurements. In the case of cranial measurements, females were significantly larger in two measurements (length of molar, mandibular toothrow) of 15 but significantly smaller in five (breadth across canines, zygomatic breadth, braincase breadth, mastoid breadth, cranial depth).

Hylonycteris underwoodi Thomas, 1903

Measurements of *Hylonycteris underwoodi* have been recorded as follows: Thomas (1903*a*), forearm and cranial measurements of the holotype and external measurements of a second specimen from Costa Rica; Elliot (1904), external and cranial measurements of one specimen; Goodwin (1942*a*, 1946), forearm and cranial measurements of the holotype from Costa Rica; Hall and Kelson (1959), forearm and cranial measurements of the holotype; Davis and Carter (1962*a*), external and cranial measurements of the holotype and two additional specimens (sex unknown) from Costa Rica, one male and four females

from Veracruz, and one male and one female from Oaxaca; Jones (1964), forearm and cranial measurements of one male and one female from Oaxaca; Villa-R. (1967), external and cranial measurements of one specimen from Tabasco; Goodwin (1969), forearm and cranial measurements of two males and two females from Oaxaca; Gardner *et al.* (1970), forearm and cranial measurements (mean, range) of 14 males and seven females from Costa Rica; Phillips and Jones (1971), forearm and cranial measurements (mean, range) of four males and six females combined, additional measurements of the female holotype of *H. u. minor* from Jalisco, comparative measurements of a Veracruz male, and a male and female from Oaxaca; Jones and Homan (1974), external and cranial measurements as given by Gardner *et al.* (1970) and Phillips and Jones (1971).

Secondary sexual variation.—Females averaged larger than males throughout the range of the species according to Phillips and Jones (1971).

Geographic variation.—Davis and Carter (1962*a*) noted that specimens from Oaxaca appeared to be smaller than those from Veracruz and Costa Rica. However, Jones (1964) found his Oaxacan male specimen to be larger than those previously reported and the measurements of his female specimens fell among the largest known individuals of the species.

Specimens from Jalisco and southern Oaxaca (Davis and Carter, 1962*a*) were included in a subspecies by Phillips and Jones (1971). They concluded that these specimens were smaller externally and cranially than *H. u. underwoodi* from northern Oaxaca, Veracruz, and Guatemala.

Leptonycteris curasoae Miller, 1900

Measurements of *Leptonycteris curasoae* have been recorded as follows: Miller (1900*b*), external and cranial measurements of the male holotype from Curaçao; Hoffmeister (1957), external measurements of the holotype and three male topotypes; Husson (1960), forearm measurements (range) of 21 specimens and cranial measurements (range) of 13 specimens from Aruba, Curaçao, and Bonaire islands; Davis and Carter (1962*b*), external and cranial measurements of four males and two females combined (mean, range); Pirlot (1965*a*), external and cranial measurements of the male holotype of *L. c. tarlosti*, a male, and three females from Margarita Island; Marinkelle and Cadena (1972), external and cranial measurements of two females from Colombia; Smith and Genoways (1974), forearm and cranial measurements of 12 specimens from Margarita Island, two from Aruba, five from Curaçao, and one from Bonaire.

Geographic variation.—In his study of this genus, Hoffmeister (1957) considered *L. curasoae* to be a subspecies of *L. nivalis*. However, Davis and Carter (1962*b*) in their review of the genus and subsequent authors have consider *L. curasoae* a distinct species. Pirlot (1965*a*) recognized specimens from Margarita Island as a distinct subspecies, however, Smith and Genoways (1974), after examining specimens from throughout the range of the species, considered the subspecific status of the island forms unwarranted.

Leptonycteris nivalis (Saussure, 1860)

Measurements of *Leptonycteris nivalis* have been recorded as follows: Saussure (1860*c*), external measurements of one specimen; Dobson (1878*a*), external measurements of one specimen; Miller (1900*b*), external and cranial measurements of a male from Colima; Elliot (1904), external and cranial measurements of one specimen; Martinez and Villa-R. (1938), external measurements of one specimen; Martinez and Villa-R. (1940), external and cranial measurements (mean, SD) of samples of males and females from Guerrero; Goodwin (1942*a*, 1946), external and cranial measurements of a male from Colima; Dalquest (1953*a*), external and cranial measurements of four males and one female from San Luis Potosí; de la Torre (1955), forearm measurements of one male from

Guerrero; Baker (1956), external and cranial measurements of two males and mean and range of five females from Coahuila; Hoffmeister (1957), cranial measurements of the holotype of *L. n. nivalis* (Veracruz), external and cranial measurements (mean) of six males and eight females combined from Texas, and external measurements (mean) of 11 males and 29 females combined from Nuevo Leon; Stains (1957), external and cranial measurements of the holotype and mean and range of the holotype and 22 topotypes of *L. n. longala* from Coahuila (see also Jones, 1958); Hall and Kelson (1959), external and cranial measurements (range) of a large series of specimens from Jalisco; Davis and Carter (1962*b*), external and cranial measurements of three males and seven females (mean, range); Alvarez (1963), external and cranial measurements of five males and five females combined (mean, range) from Tamaulipas; Baker and Cockrum (1966), external and cranial measurements of two females from Sinaloa; Villa-R. (1967), external measurements of 50 specimens (mean, SD, range) and cranial measurements of 37 (mean, SD, range) from México; Goodwin (1969), external and cranial measurements of two males and two females from Morelos, and one female from Veracruz; Barbour and Davis (1969), range of forearm length in the species; Anderson (1972), external and cranial measurements of one specimen; Matson and Patten (1975), forearm measurements (mean, range) of seven males from Zacatecas.

Individual variation.—In specimens from Guerrero, coefficients of variation for external measurements varied in males from 3.03 to 16.25 and in females from 1.04 to 16.58; CV values for cranial measurements in males ranged from 1.68 to 7.44 and in females from 1.23 to 5.58 (Martinez and Villa-R., 1940).

Geographic variation.—Hoffmeister (1957) and Davis and Carter (1962*b*) have recently reviewed this genus. Davis and Carter (1962*b*) gave characteristics by which the currently recognized species can be distinguished.

Leptonycteris sanborni Hoffmeister, 1957

Measurements of *Leptonycteris sanborni* have been recorded as follows: Hoffmeister (1957), external measurements of 22 females and cranial measurements of 21 females from Arizona, external measurements (mean) of 10 males from Chihuahua, and the mean of eight males from Colima; Davis and Carter (1962*b*), external and cranial measurements (mean, range) of five males and five females; Baker and Cockrum (1966), external and cranial measurements of one specimen from Sinaloa; Villa-R. (1967), external measurements ($N=51$) and cranial measurements ($N=39$) (mean, SD, range) of *L. yerbabuenae* (= *L. sanborni*) from México; Genoways and Jones (1968), forearm measurements (mean) of 28 males from Zacatecas; Barbour and Davis (1969), range of forearm length of the species; Anderson (1972), external measurements (mean, SD, range) of 24 specimens from Chihuahua and external and cranial measurements of one specimen from Sonora; Ramirez-Pulido and Alvarez (1972), external and cranial measurements of a lectotype and external measurements of a male and female paralectotype of *L. yerbabuenae*; Jones and Bleier (1974), forearm and cranial measurements of one male from El Salvador; Matson and Patten (1975), forearm and cranial measurements of five males (mean, range) and one female from Zacatecas.

Geographic variation.—The species was originally described as a subspecies of *L. nivalis* by Hoffmeister (1957). Davis and Carter (1962*b*) demonstrated characteristics by which this taxon could be distinguished from *L. nivalis*. Considerable controversy exists in the literature over the relationships of this taxon and *L. yerbabuenae*. Because the holotype of *yerbabuenae* has been lost and because the original series was a composite, Watkins *et al.* (1972) considered *yerbabuenae* to be a *nomen dubium*. However, as recently as Ramirez-Pulido and Alvarez (1972), authors have believed that the name *yerbabuenae* superceded *sanborni*. The reader is warned to take great care in using measurements recorded in the earlier literature concerning this genus because considerable confusion has existed in the proper identification of the species.

Lichonycteris degener Miller, 1931

Miller (1931) gave external and cranial measurements of the female holotype from Brazil.

Lichonycteris obscura Thomas, 1895

Measurements of *Lichonycteris obscura* have been recorded as follows: Thomas (1895), external and cranial measurements of the female holotype from Nicaragua; Elliot (1904), external and cranial measurements of one specimen from Nicaragua; Sanborn (1936), external and cranial measurements of a female from Costa Rica and the holotype from Nicaragua; Goodwin (1942, 1946), external and cranial measurements of two females from Costa Rica; Hall and Kelson (1959), external and cranial measurements of two females from Costa Rica; Husson (1962), external and cranial measurements of a male from Costa Rica; Davis *et al.* (1964), external and cranial measurements of a female from Nicaragua; Carter *et al.* (1966), external and cranial measurements of three females from Guatemala; Gardner *et al.* (1970), external and cranial measurements (mean, range) of one male and three females from Costa Rica; Jones *et al.* (1971*b*), external and cranial measurements of three males from Nicaragua; Marinkelle and Cadena (1972), forearm measurements (range) of three females and one unsexed specimen from Colombia; Gardner (1976), external and cranial measurements of two females from Perú.

Lionycteris spurrelli Thomas, 1913

Measurements of *Lionycteris spurrelli* have been recorded as follows: Thomas (1913), external and cranial measurements of the immature male holotype from Colombia; Goldman (1914*b*), greatest length of skull of a specimen from Colombia; Sanborn (1941), external measurements of one male and one female and cranial measurements of one specimen from Guyana, and the measurements for the holotype from Colombia.

Lonchophylla concava Goldman, 1914

Measurements of *Lonchophylla concava* have been recorded as follows: Goldman (1914*a*), external and cranial measurements of the male holotype from Panamá; Elliot (1917), external and cranial measurements of the holotype; Goodwin (1946), external and cranial measurements of the holotype from Panamá; Hall and Kelson (1959), external and cranial measurements of the holotype of *L. concava*; Davis *et al.* (1964), external and cranial measurements of one male and two females from Costa Rica; Pirlot (1968), forearm measurements of one male from Perú; Gardner *et al.* (1970), external and cranial measurements (mean, range) of five specimens from Costa Rica; Marinkelle and Cadena (1972), forearm measurements of two females from Colombia.

Lonchophylla hesperia G. M. Allen, 1908

Measurements of *Lonchophylla hesperia* have been recorded as follows: G. M. Allen (1908), external and cranial measurements of the male holotype and two additional specimens from Perú; Gardner (1976), external and cranial measurements of one male and one female from Perú.

Lonchophylla mordax Thomas, 1903

Measurements of *Lonchophylla mordax* have been recorded as follows: Thomas (1903*c*), external and cranial measurements of the male holotype from Brazil; G. M. Allen (1908), external and cranial measurements of the holotype from Brazil; Lima (1926), external measurements of a specimen from Brazil; Sanborn (1941), forearm measurements (range) of 18 males from Brazil; Cunha Vieira (1942), external measurements of a male and a female and cranial measurements of a male from Brazil; Baker (1974), external and cranial measurements of one female from Ecuador.

Lonchophylla robusta Miller, 1912

Measurements of *Lonchyphylla robusta* have been recorded as follows: Miller (1912) and Goodwin (1946), external and cranial measurements of the male holotype and a female from Panamá; Hall and Kelson (1959), external and cranial measurements of the holotype and a female topotype; Walton (1963), external and cranial measurements (mean, SD, SE, range) of specimens from Panamá ($N=27$) and Costa Rica ($N=10$); Valdivieso (1964), external and cranial measurements of one female from Colombia; Tuttle (1970), external measurements of one male and one female and cranial measurements of the female from Perú; Gardner (1976), external and cranial measurements of a male from Perú.

Secondary sexual variation.—According to Walton (1963), no sexual dimorphism in size was evident in specimens from Panamá and Costa Rica.

Geographic variation.—Walton (1963) found specimens from Panamá to be larger than those from Costa Rica. Of seven external measurements, three (total length, length of hind foot, ear length) proved to be significantly different, whereas in nine cranial measurements there were four (skull length, skull width, interorbital width, width of rostrum at canines) that showed significant differences.

Lonchophylla thomasi J. A. Allen, 1904

Measurements for *Lonchophylla thomasi* have been recorded as follows: J. A. Allen (1904), external and cranial measurements of the male holotype from Venezuela; Goodwin (1953), forearm and cranial measurements of the holotype; Husson (1962), external and cranial measurements of two males and one female from Surinam; Hill (1964), forearm and cranial measurements of a male from Guyana; Gardner (1976), external and cranial measurements (mean, range) of six males and six females combined from Perú.

Monophyllus plethodon Miller, 1900

Measurements of *Monophyllus plethodon* have been recorded as follows: Miller (1900*a*), external and cranial measurements of the male holotype of *M. plethodon* from Barbados, Lesser Antilles; Miller (1902*a*), external and cranial measurements of the male holotype of *M. p. luciae* from St. Lucia, Lesser Antilles, and of the holotype of *M. p. plethodon*; Elliot (1904), external and cranial measurements of a specimen from Barbados and one from St. Lucia; Anthony (1917), cranial measurements of the holotype and two additional specimens (sub-Recent fossils) of *M. frater* from Puerto Rico; Anthony (1918, 1925), cranial measurements of three specimens of sub-Recent fossils from Puerto Rico; Goodwin (1953), a cranial measurement of the holotype of *M. p. frater* (subfossil) from Puerto Rico; Hall and Kelson (1959), external and cranial measurements of the holotype of *M. plethodon*, *M. luciae*, and cranial measurements of the holotype and two topotypes of *M. frater*; Schwartz and Jones (1967), external and cranial measurements of specimens from Angulla, Barbuda, Antigua, Dominica, St. Lucia, and Barbados; Choate and Birney (1968), cranial measurements of six males and nine females from Dominica and of one sub-Recent fossil from Puerto Rico; Koopman (1968), forearm and cranial measurements of one male from Dominica, a specimen from Antigua, and one female from Anguilla; Homan and Jones (1975*b*), external and cranial measurements (range) of Lesser Antillean representatives of the species (after Schwartz and Jones, 1967).

Geographic variation.—Schwartz and Jones (1967) have recently reviewed geographic variation in *Monophyllus plethodon*. They recognized three subspecies occurring on Puerto Rico and the Lesser Antilles. One subspecies was known only as a fossil from Puerto Rico. Specimens of *M. plethodon* on Barbados were distinguished from all other Lesser Antillean populations by overall small size.

Monophyllus redmani Leach, 1821

Measurements of *Monophyllus redmani* have been recorded as follows: Gundlach (1872, 1877), external measurements of a Cuban specimen; Dobson (1878*a*), external measurements of one male; Miller (1900*a*), external and cranial measurements of the male holotype of *M. portoricensis* from Puerto Rico, the male holotype of *M. clinedaphus* from an unknown locality, and a male from Jamaica, as well as external measurements of one male and three females from Puerto Rico; Miller (1902*a*), external and cranial measurements of the male holotype of *M. cubanus* from Cuba and cranial measurements of one male from Jamaica; Elliot (1904), external and cranial measurements of one specimen each from Puerto Rico, Cuba, and Jamaica; Miller (1904), external measurements of eight males and seven females from Cuba; Anthony (1917), cranial measurements of a specimen from Puerto Rico; Anthony (1918, 1925), external (18 specimens) and cranial (five specimens) measurements (mean, range) of individuals from Puerto Rico; Hall and Kelson (1959), external and cranial measurements of a male from Jamaica, the holotype of *M. cubanus*, and of the holotype of *M. clinedaphus*, as well as cranial measurements of the holotype of *M. portoricensis* and the range in external measurements of five specimens from Puerto Rico; Schwartz and Jones (1967), external and cranial measurements of the three recognized subspecies from Jamaica, Cuba, Hispaniola, and Puerto Rico; Choate and Birney (1968), cranial measurements of one fossil specimen from Puerto Rico; Silva-Taboada (1974), measurements of fossil humeri, crania, and mandibles from Cuba; Buden (1975*a*), external and cranial measurements (mean, range) of specimens from Jamaica, Cuba, Hispaniola, Bahamas, and Puerto Rico; Homan and Jones (1975*a*), external and cranial measurements (range) of specimens of the three recognized subspecies (after Schwartz and Jones, 1967; Buden, 1975*a*).

Geographic variation.—Schwartz and Jones (1967) have recently reviewed geographic variation in *Monophyllus redmani*. They recognized three subspecies, all occurring in the Greater Antilles. Specimens from Jamaica were characterized by large body and cranial size but a relatively short forearm. On Cuba and Hispaniola, bats were characterized by small body, moderate skull size, and relatively long forearms. Specimens of *M. redmani* from Puerto Rico are of generally small size.

Musonycteris harrisoni Schaldach and McLaughlin, 1960

Measurements of *Musonycteris harrisoni* have been recorded as follows: Schaldach and McLaughlin (1960), external and cranial measurements of the male holotype, 10 male paratypes, and two female paratypes from Colima; Villa-R. (1967), external measurements of nine specimens (mean, range), and cranial measurements (mean, range) of six specimens from Colima; Goodwin (1969), forearm and cranial measurements of one male from Guerrero and a male and female from Colima.

Platalina genovensium Thomas, 1928

Measurements of *Platalina genovensium* have been recorded as follows: Thomas (1928*a*), external and cranial measurements of the male holotype from Perú; Sanborn (1936), external and cranial measurements of the male holotype and a second male from Perú; Sanborn (1943), forearm measurements (range) for the species from Perú; Aellen (1965), external and cranial measurements of a male in addition to the holotype (Thomas, 1928*a*), and one male (Sanborn, 1936) from Perú.

Scleronycteris ega Thomas, 1912

Thomas (1912*b*) gave external and cranial measurements of the female holotype from Ega, Brazil.

Subfamily Carolliinae

Carollia brevicauda (Schinz, 1821)

Measurements of *Carollia brevicauda* have been recorded as follows: Peters (1865*d*), external measurements of one specimen; Dobson (1878*a*), external measurements of one specimen; H. Allen (1890*b*), external measurements of three males and six females; Robinson and Lyon (1901), external measurements of two males from Venezuela; Goodwin (1942*a*), external and cranial measurements of one male and one female from Honduras (originally reported as *C. castanea*); Dalquest (1953*a*), external measurements of one male and six females (mean) and cranial measurements (mean) of six males and five females from San Luis Potosí (originally reported as *perspicillata*); Jones (1966), forearm and cranial measurements (range) of 12 specimens from Guatemala (another specimen representing *C. subrufa* is included in ranges); Goodwin (1969), external and cranial measurements of a male and a female from Chiltepec, Oaxaca (these were originally listed as *C. subrufa*, but according to Pine, 1972, these two specimens are probably *C. brevicauda*); Pine (1972), external measurements (mean, range) of four males and 10 females from San Luis Potosí, 11 males and 17 females from Veracruz, seven males and 23 females from Chiapas, 15 males and 10 females from Guatemala, one male and one female from Honduras, 20 males and 26 females from Panamá, nine males and seven females from Ecuador, eight females from Brazil, four females from Perú, one male from Bolivia, and cranial measurements (mean, range) of five males and nine females from San Luis Potosí, 11 males and 15 females from Veracruz, seven males and 23 females from Chiapas, 15 males and 10 females from Guatemala, one male and one female from Honduras, 20 males and 26 females from Panamá, nine males and seven females from Ecuador, eight females from Brazil, five males and eight females from Perú, and one male from Bolivia; Jones *et al.* (1973), external and cranial measurements (mean, range) of 20 specimens from the Yucatan Peninsula.

Geographic variation.—According to Pine (1972), specimens from the northernmost part of the geographic range of the species in México are the largest.

Carollia castanea H. Allen, 1890

Measurements of *Carollia castanea* have been recorded as follows: H. Allen (1890*b*), external measurements of the young male holotype from Costa Rica; Elliot (1904), external measurements of the holotype as given by H. Allen (1890*b*) from Costa Rica; Hahn (1907), external and cranial measurements of the holotype from Costa Rica; Goodwin (1946), forearm and cranial measurements of the holotype and a second male from Costa Rica; Hershkovitz (1949), external and cranial measurements of one male and one female from Colombia; Husson (1962), external and cranial measurements of two females from Surinam; Pirlot (1968), external and cranial measurements discussed in conjunction with *C. perspicillata*; Pine (1972), external measurements of 10 males and four females from Honduras, five males from Nicaragua, seven males and eight females from Costa Rica, 31 males and 20 females from Panamá, five males from Colombia, three males and two females from Perú, one female from Bolivia, and cranial measurements of 10 males and four females from Honduras, five males from Nicaragua, seven males and eight females from Costa Rica, 31 males and 19 females from Panamá, four females from Colombia, seven males and four females from Perú, and one female from Bolivia.

Geographic variation.—Pine (1972) could detect no geographic trends in variation in this species; therefore, he considered *C. castanea* to be monotypic.

Carollia perspicillata (Linnaeus, 1758)

Measurements of *Carollia perspicillata* have been recorded as follows: Saussure (1860*c*), external measurements of one specimen; Peters (1866*a*), external measurements of one specimen; Miller (1902*a*), external and cranial measurements of the female holotype of *C.*

tricolor from Paraguay; Elliot (1904), external and cranial measurements of a single specimen; Hahn (1907), external measurements (mean) of nine specimens from Paraguay, 10 from Brazil, 10 from Trinidad, two from Guyana, 10 from northern Ecuador, nine from Colon, Panamá, six from Panamá, Panamá, nine from Nicaragua, 13 from Veracruz, 11 from Oaxaca, two from Campeche, and 13 from Veracruz (Jaltipan), and cranial measurements (mean) of eight specimens from Paraguay, two from São Paulo, Brazil, five from Naranhoa, Brazil, five from Trinidad, two from Guyana, four from Venezuela, nine from Colombia, 10 from Ecuador, eight from Oaxaca, six from Veracruz, two from Costa Rica, two from Campeche, three from Colón, Panamá, six from Boqueron, Panamá, and six from Panamá, Panamá; Lima (1926), external measurements of a specimen from Brazil; Sanborn (1932), forearm measurement of one specimen from Bolivia; Goodwin (1934), external measurements of one specimen from Guatemala; Cunha Vieira (1942), external measurements of nine males and four females and cranial measurements of three males and one female from Brazil; Goodwin (1942*a*), external and cranial measurements of two males from Honduras; Goodwin (1946), external and cranial measurements of a male and female from Costa Rica; Hershkovitz (1949), forearm measurements (range) in 79 specimens from northern Colombia and the mean of the greatest length of skull in this sample (some specimens in this sample are *brevicauda*, see Pine, 1972); Dalquest (1951), forearm and cranial measurements (mean) of 27 specimens of both sexes combined from Trinidad; Felten (1956*a*), external measurements (mean, range) of 15 males and 28 females and cranial measurements of 10 males and 19 females from El Salvador; Felten (1956*d*), external measurements (mean, range) of specimens from El Salvador; Ryan (1960), external measurements of one male from Guatemala; Goodwin and Greenhall (1961), forearm measurements (range) of 30 specimens and cranial measurements of one male and one female from Trinidad; Husson (1962), external and cranial measurements of five males and five females from Surinam; Burt and Stirton (1961), forearm and cranial measurements (range) of 22 males and 14 females combined from El Salvador; Pirlot (1963), external measurements of specimens from Venezuela; Butterworth and Starrett (1964), cranial measurements of a male and female from Venezuela; Starrett and de la Torre (1964), external and cranial measurements of one male from Nicaragua and two males and a female from Costa Rica; Tamsitt and Valdivieso (1963*a*), external measurements (mean, range) of 28 specimens and cranial measurements of 11 from Colombia; Tamsitt and Valdivieso (1963*b*), external measurements (mean, range) of four males from Colombia; Valdivieso (1964), external and cranial measurements (mean, range) of 19 specimens from Colombia; Brosset (1965), external and cranial measurements of three males from Ecuador; Jones (1966), forearm and cranial measurements (range) of specimens from Guatemala; Pirlot (1965*b*), external measurements of 14 males and 10 females from Est du Venezuela and 19 males and 15 females from Zulia, Venezuela; Pirlot (1968), external and cranial measurements discussed in conjunction with *C. castanea*; Goodwin (1969), forearm and cranial measurements of nine males and three females from Oaxaca; Pine (1972), external and cranial measurements (mean, range) of males and females throughout the range of the species; Pirlot (1972), external measurements of a specimen from Brazil; Jones *et al.* (1973), external and cranial measurements (mean, range) of 10 specimens from the Yucatan Peninsula; Smith and Genoways (1974), forearm measurements of two specimens from Margarita Island, Venezuela; Taddei (1975*b*), external measurements (mean, SE, range) of 30 males and 30 females, and cranial measurements of 15 males and 15 females from Brazil.

Individual variation.—In specimens from Brazil, coefficients of variation for external measurements varied in 30 males from 2.70 to 6.15 and in 30 females from 2.70 to 5.94; CV values for cranial measurements in 15 males ranged from 1.78 to 4.01 and in 15 females from 1.85 to 4.11 (Taddei, 1975*b*). According to Tamsitt and Valdivieso (1963*a*), specimens from central Colombia were homogeneous in size.

Secondary sexual variation.—In specimens from Brazil, females generally averaged larger than males in external measurements and in four (head and body, ear, forearm, metacarpal

II) of 17 measurements they proved to be significantly so. Cranial measurements showed the opposite in one of 15 measurements (mastoid breadth), males proved to be significantly larger than females (Taddei, 1975*b*). Pine (1972) also found cranial measurements of males to average slightly larger than those of females. However, Tamsitt and Valdivieso (1963*a*) reported that their males and females were of the same size in a sample of 16 males and 12 females from Colombia.

Geographic variation.—Tamsitt and Valdivieso (1963*a*) found individuals from localities on each side of the East Andes not to differ in any way. Their specimens, although slightly smaller, did not differ significantly from the range of measurements given by Hershkovitz (1949) for northern Colombian specimens. According to Pine (1972), specimens from in and around the Panamá drainage are characteristically small. Dalquest (1951), comparing forearm length and cranial measurements of his specimens from Trinidad with examples from San Luis Potosí, concluded that they are alike (however, the material from San Luis Potosí was probably *C. brevicauda*).

Carollia subrufa (Hahn, 1905)

Measurements of *Carollia subrufa* have been recorded as follows: Hahn (1905), external and cranial measurements of the male holotype from Oaxaca; Hahn (1907), external measurements of eight specimens from Oaxaca, seven from Colima, four from Campeche, and one from Honduras, and cranial measurements of nine specimens from Oaxaca, four from Colima, two from Campeche, and one from Honduras; Elliot (1917), external and cranial measurements of the holotype; Goodwin (1934), external measurements of one specimen from Guatemala; Goodwin (1942*a*), external and cranial measurements of two males from Honduras; Felten (1956*a*), external measurements (mean, range) of 99 males and 99 females and cranial measurements of 27 males and 33 females from El Salvador (as a subspecies of *C. castanea*); Felten (1956*d*), external measurements (mean, range) of specimens from El Salvador; Hall and Kelson (1959), external measurements (range) of 198 (99 males, 99 females) specimens from El Salvador listed as *C. castanea*; Ryan (1960), external measurements of one female from Guatemala; Burt and Stirton (1961), external and cranial measurements of four males from El Salvador (as a subspecies of *castanea*); Starrett and de la Torre (1964), external and cranial measurements of two males from El Salvador; Jones (1966), forearm and cranial measurements of one male from Jocotán, Guatemala (others listed are *C. brevicauda*); Villa-R. (1967), external measurements (mean, SE, range) of 51 males and females combined and cranial measurements (mean, SE, range) of 38 males and females combined; Goodwin (1969), forearm and cranial measurements of six males and one female from Oaxaca, (also lists a male and a female from Chiltepec, but, according to Pine, 1972, these are probably *C. brevicauda*); Pine (1972), external measurements of one male from Colima, two males and eight females from Oaxaca, 16 males from Chiapas, one male and one female from Honduras, two males and seven females from Nicaragua, and cranial measurements of two males and five females from Colima, two males and eight females from Oaxaca, 16 males and 24 females from Chiapas, one male and one female from Honduras, and two males and seven females from Nicaragua; Watkins *et al.* (1972), external and cranial measurements of one female from Jalisco.

Geographic variation.—Pine (1972) found specimens from the northern part of the geographic range of the species to be larger than those of the southernmost part of the geographic range.

Rhinophylla alethina Handley, 1966

Handley (1966*a*) gave external measurements (mean, range) of six males and four females, and cranial measurements of the male holotype from Colombia.

Rhinophylla fischerae Carter, 1966

Measurements of *Rhinophylla fischerae* have been recorded as follows: Carter (1966), external and cranial measurements of the female holotype from Perú, six additional females and two males, all from the type locality except one female from Pucallpa, Perú; Marinkelle and Cadena (1972), external measurements of a male and female from Colombia; Mumford (1975), external and cranial measurements of an unsexed specimen from Ecuador.

Rhinophylla pumilio Peters, 1865

Measurements of *Rhinophylla pumilio* have been recorded as follows: Peters (1865*a*), external measurements of the holotype from Brazil; Dobson (1878*a*), external measurements of one specimen from Brazil; Sanborn (1936), external and cranial measurements of a male and female from Ecuador; Husson (1962), external and cranial measurements of two females from Surinam and two from Guyana; Hill (1964), forearm measurements of two males and cranial measurements of one of these from Guyana; Carter (1966), external measurements of 15 males and 10 females combined, and cranial measurements (mean, range) of 15 males and 13 females combined from Venezuela, Brazil, Ecuador, and Perú; Marinkelle and Cadena (1972), forearm and cranial measurements of a male (juvenile) and the range of three females from Colombia.

SUBFAMILY STENODERMINAE

Ametrida centurio Gray, 1847

Measurements of *Ametrida centurio* have been recorded as follows: Peters (1866*a*), external measurements of one specimen; Dobson (1878*a*), external measurements of the female holotype from Brazil; H. Allen (1894*b*), external and cranial measurements of the male holotype of *A. minor* from Surinam (type locality according to Peterson, 1965) and external measurements of a specimen of *A. centurio*; Sanborn (1938), external and cranial measurements of a male (female according to Peterson, 1965*b*) from Brazil; Husson (1960), cranial measurements of one specimen from Bonaire; Goodwin and Greenhall (1961), forearm and cranial measurements of a male from Guyana, a female from Venezuela, and a subadult from Trinidad; Husson (1962), external and cranial measurements of two males and two females (see Peterson, 1965*b*:3-4, on the question of the sex of one of these specimens) from Surinam and one male from Bonaire; Peterson (1965), forearm and cranial measurements of 12 males from Brazil, Guyana, Surinam, Venezuela, Trinidad, and Bonaire (including the holotype of *A. minor* from Surinam), 13 females from Brazil, Guyana, Venezuela, Trinidad, and Surinam (including the holotype of *A. centurio* from Brazil), and external measurements (mean, range) of males and females.

Secondary sexual variation.—Peterson (1965*b*) described distinct differences in size between the sexes with no overlap in forearm length or the following cranial measurements: condylobasal length; least interorbital width; breadth of palate (M1-M1); toothrow length (C-M3).

Ardops nichollsi (Thomas, 1891)

Measurements of *Ardops nichollsi* have been recorded as follows: Thomas (1891*a*), external and cranial measurements of the female holotype of *A. n. nichollsi* from Dominica; Thomas (1894), external and cranial measurements of the male holotype of *A. n. montserratensis* from Montserrat; Elliot (1904), external and cranial measurements of one specimen from Monsterrat, one from Dominica, and one from St. Lucia; Miller (1902*a*), external and cranial measurements of the female holotype of *A. n. luciae* from St. Lucia and of a male from Dominica; Miller (1913*a*), external and cranial measurements of the female

holotype of *A. n. annectens* and a male from Guadeloupe; Elliot (1917), external and cranial measurements of the holotype of *A. n. annectens*; G. M. Allen (1942), forearm length of taxa described at that time; Hall and Kelson (1959), external and cranial measurements of the holotypes of *A. n. monsterratensis*, *A. n. annectens*, and *A. n. luciae*; Jones and Schwartz (1967), forearm and cranial measurements of the female holotype of *A. n. nichollsi*, external measurements (mean, range) of six males and seven females, cranial measurements (mean, range) of eight males and seven females from Dominica, external and cranial measurements of a male and a female from St. Eustatius, and the male holotype of *A. n. monserratensis* from Montserrat, and the female holotype of *A. n. luciae*, cranial measurements of a female, forearm measurements of one male and four females from St. Lucia, external measurements of an adult male and the female holotype of *A. n. annectens*, cranial measurements of the holotype, two males, and two females, forearm measurements of four females from Guadeloupe, external measurements of the female holotype (*A. n. koopmani*), another female, and two males, and cranial measurements of the female holotype and a male from Martinique; Jones and Genoways (1973), some measurements as given by Jones and Schwartz (1967).

Secondary sexual variation.—In individuals from Dominica, females were clearly larger than males. This was also found to be true in one male and one female from Martinique (Jones and Schwartz, 1967).

Geographic variation.—According to Jones and Schwartz (1967), specimens from Dominica were the smallest of the species, whereas those from St. Eustatius and Montserrat were the largest. Specimens from Martinique differed from those on adjacent islands, Dominica to the north and St. Lucia to the south, in being considerably larger.

Ariteus flavescens (Gray, 1831)

Measurements of *Ariteus flavescens* have been recorded as follows: Peters (1876), external measurements of a specimen of *Peltorhinus achradophilus* (= *A. flavescens*); Dobson (1878*a*), external measurements of the female holotype of *Ariteus achradophilus* from Jamaica; Elliot (1904), external and cranial measurements of one specimen from Jamaica; G. M. Allen (1942), external measurements for the species; Howe (1974), external measurements of two males and two females from Jamaica.

Artibeus aztecus Andersen, 1906

Measurements of *Artibeus aztecus* have been recorded as follows: Andersen (1906*b*), external measurements of the male holotype of *A. aztecus* from Morelos; Andersen (1908), external and cranial measurements (range) of four specimens from Morelos; Elliot (1917), cranial measurements of the holotype; Dalquest (1953*a*), external measurements of a male and two females and cranial measurements of the male and one female from San Luis Potosí; Lukins and Davis (1957), forearm and cranial measurement (range) for the species; Villa-R. (1967), external and cranial measurements of one female from the state of México; Koopman (1961), forearm and cranial measurements (range) of four specimens (one male, three females) from Sinaloa; Baker and Greer (1962), external and cranial measurements of a female from Durango; Alvarez (1963), external and cranial measurements of three males and one female from Tamaulipas; Jones (1964), forearm and cranial measurements (mean, range) of 15 specimens (10 males and five females) from Sinaloa; Davis (1969), external and cranial measurements (mean, range) of 33 specimens from the Mexican highlands, 41 from the Guatemalan highlands, and 18 from the Costa Rican highlands, and external and cranial measurements of the male holotype of *A. aztecus aztecus* from Morelos, the male holotype of *A. a. minor* from Guatemala, and the male holotype of *A. a. major* from Costa Rica; Goodwin (1969), forearm and cranial measurements of four males and five females from Oaxaca; Alvarez and Ramirez-Pulido (1972), external and cranial measurements of two

males from Michoacán, and a female from Oaxaca; Jones *et al.* (1972), forearm and cranial measurements as given by Jones (1964).

Geographic variation.—*Artibeus aztecus*, which occurs in the Middle American highlands, was segregated into three recognizable populations—*aztecus* in the Mexican highlands, *minor* from the Guatemalan highlands, and *major* of the Costa Rican highlands. With regard to size, *A. a. major* is the largest, and *minor* is the smallest (Davis, 1969).

Artibeus cinereus (Gervais, 1855)

Measurements of *Artibeus cinereus* have been recorded as follows: Peters (1865*a*), external measurements of the holotype of *A. quadrivittatum* from Surinam; Dobson (1878*a*), external measurements of a male and a female; Robinson and Lyon (1901), external measurements of three males and six females from Venezuela; Andersen (1906*b*), cranial measurements (range) of eight specimens including the male holotype (Colombia) of *A. cinereus bogotensis* from Colombia and Venezuela and seven additional specimens of *A. c. cinereus*; Andersen (1908), external measurements (mean, range) of 10 specimens and cranial measurements (mean, range) of eight from Guyana, Trinidad, and Venezuela, external and cranial measurements (mean, range) of eight specimens from Colombia and Venezuela and the range of these measurements in three specimens of *A. quadrivittatus* from Surinam; Lima (1926), external measurements of a male from Brazil; Sanborn (1932), forearm measurements of a female and a specimen of unknown sex and cranial measurements of the female from Bolivia; Cunha Vieira (1942), external measurements of two females from Venezuela and external measurements of a male from Ecuador; Hershkovitz (1949), external and cranial measurements of a female from Colombia; Goodwin and Greenhall (1961), forearm and cranial measurements of three males and one female from Trinidad; Burt and Stirton (1961), forearm and cranial measurements (range) of four males and 14 females from El Salvador; Husson (1962), external and cranial measurements of three males, four females, and the unsexed holotype of *A. quadrivittatus* from Surinam; Tamsitt and Valdivieso (1963*a*), external measurements of four females from Colombia; Brosset (1965), external and cranial measurements of a male from Ecuador; Tamsitt and Valdivieso (1966*a*), forearm and cranial measurements of a male and female from Colombia (values for the female as given by Hershkovitz, 1949); Davis (1970*b*), external and cranial measurements (mean, range) of 36 specimens from Trinidad; Tuttle (1970), forearm measurements (range) of specimens from east of the Andes in Perú; Pirlot (1972), external measurements of two males and one female from Brazil (type description of *A. c. solimoesi*).

Artibeus concolor Peters, 1865

Measurements of *Artibeus concolor* have been recorded as follows: Peters (1865*a*), external measurements of the holotype from Surinam; Thomas (1892), forearm and cranial measurements of the holotype; Andersen (1908), external and cranial measurements of a female from Surinam and cranial measurements of the holotype from Surinam; Cabrera (1917), external and cranial measurements of a female possibly from Brazil; Cunha Vieira (1942), external measurements based on Andersen (1908); Husson (1962), external and cranial measurements of a female as given by Andersen (1908) and measurements of the holotype as given by Peters and Thomas; Hill (1964), forearm and cranial measurements of one male from Guyana; Linares (1969), external measurements of a male and two females from Venezuela; Gardner (1976), external and cranial measurements of a male from Perú.

Artibeus glaucus Thomas, 1893

Measurements of *Artibeus glaucus* have been recorded as follows: Thomas (1893), external and cranial measurements of the female holotype from Perú; Andersen (1908), external and cranial measurements of the holotype from Perú; Davis (1970*a*), cranial measurements (mean, range) of nine specimens from Perú and Ecuador.

Artibeus hirsutus Andersen, 1906

Measurements of *Artibeus hirsutus* have been recorded as follows: Andersen (1906*b*), forearm and cranial measurements (range) of eight specimens from Michoacán, Colima, and Jalisco; Andersen (1908), external and cranial measurements (mean, range) of eight specimens from Michoacán, Colima, and Jalisco; Elliot (1917), cranial measurements of the holotype; Davis and Russell (1952), external and cranial measurements of one male and five females (mean, range) from Morelos; Anderson (1960), external and cranial measurements (mean, range) of 28 specimens from Guerrero; Davis and Carter (1964), external and cranial measurements (mean, range) of six females; Villa-R. (1967), external measurements (mean, SD, range) of 55 specimens and cranial measurements of 46 specimens from Sonora, Sinaloa, Nayarit, Jalisco, Morelos, and Guerrero; Genoways and Jones (1968), forearm measurements (mean, range) of four young males and four females from Zacatecas; Goodwin (1969), forearm and cranial measurements of two males from Guerrero and two from Sonora; Anderson (1972), external and cranial measurements of three specimens from Chihuahua; Jones *et al.* (1972), forearm and cranial measurements (mean, range) of 10 specimens (five males and five females) from Sinaloa.

Secondary sexual variation.—Anderson (1960) found no significant size differences between sexes in four external and four cranial measurements in a sample of 28 specimens from Guerrero.

Artibeus inopinatus Davis and Carter, 1964

Davis and Carter (1964) reported external and cranial measurements (mean, range) of eight females from Honduras and forearm measurements of one male from Honduras and one from Nicaragua. Although Davis and Carter did not examine the specimens reported from El Salvador by Burt and Stirton (1961), under the name *Artibeus hirsutus*, they judged, and we agree, from the published measurements that the specimens are referable to *A. inopinatus*.

Artibeus jamaicensis Leach, 1821

Measurements of *Artibeus jamaicensis* have been recorded as follows: Saussure (1860*b*), external measurements of one specimen; Gundlach (1872, 1877), external measurements of a specimen from Cuba; Dobson (1878*a*), external measurements for a male of *A. perspicillatus* from Guatemala and a female; Cope (1889), external measurements of one male cotype of *Dermanura eva* from St. Martin, Lesser Antilles; H. Allen (1894*a*), external measurements from three specimens (two from México, one locality unknown) and cranial measurements (mean) of three specimens from an unspecified locality; J. A. Allen and Chapman (1897*a*), forearm measurements of four specimens from Yucatán, 10 from Jamaica, 31 females and 20 males from Cuba; Rehn (1900), cranial measurements of the two male cotypes of *Dermanura eva* Cope from St. Martin, Lesser Antilles, a specimen from Jamaica, and one from Brazil; Robinson and Lyon (1901), external measurements of a male and two females from Venezuela; Rehn (1902*b*), external measurements of the unsexed holotype of *A. hercules* (= *A. jamaicensis*) and the mean of external measurements for two additional specimens, cranial measurements of a specimen from Perú, external measurements of the male holotype, the mean for six specimens of *A. parvipes* (= *A. jamaicensis*) from Cuba, and one specimen of *A. jamaicensis* from Jamaica, the mean of six specimens and external measurements (mean) of two specimens of *A. planirostris* and cranial measurements of one from Brazil; J. A. Allen (1904), external and cranial measurements of the male holotype of *A. insularis* from St. Kitts, Lesser Antilles, and the male holotype of *A. j. yucatanicus* from Yucatán; Elliot (1904), external and cranial measurements of one specimen each of *A. coryi*, *A. jamaicensis*, *A. j. parvipes*, and *A. j. planirostris*; Miller (1904), external measurements of 12 males and 13 females from Cuba; Elliot (1905*a*), external and cranial measurements of a specimen from St. Kitts Island, Lesser Antilles; Andersen (1906), cranial measurements

(mean) of 65 specimens of *A. j. jamaicensis* and external measurements (range) of three specimens of *A. j. praeceps* from Guadeloupe; G. M. Allen (1908), external measurements of three specimens and cranial measurements of one male from Brazil, and external measurements of one specimen from Jamaica; J. A. Allen (1908*a*), forearm measurements (range) of four specimens from the Dominican Republic; J. A. Allen (1908*b*), external and cranial measurements of the male holotype of *A. j. richardsoni* from Nicaragua; Andersen (1908), external and cranial measurements (range) of 16 specimens (11 cranial) from Brazil, three from Venezuela, and three from Chiapas and Guerrero, median and range of the above combined, 13 specimens (nine cranial) from Trinidad and Tobago, nine (eight cranial) from Grenada, 41 (33 cranial) from Surinam, Cayenne, Guyana, and Lower Orinoco, 25 specimens (12 cranial) from Cuba, 14 (12 cranial) from Yucatán and Cozumel Island, 12 (nine cranial) from Central America, 27 (23 cranial) from southern México, 21 (11 cranial) from Puerto Rico, three from Dominican Republic, one from St. Kitts Island, eight (five cranial) from St. Andrews and Old Providence Island, and 95 (65 cranial) (median, range) of *A. j. jamaicensis* (including much of the above data); Elliot (1917), external and cranial measurements of the holotype; Anthony (1919), cranial measurements of fossil material from Cuba; Anthony (1924*a*), external and cranial measurements of the female holotype of *A. j. fraterculus* from Ecuador, forearm measurements (mean) of 18 specimens and cranial measurements (mean, range) of 13 others; Anthony (1918, 1925), external measurements (mean, range) of 24 specimens and cranial measurements (mean, range) of 10 specimens (five males, five females) from Puerto Rico; Goodwin (1934), external measurements of one specimen from Guatemala; Sanborn (1936), forearm measurements (range) of three males and four females and cranial measurements (range) of three specimens (one male, two females) from Barbados; Martinez and Villa-R. (1938), external measurements of five males and nine females from Morelos; Cunha Vieira (1942), external and cranial measurements of a male from Brazil; Goodwin (1942), forearm and cranial measurements of two males from Honduras, and these measurements of another specimen; Goodwin (1946), external and cranial measurements (range) for the species; Hall and Villa-R. (1949), external and cranial measurements of one female from Michoacán; Hershkovitz (1949), external and cranial measurements of a male and female (two males and a female for forearm) from Colombia; Dalquest (1951), forearm and cranial measurements (mean) of four males and eight females from Trinidad; Dalquest (1953*a*), external measurements (mean) of eight males and eight females and cranial measurements (mean) of two males and 11 females from San Luis Potosí; Goodwin (1953), forearm and cranial measurements of the male holotype of *A. coryi* from St. Andrews Island, the male holotype of *A. insularis* from St. Kitts, the male holotype of *A. j. richardsoni* from Nicaragua, the male holotype of *A. j. yucatanicus* from Yucatán, and the female holotype of *A. j. fraterculus* from Ecuador; de la Torre (1955), forearm measurements (mean, range) of five specimens (three males, two females) from Jalisco; de la Torre (1954), external and cranial measurements (mean, range) of 23 specimens from Tamaulipas; Felten (1956*a*), external measurements (mean, range) of 16 males and five females and cranial measurements of nine males (mean, range) and one female from El Salvador; Felten (1956*d*), external measurements (mean, range) of specimens from El Salvador; Anderson (1960), external and cranial measurements (range) of three specimens from Sinaloa, and four from Jalisco; Husson (1960), cranial measurements (mean, range) of specimens from Curaçao and St. Martin; Burt and Stirton (1961), forearm and cranial measurements (range) of 44 specimens (18 males, 26 females) from El Salvador; Goodwin and Greenhall (1961), forearm measurements (range) of 12 males and 18 females, and cranial measurements of one male and one female from Trinidad; Baker and Greer (1962), external and cranial measurements of a male and female from Durango; Pirlot (1963), forearm measurements (range) of 35 males and 20 females from Venezuela; Tamsitt and Valdivieso (1963*a*), external measurements of one male and three females and cranial measurements of one female from Colombia; Davis and Carter (1964), external and cranial measurements (mean, range) of eight females from Central America; Hill (1964), forearm measurements of two males and three females and cranial

measurements of two males and three females and cranial measurements of two males and two females from Guyana; Valdivieso (1964), external measurements of one male and two females and cranial measurements of one female from Colombia; Starrett and de la Torre (1964), external and cranial measurements of one male from Nicaragua and one from Costa Rica; Handley (1965), external and cranial measurements of the female holotype of *A. j. triomylus* from Guerrero and mean and range of external measurements of 10 males and nine females and cranial measurements of 12 females and 10 males from Guerrero; Pirlot (1965*b*), external measurements of 15 males and 33 females from Est du Venezuela and of 35 males and 20 females from Zulia, Venezuela; Villa-R. (1967), external measurements of 46 specimens and cranial measurements of 43 specimens of *A. j. triomylus* from México, and external measurements of 76 specimens and cranial measurements of 71 specimens of *A. j. yucatanicus* from México; Genoways and Jones (1968), mean and range of forearm measurements of six young specimens (two males, four females) and individual forearm measurements of two young males and one young female from Zacatecas; Koopman (1968), forearm and cranial measurements of the holotype of *A. praeceps* (Guadeloupe) and specimens (range) from Guadeloupe and Dominica; Pirlot (1968), forearm measurements of a female from Perú; Goodwin (1969), forearm and cranial measurements of four males and three females of *A. j. yucatanicus* from Oaxaca and three males and three females of *A. j. triomylus* from Oaxaca; Jones and Phillips (1970), forearm measurements (mean, range) of seven specimens from Barbados, 11 from St. Lucia, 20 from St. Vincent, 23 from Grenada, and 16 from Trinidad, and cranial measurements for 7, 15, 32, 15, and 11 specimens, respectively; Davis (1970*b*), external and cranial measurements of the male holotype of *A. j. richardsoni* from Nicaragua, mean and range of 13 topotypes, means of 14 from Chiapas, 12 from Guatemala (Alta Verapaz), 20 from Guatemala (Puerto Barrios), 20 from Nicaragua (Castillo), 20 from Honduras (coastal), 16 from Costa Rica (coastal), 20 from Panamá (Veraguas), 21 from Panamá (Chepo) of *A. j. richardsoni*, external and cranial measurements of the male holotype of *A. j. yucatanicus* from Yucatán, mean and range of eight topotypes, mean of 18 from Tamaulipas, 25 from San Luis Potosí, 19 from Veracruz, 14 from Campeche and Yucatán, four from British Honduras, 20 from Honduras (Bay Islands) of *A. j. yucatanicus*, forearm and cranial measurements of the female holotype of *A. j. triomylus* from Guerrero, mean and range of 20 from near the type locality, external and cranial measurements of the female holotype of *A. j. paulus* from El Salvador, means of 15 from Chiapas (below 1000 feet), 20 from Guatemala, 20 from El Salvador, 20 from Honduras (Nueva Ocotepeque), six from Honduras (Pacific lowlands), 11 from Nicaragua (San Antonio), and four from Costa Rica (Guanacaste Lowlands) of *A. j. paulus*; Tuttle (1970), cranial measurements of a female from Perú, and range in forearm length of specimens east of the Andes; Jones *et al.* (1972), forearm and cranial measurements (mean, range) of 10 specimens (five males, five females) from Sinaloa; Smith and Genoways (1974), forearm and cranial measurements (mean, range) from four localities in Venezuela (sample sizes five, 22, 17, 22) and eight specimens from Trinidad.

Age variation.—According to Davis (1970*b*), young individuals in which the cartilaginous epiphyses of finger joints were readily discernable were consistantly smaller than adults in all measurements. However, individuals in which the joint of the finger was only swollen and in which the epiphyses and diaphyses appeared to be united were as large as adults in all measurements.

Individual variation.—Within sample variation of cranial measurements was shown by Davis (1970*b*) to be usually less than 10 per cent of the minimum value of each variate tested. Of six cranial measurements tested, length of skull was the least variable and breadth across upper molars the most. Wing measurements varied more than cranial. Of four wing measurements examined, length of forearm was the least variable and length of phalanx 1, digit III the most.

Secondary sexual variation.—Davis (1970*b*) found no significant secondary sexual variation in four wing and eight cranial measurements.

Geographic variation.—Both Koopman (1968) and Jones and Phillips (1970) noted a trend toward slightly larger size in specimens from the southern part of the Lesser Antilles. Jones and Phillips (1970) found *A. jamaicensis* from Grenada to approach those from Trinidad and Tobago in size. They also found that specimens from St. Vincent averaged considerably larger than specimens from any other Antillean population.

Davis (1970*b*), studying geographic variation in Middle American populations of *Artibeus jamaicensis*, recognized four areas of differentiation. The largest individuals occurred along the Atlantic versant of Middle America (northern Chiapas to eastern Panamá). Greatest length of skull in this area averaged near 29 and forearm near 61. The population along the Atlantic versant of México (Tamaulipas to the Yucatan Peninsula and into British Honduras and on the Bay Islands of Honduras) was characterized by small size. More than 90 per cent of the individuals had a skull length of less than 28.45 combined with a zygomatic breadth of less than 17.05. Populations from the Pacific versant were also characterized by small size—those from Oaxaca and Morelos northward into Sinaloa and Durango normally possessed three upper molars and had a zygomatic breadth seldom less than 17.0. Populations from Chiapas southward to Guanacaste, Costa Rica, lacked the upper third molar.

Smith and Genoways (1974) found their material from Margarita Island, Venezuela, averaged slightly smaller in external and cranial measurements than specimens from the adjacent Venezuelan mainland and Trinidad.

Artibeus lituratus (Olfers, 1818)

Measurements of *Artibeus lituratus* have been recorded as follows: J. A. Allen and Chapman (1897*b*), external measurements of the male holotype of *A. l. palmarum* from Trinidad and a female, mean external measurements for five females, and cranial measurements of one female from Trinidad; J. A. Allen (1897), external and cranial measurements of the male holotype of *A. lituratus intermedius* from Costa Rica; Bangs (1899), external and cranial measurements of the male holotype of *Artibeus femurvillosum* from Colombia; Robinson and Lyon (1901), external measurements of five males and 15 females from Venezuela; Rehn (1902*b*), external measurements of the holotype of *A. l. hercules* from Perú, the average of these measurements for two additional specimens and cranial measurements for one; J. A. Allen (1904), external and cranial measurements of the male holotype of *A. rusbyi* from Perú; Elliot (1904), external and cranial measurements of a specimen of *A. lituratus intermedius*; G. M. Allen (1908), external measurements of three specimens and cranial measurements of one from Brazil and forearm measurements of the holotype of *A. l. intermedius* and three additional specimens from Costa Rica; Andersen (1908), external and cranial measurements (mean, range) of 12 specimens (six cranial) from Paraguay, 20 (19 cranial) from Brazil, and nine (eight cranial) from Ecuador and Colombia, means for these measurements for 15 specimens (10 cranial) from Venezuela, four (three cranial) from Trinidad and St. Vincent, 20 (15 cranial) from Central America (Panamá, Costa Rica, Nicaragua, Guatemala), four (three cranial) from México (Veracruz, Jalisco, Oaxaca) and a mean for these measurements from the latter localities, cranial measurements of six specimens of *A. l. aequatorialis* from Ecuador, and external of seven and cranial measurements of six specimens (median, range) of *A. l. aequatorialis* from Ecuador and Colombia; Lima (1926), external measurements of a male and cranial measurements of an unsexed individual from Brazil; Cunha Vieira (1942), external measurements of one male and four females and cranial measurements of three males from Brazil; Goodwin (1942*a*), external and cranial measurements of two females from Honduras; Hershkovitz (1949), external and cranial measurements (range) of specimens from Colombia; Dalquest (1950), cranial measurements (mean) of three males and two females from San Luis Potosí; Dalquest (1951), forearm and cranial measurements (mean) of three males and six females from Trinidad; Dalquest (1953*a*), external measurements of a male and two females (mean) and cranial measurements (mean) of three males and two females from San Luis Potosí; Goodwin (1953), forearm and cranial measurements of the male holotype of *A. lituratus palmarum* from Trinidad, the

male holotype of *A. lituratus intermedius* from Costa Rica, and the male holotype of *A. rusbyi* from Perú; de la Torre (1954), external and cranial measurements of three specimens from Tamaulipas; Felten (1956*c*), external measurements (mean, range) of six males and six females and cranial measurements of five males and five females from El Salvador; Felten (1956*d*), external measurements of specimens from El Salvador; Russell (1956), forearm and cranial measurements of a female from Morelos; Lukens and Davis (1957), forearm and cranial measurements (mean, range) of adult specimens, one juvenile female, and a subadult female from Guerrero; Anderson (1960), external and cranial measurements (mean, range) of 17 specimens from Sinaloa; Goodwin and Greenhall (1961), forearm measurements (range) of 14 males and 18 females and cranial measurements of one male from Trinidad; Tamsitt and Valdivieso (1963*a*), external and cranial measurements (mean, range) of 46 males and 30 females combined from Colombia; Tamsitt and Valdivieso (1963*b*), external measurements of a female from Colombia; Hill (1964), forearm and cranial measurements of a female from Guyana; Starrett and de la Torre (1964), forearm measurements of a male and female from El Salvador and a female from Costa Rica, other external and cranial measurements of a male and female from Costa Rica; Valdivieso (1964), external and cranial measurements (mean, range) of specimens from Colombia; Brosset (1965), external and cranial measurements of five males (including the lectotype of *A. fallax*) and five females from Surinam; Pirlot (1965*b*), external measurements of eight males and eight females from Est du Venezuela; Tamsitt and Valdivieso (1965*a*), forearm measurements (mean, range) of monthly samples of males from Colombia; Tamsitt and Valdivieso (1965*b*), external measurements (mean, SD, SE, range) of 80 adult and 18 young adult females from Colombia; Tamsitt and Valdivieso (1966*b*), external measurements (mean, range) of 14 specimens (four males, 10 females) and cranial measurements of five females from Colombia; Villa-R. (1967), external measurements of 46 specimens and cranial measurements of 34 specimens from México; Koopman (1968), forearm measurements (range) of seven specimens from St. Vincent; Goodwin (1969), forearm and cranial measurements of four males and four females from Oaxaca; Burt and Stirton (1969), forearm and cranial measurements (range) of five specimens from El Salvador; Villa-R. and Villa Cornejo (1969), external and cranial measurements (mean, range) of seven specimens from Argentina; Tuttle (1970), forearm measurements (range) of specimens from east of the Andes in Perú; Jones *et al.* (1972), forearm and cranial measurements (mean, range) of 10 specimens (five males, five females) from Sinaloa; Pirlot (1972), external measurements of specimens from Brazil.

Age variation.—Lukens and Davis (1957) presented forearm and cranial measurements of a juvenile female and a subadult female from Guerrero. Anderson (1960) gave external and cranial measurements of an immature female from Sinaloa.

Secondary sexual variation.—Tamsitt and Valdivieso (1963*a*) found that females from Colombia averaged larger than males in all body measurements and in four of nine cranial measurements. Anderson (1960) found no significant differences in size between males and females from Sinaloa.

Geographic variation.—San Luis Potosí material was found to be comparable in cranial size to topotypes of *A. l. palmarum* from Trinidad (Dalquest, 1950). Specimens from Girardot, Mariquita, and Puente Nacional in the Magdalena River Valley, Colombia, averaged slightly larger in body size than did those from two other localities: Mesitas del Colegio, at a higher elevation on the western slope of the East Andes, and Villavicencio, at the base of the eastern slope of the East Andes (Tamsitt and Valdivieso, 1963*a*).

Artibeus phaeotis (Miller, 1902)

Measurements of *Artibeus phaeotis* have been recorded as follows: Miller (1902*a*), external and cranial measurements of the female holotype from Yucatán; Elliot (1904), external and cranial measurements of a single specimen; Andersen (1906*b*), cranial measurements of the female holotype of *A. turpis* (= *A. phaeotis*) from Tabasco and the female holotype of *A. p.*

nanus from Guerrero; Andersen (1908), external and cranial measurements of the female holotype of *A. phaeotis* from Yucatán, the holotype of *A. jucundus* (= *A. phaeotis*) from Veracruz, the female holotype of *A. turpis* (= *A. phaeotis*) from Tabasco, and mean and range of these measurements in eight specimens from Guerrero, Sinaloa, and Colima; Goodwin (1934), external measurements of a specimen from Guatemala; Goodwin (1942*a*), forearm and cranial measurements of one specimen; Dalquest (1953*b*), forearm and cranial measurements of a male and female from Veracruz; Jones and Lawlor (1965), external and cranial measurements of a male and two females from Cozumel Island, Quintana Roo; Jones (1966), forearm and cranial measurements (mean, range) of five specimens (three males, two females) from El Peten, Guatemala, and for a male and female from Santa Rosa, Guatemala; Villa-R. (1967), external measurements of 28 specimens and cranial measurements of 22 of *A. turpis turpis*, which more or less include *A. p. phaeotis* and *A. p. palatinus* of Davis (1970*a*), external measurements of 38 specimens and cranial measurements of 35 specimens of *A. p. nanus* and two males and three females of *A. cinerus phaeotis* from Veracruz, Oaxaca, and Tabasco; Rick (1968), external measurements of three females and one male, and cranial measurements of three females, one male, and an unsexed specimen from Guatemala; Goodwin (1969), forearm and cranial measurements of four males and nine females from Oaxaca; Davis (1970*a*), cranial measurements (mean, range) of 135 specimens from the Pacific versant of Sinaloa to Guerrero, 19 from Oaxaca to Chiapas, 37 from Guatemala, El Salvador, and Nicaragua, 34 from the Pacific versant of Costa Rica and seven from the Caribbean versant, 124 from the Caribbean versant of Guatemala and British Honduras, 67 from Honduras and Nicaragua, and cranial measurements of the female holotype of *A. phaeotis phaeotis* from Yucatán, the female holotype of *A. p. nanus* from Guerrero, and the male holotype of *A. p. palatinus* from Guatemala; Jones *et al.* (1972), forearm and cranial measurements (mean, range) of five males and five females combined from Sinaloa.

Age variation.—Juveniles (cartilaginous epiphyses and unworn dental cusps) could not be distinguished from adults on the basis of seven cranial measurements (Davis, 1970*a*).

Secondary sexual variation.—Davis (1970*a*) found no significant secondary sexual dimorphism in four external and seven cranial measurements.

Geographic variation.—Davis (1970*a*) noted the following size variation throughout the geographic range of this species. Members of the population in western México (Sinaloa to Guerrero) were generally the smallest for the species. The rostrum in this population was short, which was reflected in the shortness of the palate. In the Pacific lowlands (Oaxaca to Costa Rica), specimens had a longer palate, skull, and forearm; they were, however, smaller than those from the Caribbean-Gulf versant. The population occupying the Caribbean-Gulf versant (Veracruz to South America) was the largest in the species.

Artibeus toltecus (Saussure, 1860)

Measurements of *Artibeus toltecus* have been recorded as follows: Saussure (1860*b*), external measurements of a single specimen; Miller (1902*a*), external and cranial measurements of the male holotype of *A. t. ravus* from Ecuador and a specimen from Morelos; Andersen (1908), external and cranial measurements (range) of three specimens from Costa Rica, Nicaragua, and Guatemala, two (one cranial) from Oaxaca, nine (five cranial) from Jalisco and Durango, and three from Veracruz, external measurements (mean, range) of 18 specimens (cranial of 13) from Costa Rica, Nicaragua, Guatemala, Jalisco, Durango, Oaxaca, and Veracruz, and 11 specimens (mean, range) from Ecuador; Goodwin (1934), external measurements of a specimen from Guatemala; Goodwin (1942*a*), external and cranial measurements of two males from Honduras; Goodwin (1946), external and cranial measurements (range) for the species; Dalquest (1953*a*), external measurements (mean) of two males and cranial measurements (mean) of two males and five females from San Luis Potosí; de la Torre (1954), external and cranial measurements (mean, range) of six specimens

from Tamaulipas; de la Torre (1955), forearm measurements (mean, range) of five males and three females combined from Jalisco; Felten (1956*d*), external measurements of a specimen from El Salvador; Jones *et al.* (1962), forearm and total length of skull (range) of 12 specimens from México (Oaxaca 6, Tamaulipas 3, Jalisco 2, Sinaloa 1); Alvarez (1963), external and cranial measurements of a male and two females from Tamaulipas; Jones and Alvarez (1964), forearm measurements of a female and cranial measurements of this female and a specimen of unknown sex from San Luis Potosí; Jones (1964), forearm and cranial measurements of a specimen from Sinaloa; Jones (1966), forearm and cranial measurements (mean, range) of six specimens (five males, one female) from Guatemala; Villa-R. (1967), external measurements of 20 specimens and cranial measurements of 18 from México; Genoways and Jones (1968), forearm measurements of two males and four females from Zacatecas; Davis (1969), forearm and cranial measurements (mean, range) of samples from the Pacific versant including 14 from Sinaloa and Nayarit, 12 from Guerrero, 18 from Chiapas, 18 from Guatemala, and 17 from the Honduran highlands, from the Atlantic versant including nine from Tamaulipas and San Luis Potosí, eight from Veracruz, 16 from Chiapas, 14 from Guatemala, and 29 from the Costa Rican highlands, external and cranial measurements of the male holotype of *A. t. hesperus* from Guerrero and the male neotype of *A. t. toltecus* from Veracruz; Goodwin (1969), forearm and cranial measurements of four males and four females from Oaxaca; Jones *et al.* (1971*b*), forearm and cranial measurements (mean, range) of six specimens (three males, three females) from Departamento de Matagalpa, Nicaragua, and external and cranial measurements of 10 specimens (four males, six females) from Isla de Ometepe, Rivas, Nicaragua; Alvarez and Ramirez-Pulido (1972), external and cranial measurements of two males and two females from Morelos; Jones *et al.* (1972), forearm and cranial measurements (mean, range) of 10 specimens (five males, five females) from Sinaloa.

Geographic variation.—According to Jones (1966), specimens from Guatemala averaged larger than specimens from western México. Davis (1969) showed that specimens from the Pacific versant (El Salvador to Sinaloa) averaged smaller for almost all measurements compared to those occupying the remainder of the species geographic range. Jones *et al.* (1971*b*) reported two size groups (subspecies) occurring in Nicaragua. Those of smaller size from Isla de Ometepe, Rivas, and the others from Departamento de Matagalpa.

Artibeus watsoni Thomas, 1901

Measurements of *Artibeus watsoni* have been recorded as follows: Thomas (1901*a*), forearm and cranial measurements of the male holotype and external measurements of another male from Panamá; Elliot (1904), external and cranial measurements of the holotype (after Thomas, 1901); Elliot (1906), external and cranial measurements of the holotype of *Dermanura jucundum* from Veracruz; Andersen (1908), external and cranial measurements (mean, range) of nine specimens from Panamá and Nicaragua; Sanborn (1936), external measurements of two males and cranial measurements of one male from Guatemala; Goodwin (1942*a*), external and cranial measurements of a single specimen; Goodwin (1942*b*), external and cranial measurements of the male holotype from Panamá and the range for these measurements in the species; Jones (1966), forearm and cranial measurements of a male and female from Guatemala; Davis (1970*a*), cranial measurements of the holotype, external and cranial measurements (mean, range) of 62 males and 46 females from the Pacific versant of Costa Rica, and from the Atlantic versant 25 males and 19 females from Costa Rica, 22 males and 17 females from Nicaragua, 11 males and four females from Honduras, and eight males and four females from Guatemala, and cranial measurements (mean, range) of 120 specimens from southwestern Costa Rica (near type locality).

Geographic variation.—Davis (1970*a*) considered *Artibeus watsoni* to be monotypic.

Centurio senex Gray, 1842

Measurements of *Centurio senex* have been recorded as follows: Lichtenstein and Peters (1855), external measurements of the holotype of *Centurio flavogularis*; Saussure (1860*a*), external measurements of the female holotype of *Centurio mexicanus* from México; H. Allen (1861), external measurements of the holotype of *Centurio mcmurtrii* from Veracruz; Dobson (1878*a*), external measurements of the female holotype; Ward (1891), external measurements of the female holotype of *Centurio minor* from Veracruz and measurements given by Dobson (1878*a*); Rehn (1901), external measurements from the literature including Dobson's for *C. senex*, Lichtenstein's and Peters' for *C. flavogularis*, Saussure's for *C. mexicanus* and Ward's for *C. minor*, external measurements of five and cranial of two specimens from Veracruz and external and cranial measurements of one specimen from Costa Rica; Elliot (1904), external and cranial measurements of a specimen; Sanborn (1936), external measurements (range) of 12 specimens and forearm and cranial measurements (range) of 24 specimens from Guatemala; Goodwin (1942*a*), external and cranial measurements (range) in the species; Goodwin (1946), forearm and cranial measurements (range) of 24 specimens from Guatemala (as given by Sanborn, 1936) and the holotype; Felten (1956*c*), external and cranial measurements of a female from El Salvador; Felten (1956*d*), external measurements of a specimen from El Salvador; Hall and Kelson (1959), forearm and cranial measurements (range) of specimens from Guatemala; Burt and Stirton (1961), forearm and cranial measurements of a male from El Salvador; Goodwin and Greenhall (1961), forearm measurements of four males and one female and cranial measurements of three males and one female from Trinidad; Alvarez (1963), external and cranial measurements of a female from Tamaulipas; Villa-R. (1967), external and cranial measurements (mean, SD, range) of 10 specimens from México; Paradiso (1967), forearm and cranial measurements of the female holotype of *C. s. greenhalli* from Trinidad, forearm measurements (mean, range) of 28 topotypes, cranial measurements of 11 topotypes, and forearm and cranial measurements (mean, range) of 20 specimens of *C. s. senex* from Panamá, 11 from Guatemala, and two from Oaxaca; Goodwin (1969), forearm and cranial measurements of a male and female from Oaxaca; Jones *et al.* (1971*b*), forearm and cranial measurements (mean, range) of 11 specimens (seven males, four females) from Nicaragua; Jones *et al.* (1972), external and cranial measurements of two males and one female from Sinaloa; Watkins *et al.* (1972), forearm and cranial measurements of a male and five females (mean, range) from Jalisco, and seven males and four females from Nicaragua.

Secondary sexual variation.—Females from Nicaragua averaged slightly larger than males in both external and cranial measurements (Jones *et al.*, 1971*b*).

Geographic variation.—Specimens from Trinidad were clearly larger than those from Panamá, Guatemala, and Oaxaca in most measurements. No overlap in forearm measurements were found (Paradiso, 1967). Jones *et al.* (1971*b*) reported that measurements of their specimens from Nicaragua agreed in general with those given by Paradiso (1967) for material from Panamá. Specimens from Jalisco compare favorably in size with those from the vicinity of the type locality (restricted by Goodwin, 1946) and elsewhere in Nicaragua (Watkins *et al.*, 1972).

Chiroderma doriae Thomas, 1891

Measurements of *Chiroderma doriae* have been recorded as follows: Thomas (1891*b*), forearm and cranial measurements for the species (material described by Dobson, 1878*a*, as *C. villosum* is actually *C. doriae* and formed the basis for Thomas' description); Goodwin (1958), forearm and cranial measurements of the holotype from Brazil; Baker and Genoways (1976), external and cranial measurements (mean, range) of 15 males and 21 females from Brazil.

Chiroderma improvisum Baker and Genoways, 1976

Baker and Genoways (1976) recorded external and cranial measurements of the male holotype from Guadeloupe, Lesser Antilles.

Chiroderma salvini Dobson, 1878

Measurements of *Chiroderma salvini* have been recorded as follows: Elliot (1904), external and cranial measurements of one specimen; Sanborn (1941), forearm measurements (range) of 22 specimens and cranial measurements of three from Honduras; Goodwin (1942*a*), external and cranial measurements of two males from Honduras; Goodwin (1946), external and cranial measurements of two males from Honduras and one from Costa Rica; Goodwin (1958), forearm and cranial measurements of a female from Costa Rica; Hall and Kelson (1959), external and cranial measurements of a male from Costa Rica; Brosset (1965), external and cranial measurements of a female from Ecuador; Handley (1965), external and cranial measurements of two males and 11 females (mean, range) of *C. s. scopaeum* from Chihuahua, Sinaloa, Nayarit, Jalisco, Colima, and Guerrero; Carter *et al.* (1966), external and cranial measurements of a female from Guerrero and one from Honduras; Villa-R. (1967), external and cranial measurements of a male from Costa Rica; Genoways and Jones (1968), forearm measurements of five males from Zacatecas; Alvarez and Ramirez-Pulido (1972), external and cranial measurements of one female from Puebla; Anderson (1972), external and cranial measurements of two females from Chihuahua; Baker (1974), forearm measurements of three specimens from Ecuador.

Geographic variation.—Handley (1965) distinguished specimens from western México from typical members of the species in Costa Rica and Panamá by their smaller size and paler coloration.

Chiroderma trinitatum Goodwin, 1958

Measurements of *Chiroderma trinitatum* have been recorded as follows: Goodwin (1958), external and cranial measurements of the female holotype from Trinidad; Handley (1960), external and cranial measurements of the male holotype of *C. gorgasi* (= *C. trinitatum*) from Panamá, a female paratype, and the female holotype of *C. trinitatum* from Trinidad; Goodwin and Greenhall (1961), forearm and cranial measurements of the female holotype from Trinidad; Ojasti and Linares (1971), external and cranial measurements of two females from Venezuela; Pirlot (1972), forearm measurements of a single specimen from Brazil; Gardner (1976), external and cranial measurements (mean, range) of two males and six females from Perú.

Chiroderma villosum Peters, 1860

Measurements of *Chiroderma villosum* have been recorded as follows: Thomas (1891*b*), forearm and cranial measurements for the species; J. A. Allen (1900), external and cranial measurements of the male holotype of *C. villosum jesupi* from Colombia; Miller (1912), external and cranial measurements of the female holotype of *C. isthmicum* (= *C. villosum jesupi*) from Panamá; Elliot (1917), external and cranial measurements of the holotype of *C. isthmicum*; Sanborn (1936), forearm and cranial measurements of a male from Veracruz; Goodwin (1946), external and cranial measurements of the female holotype of *C. isthmicum*; Goodwin (1953), forearm and cranial measurements of the male holotype of *C. villosum jesupi* from Colombia; Goodwin (1958), forearm and cranial measurements of the holotype of *C. v. jesupi* from Colombia, male holotype and female topotype of *C. isthmicum* from Panamá, and a male from Trinidad; Hall and Kelson (1959), external and cranial measurements of the holotype of *C. isthmicum*; Goodwin and Greenhall (1961), forearm and cranial measurements of one male and three females from Trinidad; Husson (1962), external and cranial measurements of a female from Surinam; Villa-R. (1962), cranial measurements of

three specimens from Chiapas, two from Colima, and of the holotype of *C. isthmicum*; Davis *et al.* (1964), forearm measurements (range) of 12 females from Chiapas; Hill (1964), forearm and cranial measurements of a female from Guyana; Villa-R. (1967), external and cranial measurements of three females from Chiapas; Goodwin (1969), forearm and cranial measurements of a female from Oaxaca; Gardner *et al.* (1970), forearm and cranial measurements of two males from Costa Rica; Birney *et al.* (1974), external and cranial measurements of one male from Quintana Roo.

Geographic variation.—Husson (1962) found the measurements of his female from Surinam to correspond well with those of the four specimens reported by Goodwin and Greenhall (1961) from Trinidad. According to Birney *et al.* (1974), their male specimen corresponded closely in size to a female reported by Goodwin (1969) from Oaxaca.

Ectophylla alba H. Allen, 1892

Measurements of *Ectophylla alba* have been recorded as follows: H. Allen (1892), external measurements of the holotype from Nicaragua; H. Allen (1898), external measurements of the holotype and of an Oldfield Thomas specimen; Goodwin (1946), external measurements of the holotype from Nicaragua; Casebeer *et al.* (1963), external and cranial measurements of three females from Costa Rica; Starrett and Casebeer (1968), forearm measurements of a male and two females and cranial measurements of one male from Costa Rica; Gardner *et al.* (1970), forearm measurements (eight males, two females) and cranial measurements (mean, range) of seven males and two females from Costa Rica.

Enchisthenes hartii (Thomas, 1892)

Measurements of *Enchisthenes hartii* have been recorded as follows: Thomas (1892), external and cranial measurements of the "slightly immature" male holotype from Trinidad; Andersen (1908), external and cranial measurements of the male holotype from Trinidad; Sanborn (1932), external and cranial measurements of a female from Venezuela; Goodwin (1940, 1942, 1946), external and cranial measurements of a specimen from Honduras; de la Torre (1955), forearm measurements (mean, range) of 12 specimens (eight males, four females), and cranial measurements of one male and two females from Jalisco; Hall and Kelson (1959), external and cranial measurements of a male from Honduras; Goodwin and Greenhall (1961), forearm and cranial measurements of the holotype from Trinidad; Villa-R. (1967), external measurements of a male and female from Jalisco; Baker and Lopez (1968), forearm and cranial measurements of a male from Tamaulipas and a male and female from Trinidad; Goodwin (1969), forearm and cranial measurements of a female from Oaxaca; LaVal (1969), external and cranial measurements of one female from Honduras; Gardner *et al.* (1970), forearm and cranial measurements (mean, range) of 13 specimens from Costa Rica; Gardner (1976), external and cranial measurements of a female from Perú.

Geographic variation.—When comparing one male from Tamaulipas with a male and female from Trinidad, Baker and Lopez (1968) concluded that no outstanding variation was obvious.

Mesophylla (= Ectophylla) macconnelli Thomas, 1901

Measurements of *Mesophylla macconnelli* have been recorded as follows: Thomas (1901*b*), external measurements of the female holotype and one male and cranial measurements of the holotype from Guyana; Lima (1926), external measurements of a specimen from Brazil; Cunha Vieira (1942), external and cranial measurements of a female from Brazil; Sanborn (1951), forearm and cranial measurements of one specimen from Perú; Goodwin and Greenhall (1962), external and cranial measurements of the female holotype of *M. m. flavescens* from Trinidad, forearm and cranial measurements of one male and two females (including the holotype of *M. macconnelli*) from Guyana, two males and three females from Perú, one male from Brazil, and one male and two females from Ecuador; Starrett and Casebeer (1968), forearm and cranial measurements of a female from Costa Rica.

Phyllops falcatus (Gray, 1839)

Measurements of *Phyllops falcatus* have been recorded as follows: Gundlach (1872, 1877), external measurements of a specimen from Cuba; Dobson (1878*a*), external measurements of the male holotype from Cuba; Elliot (1904), external and cranial measurements of one specimen from Cuba; G. M. Allen (1942), external measurements for the species.

Phyllops haitiensis (J. A. Allen, 1908)

Measurements of *Phyllops haitiensis* have been recorded as follows: J. A. Allen (1908*a*), external measurements of the holotype of *P. haitiensis* from the Dominican Republic; Elliot (1917), external and cranial measurements of the holotype; Sanborn (1941), external measurements of two females and cranial measurements of one from Haiti; Goodwin (1953), forearm and cranial measurements of the holotype from the Dominican Republic.

Pygoderma bilabiatum (Wagner, 1843)

Measurements of *Pygoderma bilabiatum* have been recorded as follows: Peters (1863), external measurements of the holotype of *Stenoderma* (*Pygoderma*) *microdon* from Surinam; Dobson (1878*a*), external measurements of one specimen; Elliot (1904), external and cranial measurements of a single specimen; Lima (1926), external measurements of a specimen from Brazil; Cunha Vieira (1942), external measurements of two females and two of unknown sex and cranial measurements of a female from Brazil; Goodwin (1942, 1946), external measurements of a specimen from Paraguay; Husson (1962), external and cranial measurements of two Brazilian specimens and several measurements of the male holotype of *P. microdon* from Surinam, as given by Peters (1863).

Sphaeronycteris toxophyllum Peters, 1882

Measurements of *Sphaeronycteris toxophyllum* have been recorded as follows: Peters (1882), external measurements of the holotype from tropical America; Husson (1958), external and cranial measurements of four males, five females, and one of unknown sex from Venezuela.

Stenoderma rufum Desmarest, 1820

Measurements of *Stenoderma rufum* have been recorded as follows: Peters (1869), external measurements of the holotype of *S. r. rufum*; Anthony (1918, 1925), cranial measurements of fossil material from Puerto Rico; G. M. Allen (1942), cranial measurements of a single specimen; Hall and Bee (1960), external measurements of the holotype from an unknown locality and external and cranial measurements of a male and female from St. John Island; Tamsitt and Valdivieso (1966*c*), external measurements of a female and her one-day-old young (male) from Puerto Rico; Choate and Birney (1968), cranial measurements of 10 specimens of sub-Recent material from Puerto Rico (type description of *S. r. anthonyi*), six specimens of Recent material from Puerto Rico, and two specimens from St. John; Hall and Tamsitt (1968), external and cranial measurements of the female holotype of *S. r. darioi* from Puerto Rico, and the mean and range of these measurements in three males and four females; Jones *et al.* (1971*a*), external and cranial measurements (mean, SD, range) of 15 males and seven females from Puerto Rico, and one male and female from St. John; Genoways and Baker (1972), external measurements (mean, range) of 14 males and six females and cranial measurements of 15 males and seven females from Puerto Rico (from Jones *et al.*, 1971*a*).

Individual variation.—Forearm and cranial measurements of specimens with a greyish pelage and unfused or incompletely fused phalangeal epiphyses (immature) were significantly smaller than adults (Jones *et al.*, 1971*a*).

Secondary sexual variation.—According to Choate and Birney (1968), females were larger than males in material from Puerto Rico and St. John Island. Indications also exist that this was true in sub-Recent material. Jones *et al.* (1971*a*) found females significantly larger than males in all external and cranial measurements tested.

Geographic variation.—Hall and Bee (1960) stated that cranial dimensions of Puerto Rican specimens were larger than those from St. John. Sub-Recent material from Puerto Rico was larger throughout than the Recent material from Puerto Rico and St. John (Choate and Birney, 1968).

Hall and Tamsitt (1968) assigned specimens from St. John Island and St. Thomas Island to *S. r. rufum* because they closely resembled the holotype. They named a new subspecies from Puerto Rico on the basis of external color, although they found no differences between the two in overall size or shape and size of skull.

Jones *et al.* (1971*a*) confirmed that *Stenoderma rufum* was a polytypic species with three distinct subspecies. Recent Puerto Rican specimens were characterized by marked secondary sexual dimorphism and by darker color than the other Recent race from the Virgin Islands; subfossil material from Puerto Rico was distinguished by larger size and several details of dentition.

Sturnira aratathomasi Peterson and Tamsitt, 1968

Measurements of *Sturnira aratathomasi* have been recorded as follows: Peterson and Tamsitt (1968), external and cranial measurements of the male holotype from Colombia and a male and female from Ecuador; Thomas and McMurry (1974), external and cranial measurements of the holotype and three males and three females from Colombia.

Sturnira bidens (Thomas, 1915)

Measurements of *Sturnira bidens* have been recorded as follows: Thomas (1915), external and cranial measurements of the immature male holotype from Ecuador; Gardner and O'Neill (1969), forearm and cranial measurements (mean, range) of six specimens from Perú and the holotype from Ecuador; Gardner and O'Neill (1971), forearm and cranial measurements (mean, range) of 11 specimens from Perú; Marinkelle and Cadena (1972), forearm measurements (range) of two males and seven females and cranial measurements (range) of two males and four females from Colombia.

Geographic variation.—Marinkelle and Cadena (1972) found that their specimens from Colombia averaged slightly larger in cranial measurements than those from Perú reported by Gardner and O'Neill (1969).

Sturnira erythromos (Tschudi, 1844)

Measurements of *Sturnira erythromos* have been recorded as follows: Gardner *et al.* (1969), forearm and cranial measurements (mean, range) of 24 specimens from Perú; Tuttle (1970), forearm measurement range in species.

Sturnira lilium (É. Geoffroy St.-Hilaire, 1810)

Measurements of *Sturnira lilium* have been recorded as follows: Dobson (1878*a*), external measurements of one male; Cabrera (1903), external measurements for the species in Chile; Elliot (1904), external and cranial measurements of a specimen; Goldman (1917), external and cranial measurements of the female holotype *S. l. parvidens* from Guerrero; Lima (1926), external measurements of a male from Brazil; Cunha Vieira (1942), external measurements of five males and three females and cranial measurements of four males from Brazil; Goodwin (1942*a*), external and cranial measurements of the holotype of *S. l. parvidens* and a male and female from Honduras; Goodwin (1946), external and cranial measurements of

one male from Honduras, also given by Goodwin (1942*a*); Hershkovitz (1949), external and cranial measurements of a male and female from northern Colombia; Dalquest (1953*a*), external measurements (mean) of three males and seven females combined, and cranial measurements (mean) of three males and five females combined from San Luis Potosí; de la Torre (1954), external and cranial measurements of two specimens from Tamaulipas; Felten (1956*c*), external and cranial measurements of a female from El Salvador; Felten (1956*d*), external measurements of a specimen from El Salvador; Hall and Kelson (1959), forearm measurements (mean) of 12 topotypes from Paraguay; Goodwin and Greenhall (1961), forearm and cranial measurements of a male and female from Trinidad and two males from Paraguay; Husson (1962), external and cranial measurements of one male and four females from Surinam; Pirlot (1963), external measurements of seven males and seven females from Venezuela and cranial measurements of one female; Tamsitt and Valdivieso (1963*a*), external measurements of three males and one female and cranial measurements of one female from Colombia; Tamsitt and Valdivieso (1963*b*), external measurements of two males from Colombia; Starrett and de la Torre (1964), external and cranial measurements of a male and two females from El Salvador and one female from Nicaragua; Valdivieso (1964), external and cranial measurements of a specimen from Colombia; de la Torre (1966), external and cranial measurements of the male holotype and the mean and range of four male and five female paratypes combined of *S. l. angeli* from Dominica, Lesser Antilles; de la Torre and Schwartz (1966), external and cranial measurements of the female holotype of *S. l. paulsoni* from St. Vincent, Lesser Antilles; Villa-R. (1967), external and cranial measurements (mean, SD, range) of nine specimens from México; Pirlot (1968), forearm measurement of a female from Perú; Goodwin (1969), forearm and cranial measurements of four males and five females from Oaxaca; Villa-R. and Villa Cornejo (1969), external and cranial measurements (mean, range) of 15 specimens from Argentina; Anderson (1972), external measurements of one adult specimen and cranial measurements of two from Chihuahua; Jones *et al.* (1973), greatest length of skull (mean, range) of three males and five females combined from the Yucatan Peninsula; Taddei (1975*b*), external measurements (mean, SE, range) of 20 males and 20 females and cranial measurements of 15 males and 15 females from Brazil; Jones and Phillips (1976), forearm and cranial measurements (mean and range of sexes combined) from four Lesser Antillean islands—Dominica, two males and 12 females; Martinique, four males and four females; St. Lucia, four males and three females; and St. Vincent, three males.

Individual variation.—In specimens from Brazil, coefficients of variation for external measurements varied in 20 males from 2.85 to 5.86 and in 20 females from 2.48 to 7.08; CV values for cranial measurements in 15 males ranged from 1.47 to 3.57 and in 15 females from 1.75 to 3.01 (Taddei, 1975*b*).

Secondary sexual variation.—Although males generally averaged larger than females in specimens from Brazil, no significant differences in external measurements were found. However, in 15 cranial measurements, only two (braincase breadth, cranial depth) did not differ significantly (Taddei, 1975*b*).

Geographic variation.—Comparing Mexican material with species from Paraguay, Goldman (1917) concluded that the forearm was shorter in most of the specimens available from México and that the skull was narrower. Goodwin (1942*a*) stated that size in a Honduran series, including both males and females, was smaller than specimens from México. Jones *et al.* (1973) noted that the greatest length of skull of a specimen from La Tuxpena, Campeche, which Goldman reported (1917) to be abnormally small, fell within the range of that observed for three males and five females combined from the Yucatan Peninsula—their specimens averaged only slightly smaller than specimens from adjacent Chiapas and Guatemala. Jones and Phillips (1976) stated that Antillean *S. lilium* generally fell within the size range of populations of this species from Middle and South America. They did find some variation between insular samples, although no clinal geographic trend could be

demonstrated. Bats from St. Vincent tended to be the largest cranially among Antillean populations, whereas specimens from Martinique had proportionally broader zygomatic arches and longer maxillary toothrows. Forearm length in specimens from Dominica averaged slightly larger than did specimens from other islands. No other differences in external proportions were demonstrated.

Sturnira ludovici Anthony, 1924

Measurements of *Sturnira ludovici* have been recorded as follows: Anthony (1924*b*), external and cranial measurements of the male holotype from Ecuador; Shamel (1927), external and cranial measurements of the female holotype of *S. l. bogotensis* (= *S. ludovici*) from Colombia; Goodwin (1940), external and cranial measurements of the female holotype of *S. hondurensis* (= *S. ludovici*) from Honduras; Goodwin (1942*a*), external and cranial measurements of two specimens from Honduras; Goodwin (1946), forearm and cranial measurements of the holotype of *S. hondurensis*, and a male from Costa Rica; Hershkovitz (1949), external and cranial measurements of the holotype of *S. l. bogotensis* and the range of these measurements in two males and two females combined from Colombia; de la Torre (1952), external and cranial measurements of a male and female from Michoacán; Dalquest (1953*a*), external measurements (mean) of three males and cranial measurements of one of unknown sex, from San Luis Potosí; Goodwin (1953), external and cranial measurements of the holotypes of *S. ludovici* and *S. hondurensis*; Lukins and Davis (1957), external and cranial measurements of a female from Guerrero; Baker and Greer (1962), external and cranial measurements of one male and two females from Durango; Tamsitt and Valdivieso (1963*a*), external and cranial measurements (mean, range) of six males and six females combined from Colombia; Jones and Phillips (1964), external and cranial measurements of the female holotype of *S. l. occidentalis* from Sinaloa, mean and range of these measurements for specimens from Durango and Jalisco (*S. l. occidentalis*), Puebla, Michoacán, Oaxaca, Honduras, Colombia (after Hershkovitz, 1949), and Ecuador (*S. l. ludovici*); Starrett and de la Torre (1964), external and cranial measurements of a male and female from Costa Rica; Valdivieso (1964), external and cranial measurements (mean, range) of specimens from Colombia; Jones and Dunnigan (1965), forearm and cranial measurements of 12 males and 15 females (mean, range) from Oaxaca; Villa-R. (1967), external and cranial measurements of five specimens from México; Goodwin (1969), forearm and cranial measurements of eight males and one female from Oaxaca; Jones *et al.* (1971*b*), external and cranial measurements of one male from Nicaragua; Jones *et al.* (1972), forearm and cranial measurements of the female holotype of *S. l. occidentalis* and three males from Sinaloa.

Secondary sexual variation.—Jones and Dunnigan (1965), examining the mean and extremes of forearm and six cranial measurements, suggested that males average slightly larger than females.

Geographic variation.—Lukins and Davis (1957) concluded that their female specimens from Guerrero were somewhat smaller than those recorded by Hershkovitz (1949) from Colombia and Dalquest (1953*a*) from San Luis Potosí but corresponded closely to one regarded as *S. hondurensis* from Costa Rica (Goodwin, 1946). Jones and Phillips (1964) found specimens in the northern part of the range of the species to be smaller than specimens from Central America and northern South America and described them as *S. l. occidentalis*.

Sturnira magna de la Torre, 1966

Measurements of *Sturnira magna* have been recorded as follows: de la Torre (1966), external and cranial measurements of the male holotype and mean and range of five male and three female paratypes from Perú; Peterson and Tamsitt (1968), external and cranial

measurements of the male holotype, mean and range of five males and three females (after de la Torre, 1966), and two females from Perú; Marinkelle and Cadena (1972), external measurements of one specimen from Colombia; Baker (1974), forearm measurement of a female from Ecuador; Gardner (1976), external and cranial measurements (mean, range) of one male and three females from Perú.

Sturnira mordax (Goodwin, 1938)

Measurements of *Sturnira mordax* have been recorded as follows: Goodwin (1938, 1946), external and cranial measurements of the male holotype from Costa Rica; Hall and Kelson (1959), external and cranial measurements of the holotype; Davis *et al.* (1964), external and cranial measurements of six males and two females from Costa Rica; Gardner *et al.* (1970), forearm and cranial measurements (mean, range) of 12 specimens from Costa Rica.

Sturnira nana Gardner and O'Neill, 1971

Gardner and O'Neill (1971) recorded external and cranial measurements of the female holotype and forearm and cranial measurements (mean, range) of five other specimens from Perú.

Sturnira tildae de la Torre, 1959

Measurements of *Sturnira tildae* have been recorded as follows: de la Torre (1959), external and cranial measurements of the male holotype and a female paratype from Trinidad; Goodwin and Greenhall (1961), forearm and cranial measurements of two males and two females from Trinidad; Hill (1964), external and cranial measurements of two females from Guyana; Marinkelle and Cadena (1971), external measurements of 60 males and 60 females from Colombia (mean, range), male holotype and female paratype from Trinidad (after de la Torre, 1959), two females from Guyana (after Hill, 1964), and cranial measurements of 50 males and 50 females from Colombia (mean, range), one male and five females from Guyana, holotype, paratype, and three females from Trinidad.

Geographic variation.—Marinkelle and Cadena (1971) found external measurements of Colombian specimens generally averaged larger than the holotype and paratype from Trinidad.

Sturnira thomasi de la Torre and Schwartz, 1966

Measurements of *Sturnira thomasi* have been recorded as follows: de la Torre and Schwartz (1966), external and cranial measurements of the male holotype from Guadeloupe, Lesser Antilles; Genoways and Jones (1975), external and cranial measurements of the male holotype (after de la Torre and Schwartz, 1966) and four females (including one juvenile) from Guadeloupe; Jones and Genoways (1975), external and cranial measurements (after Genoways and Jones, 1975); Jones and Phillips (1976), external and cranial measurements of the same individuals as given by Genoways and Jones (1975).

Uroderma bilobatum Peters, 1866

Measurements of *Uroderma bilobatum* have been recorded as follows: Peters (1866*a*), external measurements of a single specimen; Dobson (1878*a*), external measurements of one specimen; Rehn (1900), cranial measurements of a specimen from Brazil; Lyon (1902*a*), external and cranial measurements of the female holotype of *U. b. convexum* from Panamá and a specimen from Brazil; Elliot (1904), external and cranial measurements of the holotype of *U. b. convexum* (after Lyon, 1902*a*) from Panamá; Andersen (1906*b*), measurements (range) of two specimens, including the male holotype of *U. b. thomasi*, from

Bolivia; Andersen (1908), external and cranial measurements (range) of one specimen from Brazil, one from Amazonas, two from Perú, one from Ecuador, one from Cali, Colombia, three from Santa Marta, Colombia, and Valencia, Venezuela, two from Colón, Panamá, two from Chiriquí, Panamá, nine (eight cranial) from the islands off Panamá, and one from Costa Rica; Lima (1926), external measurements of a male from Brazil; Cunha Vieira (1942), external and cranial measurements of a male from Perú; Goodwin (1946), external and cranial measurements of two males from Costa Rica; Hershkovitz (1949), external and cranial measurements (range) of specimens from Colombia; Sanborn (1951), greatest length of skull of one female from Perú; Felten (1956*c*), external measurements of a male and four females and cranial measurements of one male and two females from El Salvador; Felten (1956*d*), external measurements (mean, range) of specimens from El Salvador; Hall and Kelson (1959), external and cranial measurements of two males from Costa Rica; Burt and Stirton (1961), forearm and cranial measurements (range) of 16 males and 13 females from El Salvador; Goodwin and Greenhall (1961), external measurements of a subadult male and four females and cranial measurements of the subadult male and two females from Trinidad; Husson (1962), external and cranial measurements of four females from Surinam; Tamsitt and Valdivieso (1963*a*), external measurements (mean, range) of nine males and five females combined from Colombia; Valdivieso (1964), external and cranial measurements (mean, range) of one male and nine females combined from Colombia; Brosset (1965), external and cranial measurements of one female from Ecuador; Villa-R. (1967), external measurements (mean, SD, range) of 22 specimens and cranial measurements of 20 from Chiapas; Davis (1968), forearm and cranial measurements of the holotype (juvenile, unsexed) of *U. b. bilobatum* from Brazil, 18 males and 30 females from Bolivia, eastern Brazil, Cayenne, Guyana, and Venezuela, external and cranial measurements of the male holotype of *U. b. trinitatum*, mean and range of eight males, and five females from Trinidad, a male paratype of *U. b. thomasi* from Bolivia, 21 males and 14 females from Ecuador, Perú, and western Bolivia, the female holotype (young) of *U. b. convexum* from Panamá, 77 males, and 124 females from western Venezuela, Colombia, Panamá (exclusive of the Bocas del Toro region), the Pacific versant of Middle America as far as Oaxaca, the male holotype of *U. b. molaris* from Chiapas, 36 males and 58 females from the Atlantic versant of Middle America from the Bocas del Toro region of Panamá northward to southern Veracruz; Goodwin (1969), forearm and cranial measurements of one male and two females from Oaxaca and one subadult male and two females of *Uroderma* sp. from Oaxaca; Baker and McDaniel (1972), forearm and cranial measurements of the female holotype of *U. b. davisi* from El Salvador, forearm and cranial measurements (mean, SD) of 16 males and 10 females from Chiapas and El Salvador (*U. b. davisi*), 33 males and 29 females from Nicaragua, Costa Rica, and Colombia (*U. b. convexum*), and 25 males and 26 females from Tabasco, Honduras, Nicaragua, and Costa Rica (*U. b. molaris*).

Secondary sexual variation.—Baker *et al.* (1972*a*) described sexual dimorphism in this species with males larger than females.

Geographic variation.—According to Davis (1968), specimens from Trinidad (*U. b. trinitatum*) were noticeably larger than those from the adjacent mainland (*U. b. bilobatum*) but were difficult to separate from specimens from Ecuador, Perú, and western Bolivia (*U. b. thomasi*). Specimens from western Bolivia were larger than specimens from Colombia and the Pacific versant of Central America (*U. b. convexum*). *U. b. convexum*, again, was smaller in most measurements than specimens from Bolivia, eastern Brazil, the Guianas, and Venezuela (*U. b. bilobatum*). Specimens from the Atlantic versant of Middle America (*U. b. molaris*) from Bocas de Toro, Panamá, northwest to Veracruz, México, were of moderate size for the species. *Uroderma b. davisi* from the Pacific versant of Middle America (Chiapas, El Salvador, Honduras) averaged smaller both externally and cranially than either *convexum* or *molaris* (Baker and McDaniel, 1972).

Uroderma magnirostrum Davis, 1968

Measurements of *Uroderma magnirostrum* have been recorded as follows: Davis (1968), external and cranial measurements of the male holotype from Honduras and 26 males and 51 females (mean, range) from Oaxaca, Chiapas, El Salvador, Honduras, Nicaragua, Panamá, Colombia, Perú, Bolivia, Venezuela, and Brazil; Jones *et al.* (1971*b*), external and cranial measurements of one male and two females from Nicaragua.

Geographic variation.—Davis (1968) found little evidence of geographic variation but his findings were based on relatively small sample sizes of *U. magnirostrum.*

Vampyressa bidens (Dobson, 1878)

Measurements of *Vampyressa bidens* have been recorded as follows: Dobson (1878*a*), external measurements of the female holotype from Perú; Sanborn (1936), forearm measurements (range) of two males and one female, wing measurements of one male and one female from Ecuador, cranial measurements of a male and female from Ecuador and the range of these measurements in three males and one female from Perú; Cunha Vieira (1942), external measurements of a male and female and cranial measurements of a male from Brazil; Hill (1964), forearm and cranial measurements of four males and one female from Guyana; Marinkelle and Cadena (1972), external and cranial measurements of one female from Colombia; Davis (1975), external and cranial measurements of 13 males and 10 females (mean, SD, range) from Perú.

Individual variation.—Coefficients of variation, as given by Davis (1975), varied from 1.28 in greatest length of skull in females to 3.27 in postorbital constriction of females. The two external measurements, which were tested, fell within this range.

Secondary sexual variation.—Comparing two external and eight cranial measurements of 13 males with those of 10 females showed no significant differences. Females generally averaged larger than males (Davis, 1975).

Vampyressa brocki Peterson, 1968

Measurements of *Vampyressa brocki* have been recorded as follows: Peterson (1968), external and cranial measurements of the female holotype from Guyana; Baker *et al.* (1972*b*), external and cranial measurements of three females from Colombia; Peterson (1972), external and cranial measurements of the holotype and a male from Guyana; Davis (1975), forearm and cranial measurements (range) of published data.

Vampyressa melissa Thomas, 1926

Measurements of *Vampyressa melissa* have been recorded as follows: Thomas (1926), external and cranial measurements of the female holotype from Perú; Goodwin (1963), forearm and cranial measurements of the female holotype; Peterson (1968), forearm and cranial measurements of one specimen; Gardner (1976), external and cranial measurements of four specimens (one male, three females) from Perú.

Vampyressa nymphaea Thomas, 1909

Measurements of *Vampyressa nymphaea* have been recorded as follows: Thomas (1909), forearm and cranial measurements of the male holotype from Colombia; Hall and Kelson (1959), forearm and cranial measurements of the holotype and external measurements of a specimen from Panamá; Goodwin (1963), forearm and cranial measurements of two males from Colombia and two females from Panamá; Peterson (1968), forearm and cranial measurements (range) in specimens of the species; Gardner *et al.* (1970), forearm and cranial measurements (mean, range) of five specimens (three males, two females) from Costa Rica; Jones *et al.* (1971*b*), external and cranial measurements of one female from Nicaragua.

Vampyressa pusilla (Wagner, 1843)

Measurements of *Vampyressa pusilla* have been recorded as follows: Peters (1866*a*), external measurements of a specimen from Brazil; Dobson (1878*a*), external measurements of one specimen from Brazil; Thomas (1909), forearm and cranial measurements of the male holotype of *V. p. thyone* from Colombia; Miller (1912), external and cranial measurements of the immature female holotype of *V. minuta* (= *V. pusilla*) from Panamá; Elliot (1917), external and cranial measurements of the holotype of *V. minuta*; Cunha Vieira (1942), external measurements of a specimen from Brazil; Goodwin (1946), external and cranial measurements of the female holotype of *V. minuta* from Panamá and those of a male from Costa Rica; Hershkovitz (1949), external and cranial measurements of one female from Colombia; Sanborn (1953), forearm and cranial measurements (range) of two males and one female from Perú; Hall and Kelson (1959), cranial measurements of the holotype of *V. p. thyone*; Davis *et al.* (1964), external and cranial measurements of a female from Chiapas; Goodwin (1963), external and cranial measurements of the male holotype of *V. pusilla* from Brazil, the male holotype of *V. nattereri* (= *V. pusilla*) from Brazil, and forearm and cranial measurements of the female holotype of *V. p. venilla* from Perú, three females from Panamá, two males from Costa Rica, one male and three females from Colombia, two males and one female from Ecuador, five males and five females from Perú, and one female from Venezuela; Starrett and de la Torre (1964), external and cranial measurements of one female from Nicaragua; Peterson (1965*a*), external and cranial measurements of a female from British Honduras; Tamsitt and Valdivieso (1966*a*), forearm and cranial measurements of a male and female from Colombia (the latter as given by Hershkovitz, 1949); Rick (1968), external and cranial measurements of one male and female from Guatemala; Gardner *et al.* (1970), forearm and cranial measurements (mean, range) of five specimens (one male, four females) from Costa Rica; Jones *et al.* (1971*b*), forearm and cranial measurements of two males and mean and range of six females from Nicaragua; Baker *et al.* (1973), external and cranial measurements of 36 specimens from Colombia, Ecuador, and Venezuela, four specimens from the Darien of Panamá, 14 from the remainder of Panamá, and seven from Nicaragua; Jones *et al.* (1973), external and cranial measurements of one female from Campeche.

Individual variation.—Baker *et al.* (1973) found coefficients of variation for forearm and cranial measurements in four samples from Central and South America ranged between 1.5 and 7.2. Lowest values were for breadth across upper molars in the sample from the Darien of Panamá and postorbital breadth in the sample from Nicaragua; the highest CV value was for postorbital breadth in the sample from the Darien of Panamá. All samples had coefficients of variation exceeding 4.0 for palatal length.

Geographic variation.—Goodwin (1963), in his review of the genus, recognized three subspecies of *V. pusilla*. These were based primarily on minor details of coloration and slight size differences. Handley (1966*b*) believed that the subspecific variations noted by Goodwin could be attributed to variation with age and chose to consider *V. pusilla* as being monotypic. Two years later, Peterson (1968) recognized two subspecies—one from southeastern Brazil and the other occupying the remainder of the geographic range of the species in South and Central America. He did not give, however, the characteristics used to distinguish them.

Starrett and de la Torre (1964) concluded that their female specimen from Nicaragua was similar in size to measurements given by Goodwin (1946) for the holotype of *V. minuta* (= *V. pusilla*) from Panamá and for a specimen from Costa Rica. They also found their specimen from Nicaragua indistinguishable from three specimens from Perú.

Baker *et al.* (1973) found no significant differences in forearm and cranial measurements of specimens from four geographic areas including Colombia, Ecuador, Venezuela, the Darien and remainder of Panamá, and Nicaragua.

Jones *et al.* (1973) followed Handley (1966*b*) in considering *V. pusilla* monotypic when assigning their specimen from Campeche.

Vampyrodes caraccioli (Thomas, 1889)

Measurements of *Vampyrodes caraccioli* have been recorded as follows: Thomas (1889), external and cranial measurements of the holotype from Trinidad; G. M. Allen (1908), external and cranial measurements of the female holotype of *V. major* from Panamá; Sanborn (1936), forearm and cranial measurements (range) of two males, one female, and one unsexed specimen, and wing measurements of one male from Guatemala; Sanborn (1941), external and cranial measurements of a male from Trinidad; Goodwin (1942*a*), external and cranial measurements of the female holotype of *V. major* from Panamá; Goodwin (1946), external and cranial measurements of the holotype of *V. major* (as in Goodwin, 1942) and of one specimen from Nicaragua; Husson (1954), external and cranial measurements of four males from Tobago; Hall and Kelson (1959), cranial measurements of a male from Guatemala; Goodwin and Greenhall (1961), forearm and cranial measurements of the unsexed holotype from Trinidad and a female from Tobago; Villa-R. (1967), external and cranial measurements of two males and one female from Veracruz; Starrett and Casebeer (1968), forearm measurements of three males and nine females, and cranial measurements of three males and two females from Costa Rica; Goodwin (1969), forearm and cranial measurements of one male from Oaxaca; Linares (1969), external and cranial measurements of one specimen from Venezuela; Gardner *et al.* (1970), forearm measurement of a female from Costa Rica.

Geographic variation.—According to Sanborn (1936), his series of specimens from Guatemala agreed closely in measurements with the original description of *V. major* from Panamá. Gardner *et al.* (1970) noted that the forearm length of their female from Costa Rica greatly exceeded the range for three males and nine females recorded by Starrett and Casebeer (1968) from Costa Rica.

Vampyrops aurarius Handley and Ferris, 1972

Measurements of *Vampyrops aurarius* have been recorded as follows: Handley and Ferris (1972), external and cranial measurements of the male holotype from Venezuela; Carter and Rouk (1973), forearm and cranial measurements of the male holotype from Venezuela and the mean and range for Peruvian specimens.

Vampyrops brachycephalus Rouk and Carter, 1972

Measurements of *Vampyrops brachycephalus* have been recorded as follows: Rouk and Carter (1972), external and cranial measurements of the male holotype from Huánuco, Perú and mean and range for 13 specimens from Loreto, Perú, six from Huánuco, Perú, three from Colombia, and 13 from Venezuela; Gardner and Carter (1972*b*), external and cranial measurements of the male holotype and measurements (mean, range) of 13 specimens from Loreto and six specimens from Huánuco, Perú (see also Rouk and Carter, 1972); Handley and Ferris (1972), external and cranial measurements of the male holotype of *V. latus* (= *V. brachycephalus*) from Perú and similar measurements for the male holotype of *V. latus saccharus* from Venezuela; Carter and Rouk (1973), forearm and cranial measurements of the holotype of *V. latus* and *V. latus saccharus* as well as mean and range of these measurements for 13 specimens from Loreto, Perú, and an unspecified number of specimens from Tingo María, Perú.

Vampyrops dorsalis Thomas, 1900

Measurements of *Vampyrops dorsalis* have been recorded as follows: Thomas (1900), external and cranial measurements of the holotype from Ecuador; Lyon (1902*b*), external and cranial measurements of the female holotype of *V. umbratus* from Colombia; Thomas (1914), external and cranial measurements of the male holotype of *V. oratus* from Venezuela; Sanborn (1951), forearm and cranial measurements of the holotype and a male from Perú;

Sanborn (1955), external measurements of two males and cranial measurements (range) of 10 specimens (eight males, one female, one unsexed) from Colombia, Ecuador, Perú, and Venezuela; Tamsitt and Valdivieso (1966*a*), forearm and cranial measurements (range) of four males from Colombia, and those given by Sanborn (1955), Handley and Ferris (1972), external and cranial measurements of the female holotype of *V. aquilus* from Panamá; Gardner and Carter (1972*b*), external and cranial measurements of the immature male holotype from Ecuador and mean and range for one specimen from Ecuador and eight from Perú; Carter and Rouk (1973), forearm and cranial measurements of the holotype of *V. aquilus* (= *V. dorsalis*) as reported by Handley and Ferris (1972) and mean and range for specimens from Perú of *V. dorsalis* reported by Gardner and Carter (1972*b*).

Vampyrops helleri Peters, 1866

Measurements of *Vampyrops helleri* have been recorded as follows: Peters (1866*a*), external measurements of the holotype from México; Dobson (1878*a*), measurements of one specimen from México; H. Allen (1891), external and cranial measurements of the female holotype of *Vampyrops zarhinus* from Brazil (holotype now considered to be from Panamá according to Jones and Carter, 1976); Robinson and Lyon (1901), external measurements of four females from Venezuela; Elliot (1904), external and cranial measurements of one specimen; Thomas (1912*a*), external and cranial measurements of the male holotype of *V. incarum* from Perú; Cunha Vieira (1942), external measurements of a male and female and cranial measurements of a male of *Vampyrops zarhinus* (= *V. helleri*) from Brazil; Goodwin (1942*a*), external and cranial measurements of a single specimen; Goodwin (1946), forearm and cranial measurements of one female from Costa Rica; Sanborn (1949*b*), forearm measurement of one female and cranial measurements of two females from Perú; Sanborn (1955), external and cranial measurements (range) of specimens from Oaxaca, Honduras, Costa Rica, Panamá, Cayenne, Trinidad, Brazil, Venezuela, Colombia, and Perú; Sherman (1955), external measurements of a male from Paraguay; Hall and Kelson (1959), forearm and cranial measurements of one female from Costa Rica; Goodwin and Greenhall (1961), external and cranial measurements of one male and three females from Trinidad; Husson (1962), external and cranial measurements of eight males from Surinam; Tamsitt and Valdivieso (1963*a*), external measurements of three males and one female and cranial measurements of three males from Colombia; Starrett and de la Torre (1964), external and cranial measurements of a female from Costa Rica; Davis *et al.* (1964), external and cranial measurements (mean, range) of six specimens from Chiapas and Central America; Valdivieso (1964), external measurements of one specimen from Colombia; Villa-R. (1967), external and cranial measurements of a male and two females from Oaxaca, Chiapas, and Tabasco; Rick (1968), external and cranial measurements of a male and female from Guatemala; Goodwin (1969), forearm and cranial measurements of one female from Oaxaca; Gardner and Carter (1972*b*), external measurements of the holotype (sex unknown) from México, and external and cranial measurements (mean, range) of four specimens from Perú; Rouk and Carter (1972), forearm and cranial measurements (mean, range) of four specimens from Perú, one from Ecuador, nine from Colombia, three from Venezuela, one from Panamá, two from Costa Rica, 20 from Nicaragua, and 12 from Honduras.

Vampyrops infuscus Peters, 1880

Measurements of *Vampyrops infuscus* have been recorded as follows: Peters (1880), external measurements of the holotype from Perú; Miller (1902*a*), external and cranial measurements of the female holotype of *V. fumosus* from Brazil; Sanborn (1936), forearm and cranial measurements (range) of three males and one female from Ecuador; Cunha Vieira (1942), external measurements of the holotype of *V. fumosus* based on Miller (1902*a*); Sanborn (1951), forearm measurements of the holotype of *V. infuscus* from Brazil

and a series of specimens from Perú, Ecuador, and Colombia; Marinkelle (1970), external and cranial measurements of the female holotype of *V. intermedius* from Colombia and the range of these measurements in the paratypes (five males, ten females); Gardner and Carter (1972*b*), external and cranial measurements of the adult male neotype of *V. infuscus* and the mean and range of several external and cranial measurements of six specimens, including the neotype from Perú.

Secondary sexual variation.—Marinkelle (1970) found no significant differences in size between five males and 10 females from Colombia.

Vampyrops lineatus (É. Geoffroy St.-Hilaire, 1810)

Measurements of *Vampyrops lineatus* have been recorded as follows: Dobson (1878*a*), external measurements of the holotype; H. Allen (1891), external and cranial measurements of one specimen; Elliot (1904), external measurements of a single specimen; Lima (1926), external measurements of a specimen from Brazil; Cunha Vieira (1942), external measurements of three males, three females, and one unsexed specimen, and cranial measurements of three males and one female from Brazil; Goodwin (1946), external and cranial measurements of a male from Paraguay; Hershkovitz (1949), external measurements of four males and a female and cranial measurements of one male from Colombia; Sanborn (1955), external measurements of one male and seven females and cranial measurements of an unspecified number of specimens from Brazil, Paraguay, and Bolivia.

Vampyrops nigellus Gardner and Carter, 1972

Gardner and Carter (1927*a*, 1972*b*) gave external and cranial measurements of the male holotype from Perú and mean and range of measurements of 17 specimens from Perú.

Vampyrops recifinus Thomas, 1901

Measurements of *Vampyrops recifinus* have been recorded as follows: Thomas (1901*c*), external and cranial measurements of the male holotype from Brazil; Cunha Vieira (1942), external measurements of a male and a female from Brazil; Sanborn (1955), external and cranial measurements (range) of specimens from Brazil and Guyana.

Vampyrops vittatus (Peters, 1859)

Measurements of *Vampyrops vittatus* have been recorded as follows: Dobson (1878*a*), external measurements of one specimen; Goodwin (1946), external and cranial measurements of a specimen from Costa Rica; Sanborn (1955), forearm and cranial measurements (range) of specimens from Venezuela, Colombia, Brazil, Ecuador, and Perú (he considered *V. vittatus* and *V. fuscus* conspecific); Hall and Kelson (1959), external and cranial measurements of a single specimen from Colombia; Davis *et al.* (1964), external and cranial measurements of a male and two females from Costa Rica; Gardner *et al.* (1970), forearm and cranial measurements (mean, range) of six males and nine females from Costa Rica; Gardner and Carter (1972*b*), external and cranial measurements of the male holotype from Venezuela and several of these measurements (mean, range) for six specimens from Perú.

Geographic variation.—According to Gardner and Carter (1972*b*) measurements of six specimens from Perú were much the same as those reported by Gardner *et al.* (1970) for 19 specimens from Costa Rica.

Subfamily Brachyphyllinae

Brachyphylla cavernarum Gray, 1834

Measurements of *Brachyphylla cavernarum* have been recorded as follows: Gray (1834), external measurements of the holotype from St. Vincent; Dobson (1878*a*), external measure-

ments of one specimen; Miller (1902*a*), cranial measurements of a male topotype from St. Vincent; Miller (1902*b*), external measurements of a female specimen; Elliot (1904), external and cranial measurements of one specimen; Miller (1913*a*), external and cranial measurements of the female holotype of *B. c. minor* from Barbados and cranial measurements for an additional male; Elliot (1917), external and cranial measurements of the holotype of *B. c. minor*; Anthony (1918, 1925), external measurements (mean, range) of 11 specimens (2 males, 9 females) and cranial measurements of 10 specimens (3 males, 7 females) from Puerto Rico; Hall and Kelson (1959), external and cranial measurements (range) of 10 specimens and external and cranial measurements of the holotype of *B. b. minor* from Barbados; Husson (1960), forearm and cranial measurements (range) of 18 specimens from St. Martin and Saba; Choate and Birney (1968), cranial measurements of two samples of sub-Recent material from Puerto Rico; Koopman (1968), cranial measurements of a male and female from Barbados (as given by Miller, 1913*a*) and the range of a series of males from Anguilla and females from St. Martin; Buden (1977), forearm measurements (mean, range) of three males and eight females, cranial measurements of four males and eight females from Puerto Rico, forearm measurements (mean, range) of seven males and three females, and cranial measurements of 11 males and four females from St. John.

Geographic variation.—Buden (1977) treated all members of the genus as a single species. Within the species, he recognized several areas of morphological variation. Individuals from Puerto Rico, Virgin Islands, and most of the Lesser Antilles were the largest. Specimens from Barbados in the Lesser Antilles were small compared to populations on adjacent islands. Specimens from Cuba, Hispaniola, and the Bahamas were also small, with Cuban material being distinguished by deeper and more robust zygomatic arches. However, Silva-Taboada (1976), after examining this group, concluded that it contained two species, each with two subspecies.

Initially, populations from Barbados (*minor*) and the remainder of the Lesser Antilles (*cavernarum*) were considered two separate species. Koopman (1968), however, showed that there was overlap in size among both males and females and concluded from this that the two were subspecies of *B. cavernarum*.

Brachyphylla nana Miller, 1902

Measurements of *Brachyphylla nana* have been recorded as follows: Gundlach (1872, 1877), external measurements of a specimen from Cuba; Miller (1902*a*), cranial measurements of the holotype from Cuba; Miller (1902*b*), external measurements of one female from Cuba; Elliot (1904), external and cranial measurements of a single specimen; Miller (1918), cranial measurements of the holotype and an additional specimen of *B. nana pumila* from the type locality on Haiti; Miller (1929), cranial measurements of one specimen from Haiti; Goodwin (1933), external measurements of five males from the Dominican Republic and one female from Cuba; Sanborn (1941), external measurements of three females (range) and cranial measurements of one female from Haiti; Hall and Kelson (1959), cranial measurements of the holotype of *Brachyphylla nana* and *B. pumila*; Silva-Taboada (1974), measurements of fossil humeri, crania, and mandibles from Cuba; Buden (1977), forearm measurements (mean, range) of eight males and 13 females, cranial measurements (mean, range) of five males and nine females from Cuba, forearm measurements of seven males and three females, and cranial measurements of 10 males and three females from Hispaniola and of seven males and 12 females from Middle Caicos, Bahamas.

Geographic variation.—Buden (1977), considering *B. nana* and *B. cavernarum* conspecific, found populations from Middle Caicos, Cuba, and Hispaniola (*nana*) to be distinctly smaller than individuals from Puerto Rico, Virgin Islands, and the remainder of the Lesser Antilles (*cavernarum*). Many characters of specimens from Caicos and Hispaniola overlap broadly, but Buden distinguished specimens from the two areas by the deeper and more robust zygomatic arch of specimens from Cuba.

Erophylla bombifrons (Miller, 1899)

Measurements of *Erophylla bombifrons* have been recorded as follows: Miller (1899), external and cranial measurements of the male holotype from Puerto Rico; Elliot (1904), external and cranial measurements of the holotype from Puerto Rico as given by Miller (1899); Elliot (1905*b*), external and cranial measurements of the holotype of *E. b. santacristobalensis* from the Dominican Republic; Elliot (1917), external and cranial measurements of the holotype of *E. b. santacristobalensis*; Anthony (1918, 1925), external measurements (mean, range) of six specimens and cranial measurements (mean, range) of three specimens from Puerto Rico; Miller (1929), cranial measurements of three specimens from Haiti and three from Puerto Rico; Hall and Kelson (1959), forearm and cranial measurements of the holotype of *E. b. bombifrons*; Buden (1976), external and cranial measurements (mean, SD, range) of 49 specimens (21 cranial) from Hispaniola and 47 (18 cranial) from Puerto Rico.

Individual variation.—Coefficients of variation in external measurements of specimens from Hispaniola and Puerto Rico varied from 1.98 to 4.94 and in cranial measurements from 1.84 to 3.45 (Buden, 1976).

Geographic variation.—Buden (1976) treated the two recognized species (*bombifrons* and *sezekorni*) of the genus as conspecifics and relegated them to subspecific status. Differences between many of the currently recognized taxa were considered slight. Skull shape was considered the main diagnostic factor in distinguishing *bombifrons* and *sezekorni*.

Erophylla sezekorni (Gundlach, 1861)

Measurements of *Erophylla sezekorni* have been recorded as follows: Gundlach (1877), external measurements of a specimen from Cuba; Dobson (1878*a*), external measurements of a single specimen; Miller (1899), external and cranial measurements of the male holotype of *E. s. plantifrons* from the Bahamas; Elliot (1904), external and cranial measurements of two specimens; G. M. Allen (1917), external and cranial measurements of the male holotype from Jamaica; Shamel (1931), external and cranial measurements of the male holotype of *E. s. mariguanensis* from Mariguana Island, southern Bahamas, cranial measurements (range) of eight additional specimens, and eight from the northern Bahamas; Buden (1976), external and cranial measurements (mean, SD, range) of 50 specimens (19 cranial) from New Providence, Bahamas, 35 (six cranial) from Mayaguana, Bahamas, 88 (44 cranial) from Cuba, and 66 (29 cranial) from Jamaica.

Individual variation.—Coefficients of variation in external measurements of specimens from the Bahamas, Cuba, and Jamaica varied from 2.06 to 4.40 and in cranial measurements from 1.58 to 2.93 (Buden, 1976).

Geographic variation.—See geographic variation in *E. bombifrons*.

Phyllonycteris aphylla (Miller, 1898)

Measurements of *Phyllonycteris aphylla* have been recorded as follows: Miller (1898), external and cranial measurements of the male holotype from Jamaica; Elliot (1904), external and cranial measurements of one specimen; G. M. Allen (1942), external and cranial measurements for the species; Hall and Kelson (1959), external and cranial measurements of the holotype; Henson and Novick (1966), external measurements of a female from Jamaica; Howe (1974), external measurements of three females from Jamaica.

Phyllonycteris major Anthony, 1917

Measurements of *Phyllonycteris major* have been recorded as follows: Anthony (1917, 1918, 1925), cranial measurements of the holotype and eight additional specimens (sub-Recent fossils) from Puerto Rico; G. M. Allen (1942), cranial measurements for the

species; Goodwin (1953), cranial measurements of the holotype from Puerto Rico; Choate and Birney (1968), measurements (mean, range) of partial crania and partial lower jaws from Puerto Rico.

Phyllonycteris poeyi Gundlach, 1861

Measurements of *Phyllonycteris poeyi* have been recorded as follows: Gundlach (1872, 1877), external measurements of a specimen from Cuba; Dobson (1878*a*), external measurements of one specimen from Cuba; Elliot (1904), external and cranial measurements of a single specimen from Cuba; Miller (1904), external measurements of a single specimen from Cuba; Miller (1904), external measurements of 12 males and 13 females from Cuba; Anthony (1917, 1918, 1925), cranial measurements of two specimens from Cuba; Miller (1929), cranial measurements of the holotype of *P. p. obtusa* and an additional specimen from Haiti; G. M. Allen (1942), cranial measurements for *P. p. obtusa*; Hall and Kelson (1959), cranial measurements of the holotype of *P. p. obtusa* and two specimens of *P. p. poeyi*; Silva-Taboada (1974), measurements of fossil humeri, crania, and mandibles from Cuba.

Subfamily Desmodontinae

Desmodus rotundus (É. Geoffroy St.-Hilaire, 1810)

Measurements of *Desmodus rotundus* have been recorded as follows: Dobson (1878*a*), external measurements of one specimen; Flower and Lydekker (1891), forearm length of the species; Jentink (1893), external measurements probably of a female from Guyana; H. Allen (1896), cranial measurements of a single specimen; Cabrera (1903), external measurements for the species in Chile; Elliot (1904), external and cranial measurements of one specimen; J. A. Allen (1906), external measurements (mean, range) of five specimens from Jalisco; Miller (1912), external and cranial measurements of a female from Taboga Island, Panamá; Lima (1926), external and cranial measurements of a specimen from Brazil; Goodwin (1934), external measurements of one specimen from Guatemala; Martinez and Villa-R. (1940), external and cranial measurements of males and females combined from Guerrero; Cunha Vieira (1942), external measurements of four males and four females and cranial measurements of three males and one female from Brazil; Goodwin (1942*a*), external and cranial measurements of two females from Honduras; Osgood (1943), forearm measurements of two specimens from Chile; Goodwin (1946), external and cranial measurements of a male and female from Costa Rica; Hershkovitz (1949), external and cranial measurements (range) of 14 females and a large male obtained in a sample from Colombia; Dalquest (1953*a*), external measurements (mean) of 10 males and 10 females and cranial measurements of one male and one female from San Luis Potosí; de la Torre (1954), external and cranial measurements of a female from Tamaulipas; de la Torre (1955), forearm measurements of one male and one female from Guerrero; Felten (1956*c*), external measurements (mean, range) of 33 males and 23 females and cranial measurements (mean, range) of 19 females and eight females from El Salvador; Felten (1956*d*), cranial measurements of a single specimen from El Salvador; Jones (1958), cranial measurements (mean, range) of three males and seven females (combined) from Tamaulipas; Koopman (1958), cranial measurements of a sub-Recent fossil from Cuba and the range of these measurements in seven specimens from Tamaulipas; Hall and Kelson (1959), external and cranial measurements of a male and female from Costa Rica; Burt and Stirton (1961), forearm and cranial measurements (range) of 14 males and 23 females; Goodwin and Greenhall (1961), forearm measurements (range) of 15 males and 16 females and cranial measurements of one male and one female from Trinidad; Husson (1962), external and cranial measurements of a male and five females from Surinam; Tamsitt and Valdivieso (1962), external measurements of a male from Colombia and a large male reported from Colombia by Hershkovitz (1949); Tamsitt and Valdivieso (1963*a*), external measurements of one male and one female from Colombia; Valdivieso (1964), external measurements of a

specimen from Colombia; Aellen (1965), forearm measurements of two males, the range of eight females, and cranial measurements of one male from Perú; Brosset (1965), external measurements of two males and a female and cranial measurements of a male and female from Ecuador; Tamsitt and Valdivieso (1966*a*), forearm and cranial measurements of one male and the range of four females from Colombia; Villa-R. (1967), external measurements (mean, SD, range) of 53 specimens and cranial measurements (mean, SD, range) of 42 specimens from México; Genoways and Jones (1968), forearm measurements (mean, range) of 10 young specimens (seven males, three females) from Zacatecas; Goodwin (1969), forearm and cranial measurements of seven males and seven females from Oaxaca; Anderson (1972), external measurements (mean, SD, range) of 21 specimens and cranial measurements (mean, SD, range) of six specimens from Chihuahua; Smith and Genoways (1974), external and cranial measurements of a male from Margarita Island, Venezuela, and mean and range of four males from the adjacent mainland; Woloszyn and Mayo (1974), cranial measurements of the holotype of the sub-Recent *D. r. puntajudensis* from Cuba, one sub-Recent specimen from México, 10 Recent specimens (mean, range) from México, and measurements after Koopman (1958) and Husson (1962).

Individual variation.—In specimens from Guerrero, coefficients of variation for external measurements of sexes combined varied from 2.51 to 16.80 and for cranial measurements from 1.48 to 4.41 (Martinez and Villa-R., 1940).

Secondary sexual variation.—Hershkovitz (1949) noted that males were smaller than females, and Husson (1962) concluded from published accounts that males were smaller than females.

Geographic variation.—Measurements of individuals from Surinam agreed well, according to Husson (1962), with those from Colombia (Hershkovitz, 1949) and Trinidad (Goodwin and Greenhall, 1961).

Diaemus youngii (Jentink, 1893)

Measurements of *Diaemus youngii* have been recorded as follows: Jentink (1893), external measurements of the male holotype of *D. y. youngii* from Guyana; Thomas (1928*b*), external and cranial measurements of the female holotype of *D. y. cypselinus* from Perú; Cunha Vieira (1942), external and cranial measurements of a male and female from Brazil; Sanborn (1949), external and cranial measurements of one specimen from Venezuela and another from Perú; Goodwin and Greenhall (1961), forearm measurements of one male and two females and cranial measurements of one male and female from Trinidad; Husson (1962), external and cranial measurements of the holotype from Guyana; Lay (1962), external and cranial measurements of a male and female from Tabasco; Villa-R. (1965), external and cranial measurements of a female from Tamaulipas; Villa-R. (1967), external and cranial measurements of a specimen from México; Gardner *et al.* (1970), external and cranial measurements of a male from Costa Rica; Smith and Genoways (1974), external and cranial measurements of one specimen from Margarita Island, Venezuela, three males (mean, range) and one female from the adjacent mainland, and the holotype of *D. youngii*.

Geographic variation.—Gardner *et al.* (1970) reported that measurements of their Costa Rican specimen were much larger than the holotype of *D. y. youngii* from Guyana but that it agreed closely with the holotype of *D. y. cypselinus* from Perú and with a specimen from Tamaulipas recorded by Villa-R. (1965). Measurements of two specimens from Tabasco (Lay, 1962) were somewhat larger than those of a specimen from Costa Rica (Gardner *et al.*, 1970).

Diphylla ecaudata Spix, 1823

Measurements of *Diphylla ecaudata* are recorded as follows: Dobson (1878*a*), external measurements of a specimen from Brazil; H. Allen (1896), external measurements of two

specimens and cranial measurements of one from México; Thomas (1903*b*), external and cranial measurements of the male holotype of *D. e. centralis* from Panamá; Elliot (1904), external and cranial measurements of the male holotype of *D. e. centralis* from Panamá (after Thomas, 1903*b*) and another specimen; Lima (1926), external measurements of a specimen from Brazil; Sanborn (1936), external and cranial measurements of one female from Ecuador; Cunha Vieira (1942), external and cranial measurements of a male from Brazil; Goodwin (1942*a*), external and cranial measurements of two males from Honduras; Goodwin (1946), external and cranial measurements of two males from Honduras (as given by Goodwin, 1942*a*) and the holotype of *D. e. centralis* from Panamá; Dalquest (1950), cranial measurements (mean) of seven males and three females from San Luis Potosí; Dalquest (1953*a*), external measurements (mean) for two males and 13 females and cranial measurements (mean) of seven males and three females from San Luis Potosí; de la Torre (1954), external and cranial measurements of a male from Tamaulipas; Felten (1956*c*), cranial measurements of five males from El Salvador; Felten (1956*d*), external measurements of one specimen from El Salvador; Hall and Kelson (1959), external and cranial measurements of the holotype of *D. e. centralis*; Burt and Stirton (1961), forearm and cranial measurements (range) of six males and nine females from El Salvador; Villa-R. (1967), external measurements of 20 specimens and cranial measurements of 19 from México; Reddell (1968), external measurements of one female from Texas; Goodwin (1969), forearm and cranial measurements of a male from San Luis Potosí and a female from Yucatán; Ojasti and Linares (1971), forearm measurements (mean, SE, range) of 16 males and 10 females and cranial measurements of 10 males and nine females from Venezuela; Starrett (1976), forearm measurement of a single female from Costa Rica.

Geographic variation.—Ojasti and Linares (1971) compared length of forearm and length of skull of specimens of *Diphylla ecaudata* from Central and South America. They concluded that these populations were sufficiently distinct to warrant recognition as separate subspecies.

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APPENDIX 1.—*Selected measurements of phyllostomatid bats. Museum acronyms used are as follows: AMNH, American Museum of Natural History; AS, Albert Schwartz Collection; BMNH, British Museum (Natural History), CM, Carnegie Museum of Natural History, COLU, Department of Biology, Colgate University; FHKSC, Museum of the High Plains, Fort Hays Kansas State College; KU, Museum of Natural History, University of Kansas; LACM, Natural History Museum of Los Angeles County; LSU, Museum of Zoology, Louisiana State University; ROM, Royal Ontario Museum; TCWC, Texas Cooperative Wildlife Collection, Texas A&M University; TTU, The Museum, Texas Tech University; USNM, National Museum of Natural History.*

Museum, catalogue no., and sex	Locality	Forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Postorbital constriction	Breadth of braincase	Length of maxillary toothrow	Breadth across upper molars
			Phyllostomatinae						
			Chrotopterus auritus						
KU 23661 ♀	Veracruz	78.9	36.7	31.2	19.2	5.9	13.4	12.9	12.0
KU 93385 ♀	Yucatán	78.7	36.2	31.1	18.5	6.3	13.3	12.7	11.5
USNM 305204 ♀	Panamá	83.1	37.8	31.8	19.5	6.2	14.0	13.5	12.4
USNM 335156 ♀	Panamá	82.5	37.1	31.7	19.6	6.2	14.5	13.2	12.6
TTU 9339 ♂	Veracruz	81.1	35.7	30.4	18.5	5.9	12.9	13.0	12.0
KU 23622 ♂	Veracruz	79.1	35.7	30.6	18.1	6.1	12.9	13.0	11.6
KU 93383 ♂	Yucatán	80.8	36.0	31.0	18.2	6.3	13.3	12.9	11.6
KU 105962 ♂	Nicaragua	79.8	36.2	31.0	18.2	6.0	13.2	12.6	11.3
			Lonchorhina aurita						
USNM 305186 ♀	Panamá	50.5	20.0	17.9	10.4	4.8	8.4	6.3	7.0
TTU 5320 ♀	Trinidad	47.1	20.8	19.1	10.4	4.9	8.9	6.7	7.1
TTU 5322 ♀	Trinidad	50.3	20.5	18.6	10.8	4.9	8.8	6.6	7.0
TTU 8984 ♀	Trinidad	51.1	20.6	18.7	10.8	4.9	8.9	6.6	7.0
TTU 5321 ♂	Trinidad	49.0	20.7	18.9	10.5	4.9	8.7	6.6	7.0
TTU 5323 ♂	Trinidad	50.0	20.4	19.0	10.8	4.8	8.7	6.6	7.1
TTU 9827 ♂	Trinidad	49.9	20.7	18.7	10.4	5.0	8.7	6.6	7.1
TTU 9829 ♂	Trinidad	49.8	20.5	18.7	10.4	4.9	8.7	6.6	7.0
			Lonchorhina orinocensis						
USNM 373254 ♀	Venezuela	42.3	19.0	16.4	9.3	4.0	8.0	5.9	6.0
USNM 373255 ♀	Venezuela	42.2	19.1	16.4	9.6	4.1	8.2	5.9	6.0
USNM 373256 ♀	Venezuela	43.7	19.2	16.8	9.6	4.2	8.0	6.0	6.0
USNM 373260 ♀	Venezuela	41.5	18.3	16.2	9.1	3.8	8.2	5.7	5.7
USNM 373248 ♂	Venezuela	41.4	19.5	17.0	9.7	4.2	8.3	6.0	5.9
USNM 373249 ♂	Venezuela	42.6	19.5	17.0	9.6	4.0	8.0	6.3	6.1
USNM 373257 ♂	Venezuela	41.5	19.3	17.0	9.7	4.0	8.3	6.0	5.9
USNM 373258 ♂	Venezuela	43.0	19.5	16.8	9.8	4.0	8.1	6.1	6.1
			Macrophyllum macrophyllum						
AMNH 177666 ♀	Nicaragua	36.9	17.1	14.5	9.2	3.4	8.2	5.5	6.1
AMNH 177669 ♀	Nicaragua	36.2	17.0	14.7	9.5	3.1	7.8	5.7	6.4
AMNH 177670 ♀	Nicaragua	37.4	17.4	14.7	9.5	3.0	8.0	5.5	6.2
AMNH 177671 ♀	Nicaragua	37.4	17.1	14.7	9.4	3.0	8.1	5.6	6.2
KU 70478 ♂	Nicaragua	35.6	16.6	13.6	9.2	3.0	7.8	5.2	6.1
USNM 311944 ♂	Panamá	35.0	16.8	14.2	8.9	3.2	7.8	5.5	6.1
USNM 312963 ♂	Panamá	37.2	17.7	14.9	9.8	3.2	8.0	5.7	6.7
USNM 315212 ♂	Panamá	34.3	17.2	14.2	10.0	3.2	8.0	5.7	6.8
			Macrotus californicus						
FHKSC 2442 ♀	Arizona	49.0	22.7	19.9	10.4	3.3	8.1	8.9	7.4
TTU 10529 ♀	Sonora	49.4	22.3	19.9	10.8	3.5	8.1	9.0	7.0
TTU 10584 ♀	Sonora	51.8	22.9	20.7	11.2	3.5	9.0	8.8	7.1

APPENDIX 1.—*Continued.*

TTU 10588 ♀	Sonora	51.7	23.0	20.4	11.2	3.7	8.4	8.9	7.0
FHKSC 1994 ♂	Arizona	50.7	23.2	20.5	11.4	3.8	8.5	8.7	7.5
TTU 10582 ♂	Sonora	49.7	23.8	20.1	11.7	3.5	8.5	9.5	7.4
TTU 10585 ♂	Sonora	48.3	22.6	20.2	10.6	3.6	8.1	8.9	7.0
TTU 10587 ♂	Sonora	50.0	23.2	20.1	11.1	3.6	8.3	9.2	7.3
		Macrotus waterhousii							
TTU 10566 ♀	Sonora	49.2	22.2	19.5	10.6	3.9	8.5	8.4	7.2
TTU 21470 ♀	Jamaica	53.9	25.3	21.5	12.2	4.1	9.2	9.4	7.8
TTU 21471 ♀	Jamaica	55.0	25.8	21.9	12.5	4.2	9.2	9.7	8.0
TTU 21505 ♀	Jamaica	54.1	26.0	22.0	12.0	4.2	8.8	9.6	7.5
TTU 6267 ♂	Sonora	47.2	23.2	20.0	11.1	4.2	8.6	8.9	7.5
TTU 10564 ♂	Sonora	49.6	23.0	20.0	11.2	4.1	8.6	8.8	7.4
TTU 10565 ♂	Sonora	48.3	22.4	19.4	10.9	4.1	8.5	8.6	7.4
TTU 21501 ♂	Jamaica	54.7	26.4	22.0	12.4	4.4	9.5	9.7	7.9
		Micronycteris behni							
BMNH 69.5.13.3 ♀	Perú					4.7		8.1	7.2
		Micronycteris brachyotis							
USNM 323059 ♀	Panamá	42.2	22.4	19.3	11.4	5.0	9.0	8.3	7.3
TTU 5237 ♀	Trinidad	39.4	21.3	18.5	10.2	5.0	8.6	8.1	6.7
TTU 5315 ♀	Trinidad	40.9	21.6	19.0	10.4	5.1	8.4	8.6	6.9
AMNH 175633 ♀	Trinidad	40.3	21.4	18.7	10.5	5.0	8.5	8.1	6.9
USNM 245153 ♂	Guatemala	40.9	21.7	19.3	10.7	5.1	8.7	8.2	6.9
USNM 306546 ♂	Panamá	40.8	22.8	19.9	11.1	5.2	8.9	8.2	7.0
USNM 323060 ♂	Panamá	40.2	21.3	18.7	10.8	4.8	8.4	7.9	6.9
TTU 5314 ♂	Trinidad	39.4	21.9	19.2	10.5	5.2	8.9	8.2	7.0
		Micronycteris daviesi							
BMNH 64.767 ♀	Guyana	57.1	27.3	23.7	13.3	6.5	10.8	11.0	9.3
USNM 335104 ♂	Panamá	54.0	27.3	23.5	13.2	6.7	10.5	10.7	9.2
USNM 460089 ♂	Brazil	54.7	26.1	22.8	12.8	6.2	10.6	10.5	9.1
		Micronycteris hirsuta							
TTU 13158 ♀	Nicaragua	42.5	23.8	20.6	11.8	5.0	8.4	9.4	7.3
CM 2659 ♀	Colombia	42.9	23.0	19.9	11.3	4.7	8.9	8.8	6.9
USNM 418876 ♀	Venezuela	42.2	24.0	20.6	11.6	4.8	8.6	9.3	7.5
TTU 5299 ♀	Trinidad	43.0	23.8	20.6	11.8	5.2	8.8	9.4	7.5
TTU 13155 ♂	Nicaragua	39.5	22.8	19.4	11.0	4.7	8.5	8.7	7.2
TTU 5410 ♂	Trinidad	42.1	24.0	20.2	11.6	5.0	8.9	9.2	7.4
TTU 5449 ♂	Trinidad	42.3	23.7	20.3	11.3	4.9	8.7	8.9	7.2
TTU 10116 ♂	Trinidad	42.7	24.3	20.7	11.5	5.0	8.5	9.2	7.3
		Micronycteris megalotis							
KU 70474 ♀	Nicaragua	38.0	20.2	17.4	9.7	4.2	8.0	7.5	6.5
KU 97407 ♀	Nicaragua	33.6	19.6	17.2	9.2	4.1	7.7	7.1	6.2
KU 97409 ♀	Nicaragua	36.7	19.6	17.1	9.0	3.9	7.7	7.3	6.3
KU 114772 ♀	Nicaragua	34.7	18.6	16.3	9.1	4.0	7.4	7.0	6.0
TTU 5438 ♂	Trinidad	32.6	18.4	16.0	8.9	4.0	7.5	6.9	6.0
TTU 5446 ♂	Trinidad	35.5	19.1	16.3	8.7	3.9	7.5	7.0	5.9
TTU 5495 ♂	Trinidad	32.2	18.7	16.2	8.6	3.8	7.4	6.9	6.0
TTU 9788 ♂	Trinidad	33.3	18.8	16.1	8.8	4.1	7.5	7.1	5.9
		Micronycteris minuta							
TTU 5226 ♀	Trinidad	36.5	18.5	15.9	8.6	4.3	7.6	6.6	5.7
TTU 5437 ♀	Trinidad	35.6	18.6	15.8	8.6	4.0	7.5	6.5	5.7
TTU 5443 ♀	Trinidad	34.6	18.4	16.0	8.4	4.0	7.6	6.5	5.5
TTU 5444 ♀	Trinidad	36.5	18.8	16.4	8.5	4.0	7.5	6.7	5.6
TTU 5225 ♂	Trinidad	35.3	18.8	16.5	8.6	4.2	7.4	6.8	5.6
TTU 5239 ♂	Trinidad	35.2	18.7	16.5	8.7	4.1	7.6	6.4	5.5
TTU 5294 ♂	Trinidad	34.9	18.3	16.0	8.7	4.2	7.5	6.7	5.5
TTU 5295 ♂	Trinidad	35.5	19.0	16.2	8.3	4.0	7.4	6.7	5.5

APPENDIX 1.—*Continued.*

		Micronycteris nicefori							
TTU 5257 ♀	Trinidad	40.2	22.0	19.6	9.8	4.5	8.3	7.8	6.3
TTU 5297 ♀	Trinidad	40.0	21.4	19.3	9.5	4.1	8.2	7.7	6.0
TTU 5298 ♀	Trinidad	38.8	21.2	19.9	9.4	4.2	7.6	7.6	6.3
TTU 8954 ♀	Trinidad	38.4	21.1	19.0	9.8	4.4	8.3	7.5	6.3
TTU 8963 ♂	Trinidad	36.8	21.1	18.9	9.5	4.0	8.0	7.6	6.2
TTU 8964 ♂	Trinidad	37.1	20.7	18.2	9.5	4.3	8.3	7.2	6.3
TTU 8965 ♂	Trinidad	36.3	20.8	18.7	9.6	4.2	8.2	7.6	6.1
TTU 8966 ♂	Trinidad	39.1	20.8	18.4	9.3	4.0	8.5	7.5	6.3
		Micronycteris pusilla							
AMNH 78830 ♂	Brazil	34.3		15.2	8.9	4.2	7.6	6.7	5.7
AMNH 78831 ♂	Brazil	33.7	17.8	15.4		4.5	7.8	6.8	6.0
		Micronycteris schmidtorum							
USNM 388704 ♀	Venezuela	34.7	19.5	16.9	9.3	4.2	7.5	7.5	6.1
USNM 388713 ♀	Venezuela	34.2	19.8	17.1	9.2	4.4	7.7	7.4	6.0
USNM 407257 ♀	Venezuela	33.9	19.4	17.1	9.4	4.2	7.9	7.2	6.1
USNM 415210 ♀	Venezuela	35.1	18.9	17.0	9.1	4.1	7.4	7.4	5.9
AMNH 130715 ♂	Venezuela	36.9	20.0	17.7	9.7	4.2	7.8	7.8	6.5
AMNH 130718 ♂	Venezuela	36.0	20.1	17.4	9.5	4.0	7.6	7.5	6.4
AMNH 130725 ♂	Venezuela	36.8	20.2	17.8	9.8	4.1	7.6	7.8	6.7
USNM 444235 ♂	Venezuela	37.3	20.2	17.7	9.6	4.2	7.6	7.9	6.6
		Micronycteris sylvestris							
KU 96970 ♀	Nayarit	43.8	21.2	18.7	10.2	4.9	8.5	8.4	6.7
KU 23646 ♀	Veracruz	42.1	20.5	18.7	10.4	4.8	8.5	8.4	7.0
USNM 396399 ♀	Panamá	42.0	19.8		10.7	4.5	8.7	7.9	7.2
KU 23651 ♂	Veracruz	41.2	21.0	18.7	10.2	4.9	8.6	8.3	7.0
KU 23653 ♂	Veracruz	40.3	20.7	18.5	10.1	4.9	8.4	8.1	6.9
KU 29594 ♂	Veracruz	38.3	21.0	18.7	10.2	4.9	8.8	8.5	6.9
BMNH 96.10.1.2 ♂	Costa Rica	39.5	20.1	17.1	9.9	4.5	8.2	7.9	6.8
		Mimon bennettii							
BMNH 3.7.1.153 ♀	Brazil	56.6	26.1	22.8	13.8	4.6	9.8	9.4	9.1
BMNH 3.7.1.155 ♀	Brazil	56.0	25.4	21.8		4.6	9.8	9.0	8.6
USNM 391027 ♀	Brazil	58.4	26.3	22.9	14.1	4.7	10.0	9.4	9.5
BMNH 65.618 ♂	Guyana	53.1	25.6	22.0	13.9	4.5	9.6	9.0	9.5
USNM 123393 ♂	Brazil	53.7	24.5	21.8		4.7	9.1	9.1	9.3
		Mimon cozumelae							
KU 23658 ♀	Veracruz	57.5	26.7	23.3	14.3	4.8	10.1	9.5	9.7
KU 32092 ♀	Veracruz	55.1	26.1	22.6	14.2	4.4	10.0	9.5	9.8
KU 91548 ♀	Yucatán	59.0	27.0	23.0	13.8	4.5	9.6	9.5	9.3
KU 93380 ♀	Yucatán	54.9	25.2	22.1	13.6	4.4	9.8	9.1	8.8
KU 19171 ♂	Veracruz	55.1	26.5	22.6	13.3	4.5	9.9	9.4	9.4
KU 23656 ♂	Veracruz	55.4	26.0	22.2	13.8	4.6	9.9	9.4	9.7
KU 91546 ♂	Yucatán	56.4	25.6	22.5	13.1	4.4	9.5	9.3	8.8
TTU 9340 ♂	Yucatán	56.6	26.0	22.7	13.8	4.7	9.8	9.1	9.1
		Mimon crenulatum							
USNM 371497 ♀	Venezuela	48.8	21.3	18.5	11.7	3.9	8.7	7.6	8.4
USNM 371503 ♀	Venezuela	50.4	21.9	18.9	12.1	3.8	8.8	7.7	7.9
TTU 5340 ♀	Trinidad	45.9	22.0	19.2	12.5	4.0	8.4	7.9	9.0
TTU 5374 ♀	Trinidad	48.7	22.6	19.5	12.0	4.3	8.6	7.7	8.4
TTU 5264 ♂	Trinidad	47.0	21.6	18.7	11.6	3.9	7.9	7.5	8.5
TTU 5375 ♂	Trinidad	51.0	22.4	19.6	11.8	4.2	8.7	7.6	8.6
TTU 5379 ♂	Trinidad	47.3	21.6	18.5	11.7	3.9	8.4	7.7	8.4
TTU 5460 ♂	Trinidad	48.2	21.9	19.0	11.7	4.1	8.3	7.7	8.5
		Mimon koepckeae							
LSU 16447 ♀	Perú*	47.4	21.9	18.9	11.6	4.2	8.6	7.5	8.2
LSU 15675 ♂	Perú	46.3	21.7	18.5	11.4	4.1	8.3	7.1	8.0
LSU 15676 ♂	Perú	49.8	21.5	18.9	11.7	3.9	8.2	7.4	8.1

APPENDIX 1.—*Continued.*

		Phylloderma stenops							
USNM 388843 ♀	Venezuela	71.8	30.9	26.0	14.9	8.9	12.7	9.7	9.7
USNM 388844 ♀	Venezuela	71.6	32.2	28.3	16.0	9.2	13.4	10.0	10.2
USNM 388848 ♀	Venezuela	71.2	30.3	26.3	14.8	9.0	12.9	9.7	9.4
TTU 5318 ♀	Trinidad	65.8	30.0	25.3	14.6	8.9	12.1	9.6	9.8
USNM 335144 ♂	Panamá	73.4	31.8	27.3	15.6	9.1	13.0	10.2	9.6
USNM 388842 ♂	Venezuela	72.2	31.2	27.4	14.7	8.9	12.7	9.8	9.6
USNM 388845 ♂	Venezuela	69.5	30.3	26.5	14.7	8.7	12.7	9.6	9.4
USNM 388846 ♂	Venezuela	73.3	30.8	26.5	16.3	9.0	13.1	10.3	10.6
		Phyllostomus discolor							
KU 114811 ♀	Nicaragua	61.7	30.8	27.1	15.0	6.5	12.1	9.5	10.3
KU 114812 ♀	Nicaragua	64.9	31.8	26.8	16.1	6.6	12.2	9.9	10.5
KU 114813 ♀	Nicaragua	61.6	29.5	26.2	15.3	6.2	11.7	9.5	10.0
TTU 5452 ♀	Trinidad	59.9	29.7	25.6	15.4	6.2	12.1	9.0	9.6
KU 110701 ♂	Nicaragua	62.9	31.0	27.3	15.5	6.6	11.8	9.8	10.0
KU 110702 ♂	Nicaragua	64.3	32.1	28.5	16.4	6.4	12.6	10.0	10.4
KU 114800 ♂	Nicaragua	61.8	31.7	28.5	16.1	6.6	12.3	9.8	10.4
TTU 5412 ♂	Trinidad	60.9	30.5	27.0	15.4	6.3	11.9	9.6	9.8
		Phyllostomus elongatus							
USNM 364304 ♀	Perú	67.5	30.6	26.3	16.1	5.4	10.9	10.6	11.2
USNM 364306 ♀	Perú	66.2	30.0	25.2	16.7	5.4	11.1	10.3	11.4
USNM 364310 ♀	Perú	64.3	29.0	25.2	16.6	5.3	10.9	10.2	11.3
USNM 499015 ♀	Perú	64.6	29.0	25.4	16.3	5.4	10.8	10.0	11.3
USNM 483339 ♂	Colombia	60.8	28.9	24.7	15.4	5.1	10.5	10.3	11.0
USNM 361515 ♂	Brazil	64.5	30.5	25.6	16.5	5.3	10.9	10.3	11.5
USNM 364303 ♂	Perú	67.2	30.2	25.8	16.9	5.7	11.2	10.4	11.3
USNM 364305 ♂	Perú	67.7	29.1	25.5	16.5	5.6	10.8	10.1	11.0
		Phyllostomus hastatus							
KU 110716 ♀	Nicaragua	90.4	39.3	33.9	21.0	7.3	14.9	13.2	13.5
KU 110717 ♀	Nicaragua	92.6	40.7	34.3	21.3	7.1	14.6	14.1	14.2
KU 110720 ♀	Nicaragua	88.2	40.8	34.5	21.9	7.3	15.1	13.9	14.4
CM 2667 ♀	Colombia	84.7	38.9	32.5	20.7	7.2	14.2	13.0	14.0
KU 110718 ♂	Nicaragua	91.1	41.5	35.8	22.4	7.7	15.2	14.3	14.3
KU 110719 ♂	Nicaragua	94.4	43.1	36.1	23.2	7.7	15.5	13.8	14.3
ROM 31469 ♂	Trinidad	82.8	37.6	32.1	19.9	6.8	13.8	12.8	12.8
ROM 50233 ♂	Brazil	86.9	39.0	32.5	21.0	7.4	14.1	12.9	13.9
		Phyllostomus latifolius							
BMNH 1.6.4.44 ♀	Guyana	59.6	28.0	23.5	15.1	4.9	10.3	10.0	10.3
BMNH 1.6.4.45 ♀	Guyana	59.8	28.4	24.0	15.1	5.2	10.4	9.9	10.7
BMNH 1.6.4.40 ♂	Guyana	58.7	28.3	24.1	15.5	5.1	10.3	10.0	10.5
BMNH 1.6.4.41 ♂	Guyana	59.2	28.3	24.4		4.8	10.3	10.4	10.6
BMNH 1.6.4.42 ♂	Guyana	58.9	28.6	24.5	15.8	5.1	10.4	10.3	11.2
BMNH 1.6.4.43 ♂	Guyana	58.5	28.2	24.1	15.8	5.0	10.5	10.0	10.9
		Tonatia bidens							
USNM 315218 ♀	Panamá	58.8	28.9	24.0	14.0	5.7	10.7	9.7	8.9
TTU 5260 ♀	Trinidad	55.8	27.9	23.7	13.7	5.3	10.2	9.6	8.3
TTU 9774 ♀	Trinidad	54.8	28.3	24.1	14.3	5.4	10.6	9.3	8.4
TTU 9778 ♀	Trinidad	55.2	28.3	23.5	14.0	5.2	10.4	9.6	8.6
TTU 13108 ♂	Nicaragua	57.0	28.9	24.5	14.5	5.7	10.6	10.4	9.4
TTU 5261 ♂	Trinidad	55.1	28.6	24.2	14.5	5.6	10.6	9.6	8.5
TTU 5338 ♂	Trinidad	54.9	27.6	23.1	13.9	5.1	10.7	9.4	8.4
TTU 5339 ♂	Trinidad	51.5	27.3	23.1	13.8	5.6	10.6	9.5	8.6
		Tonatia brasiliense							
AMNH 95497 ♀	Perú	35.7	20.0	16.6	9.4	3.3	8.1	6.8	6.5
AMNH 95498 ♂	Brazil	35.8	20.0	17.0	9.5	3.2	7.9	6.8	6.3
LSU 16440 ♂	Perú	37.9	20.8	17.0	9.4	3.2	8.3	6.8	6.1

APPENDIX 1.—*Continued.*

		Tonatia carrikeri							
AMNH 30180 ♀	Venezuela	46.0	25.2	20.3	11.5	3.6	9.4	8.0	7.8
AMNH 30183 ♀	Venezuela	46.8	24.8	20.0	10.8	3.6	9.3	8.3	7.5
AMNH 209322 ♀	Bolivia	45.6	24.5	20.2	11.1	3.6	9.4	8.1	7.7
AMNH 30181 ♂	Venezuela	48.4	25.8	21.5	12.2	3.9	9.7	8.6	8.0
ROM 67468 ♂	Guyana	43.9	23.9	19.5	11.5	3.7	9.4	7.8	7.3
		Tonatia minuta							
USNM 314221 ♀	Panamá	33.3	18.9	15.8	8.8	2.9	7.6	6.7	5.8
USNM 362457 ♀	Panamá	34.0	19.2	16.3	9.0	2.9	7.8	6.8	6.2
USNM 362458 ♀	Panamá	35.0	19.2	16.0	9.2	3.0	7.6	6.7	6.1
TTU 5238 ♀	Trinidad	35.8	20.1	16.9	9.6	2.9	8.0	6.9	6.2
TTU 5222 ♂	Trinidad	36.3	20.2	16.8	9.6	3.2	8.4	7.0	6.1
TTU 5309 ♂	Trinidad	34.5	20.2	16.8	9.6	3.1	8.2	6.7	6.4
TTU 5422 ♂	Trinidad	35.5	20.6	17.6	10.0	3.4	8.5	7.0	6.7
TTU 10119 ♂	Trinidad	35.2	20.8	17.3	10.0	3.3	8.4	6.9	6.4
		Tonatia silvicola							
USNM 306549 ♀	Panamá	51.6	27.0	22.8	12.9	3.9	10.5	8.9	8.1
USNM 309357 ♀	Panamá	50.0	26.4	22.2	12.7	3.9	10.1	9.5	8.7
USNM 323068 ♀	Panamá	53.3	26.7	22.6	12.9	3.9	10.2	9.0	8.3
USNM 364278 ♀	Perú	55.0	28.7	23.6	13.1	4.0	10.4	9.8	9.0
USNM 323074 ♂	Panamá	54.7	27.9	23.1	13.5	4.1	10.6	9.3	8.8
USNM 323076 ♂	Panamá	53.5	27.8	23.3	13.3	4.1	10.5	9.2	8.7
USNM 407291 ♂	Venezuela	51.4	28.3	23.6	13.7	4.3	11.1	9.7	8.6
USNM 364275 ♂	Perú	55.2	30.4	24.8	14.1	4.1	10.8	10.4	9.6
		Tonatia venezuelae							
USNM 102919 ♀	Venezuela	39.8	21.5	17.9	10.5	3.1	8.3	7.5	6.9
USNM 142567 ♀	Venezuela	38.9	21.7	17.9	10.0	3.2	8.3	7.4	6.7
BMNH 11.5.25.41 ♂	Venezuela	39.1	21.5	17.7	10.6	3.4	8.6	7.4	7.0
		Trachops cirrhosus							
KU 93381 ♀	Campeche	57.9	27.8	24.1	13.6	5.0	11.1	9.7	9.7
TTU 13172 ♀	Costa Rica	60.1	28.0	24.2	13.8	5.3	11.5	10.3	9.7
TTU 9777 ♀	Trinidad	60.1	29.0	25.4	14.8	5.3	11.9	10.8	10.4
TTU 9780 ♀	Trinidad	61.2	29.6	25.7	14.9	5.2	11.7	11.4	10.5
TTU 6077 ♂	Oaxaca	59.3	28.2	24.5	13.8	5.0	11.5	10.0	9.7
TTU 6115 ♂	Chiapas	59.5	28.2	24.5	13.5	4.9	11.1	10.1	9.8
KU 114818 ♂	Nicaragua	57.3	27.6	24.2	13.9	4.8	11.4	9.8	9.4
TTU 9779 ♂	Trinidad	60.7	30.4	26.4	15.4	5.5	12.1	11.1	10.8
		Vampyrum spectrum							
USNM 335161 ♀	Panamá	106.0	51.9	43.1	24.5	8.5	15.9	20.2	14.8
USNM 335162 ♀	Panamá	107.1	53.6	43.7	25.4	7.9	15.6	19.8	15.0
TTU 5357 ♀	Trinidad	102.0	51.2	42.9	23.3	8.0	15.8	20.9	14.5
TTU 9837 ♀	Trinidad	103.3	51.6	44.0	23.4	7.7	15.7	21.1	15.4
AMNH 28993 ♂	Nicaragua	105.7	50.4	42.3	24.5	8.0	15.6	19.7	14.4
KU 88190 ♂	Costa Rica	110.4	50.7	43.0	23.4	8.1	15.8	19.9	14.3
TTU 9836 ♂	Trinidad	106.1	52.4	44.1	24.2	7.8	15.8	21.1	15.2
TTU 11439 ♂	Trinidad	107.1	52.0	43.2	25.2	8.4	16.4	20.6	15.4
		Glossophaginae							
		Anoura brevirostrum							
AMNH 214324 ♀	Perú	39.8	23.5	22.5	9.6	5.0	9.4	8.3	5.7
AMNH 233263 ♀	Perú	38.9	23.3	22.3	9.4	4.9	9.1	8.0	5.4
TCWC 11881 ♀	Perú	38.0	23.1	22.3	9.4	4.8	9.2	7.7	5.3
TCWC 11882 ♀	Perú	40.0	23.1	22.0	9.5	4.6	9.2	8.2	5.6
LSU 17941 ♂	Perú	40.2	23.3	22.6	10.3	5.0	9.3	8.0	5.7
TCWC 11880 ♂	Perú	39.6	23.3	22.5	10.0	4.8	9.3	8.1	5.4
		Anoura caudifer							
USNM 373705 ♀	Venezuela	38.5	24.6	23.8	9.5	4.6	9.3	9.1	5.5
USNM 373761 ♀	Venezuela	36.0	22.0	21.3	8.9	4.3	8.6	8.0	5.3

APPENDIX 1.—*Continued.*

USNM 389076 ♀	Venezuela	35.1	22.1	21.4	9.1	4.6	8.9	8.2	5.6
USNM 389108 ♀	Venezuela	36.4	23.0	22.3	9.2	4.6	8.9	8.3	5.3
USNM 370109 ♂	Venezuela	37.2	24.0	23.2	9.4	4.6	8.8	8.8	5.3
USNM 373704 ♂	Venezuela	37.4	24.3	23.4	10.1	4.6	9.2	8.9	5.8
USNM 385771 ♂	Venezuela	36.8	22.0	21.5	9.3	4.5	9.0	8.0	5.3
USNM 385773 ♂	Venezuela	37.2	22.0	21.3	9.3	4.4	9.0	8.0	5.4
		Anoura cultrata							
USNM 309400 ♀	Panamá	43.8	26.4	25.5	10.9	5.0	10.0	9.3	6.0
USNM 319249 ♀	Panamá	41.7	26.3	25.5	10.3	5.1	10.0	9.2	6.0
USNM 419465 ♀	Venezuela	41.4	25.4	24.6	10.6	5.0	9.8	8.9	6.2
USNM 419466 ♀	Venezuela	41.1	25.6	24.5	10.4	5.0	10.0	8.7	6.2
USNM 309396 ♂	Panamá	43.0	26.4	25.6	10.7	5.3	10.3	9.1	5.7
USNM 309397 ♂	Panamá	44.3	26.6	25.8	11.0	5.3	10.0	9.4	6.1
USNM 309398 ♂	Panamá	43.6	26.7	26.0	11.1	5.3	10.0	9.3	6.1
USNM 337991 ♂	Panamá	42.3	26.2	25.4	11.0	5.3	10.0	9.3	6.3
		Anoura geoffroyi							
USNM 362594 ♀	Panamá	43.7	26.3	25.7	11.0	4.9	9.8	10.1	6.3
USNM 385802 ♀	Venezuela	42.7	25.0	24.1	10.7	4.9	9.7	9.5	6.2
TTU 5825 ♀	Trinidad	42.7	25.0	24.2	10.8	4.8	9.7	9.5	6.3
TTU 8977 ♀	Trinidad	42.0	24.8	24.1	10.6	5.1	9.8	9.3	6.2
USNM 385852 ♂	Venezuela	42.0	25.3	25.1	10.8	4.8	9.7	9.5	6.0
TTU 5370 ♂	Trinidad	41.0	24.9	24.1	10.8	5.1	9.6	9.2	6.1
TTU 5823 ♂	Trinidad	43.0	24.7	24.2	11.3	5.1	9.8	9.2	6.3
TTU 5826 ♂	Trinidad	40.5	24.5	24.0	11.0	4.9	9.8	9.0	6.3
		Anoura werckleae							
LACM 25438 ♀	Costa Rica	43.1	26.1	25.3	10.5	5.2	10.1	9.3	6.0
LACM 15186 ♂	Costa Rica**	40.7	25.8	25.1	10.8	5.3	10.2	9.0	6.1
		Choeroniscus godmani							
KU 90650 ♀	Sinaloa	33.8	20.7	20.0		3.2	8.2	7.3	4.2
AMNH 186162 ♀	Oaxaca	35.1	20.8	20.1		3.2	8.4	7.3	4.2
USNM 337550 ♀	Nicaragua	34.4	21.2	20.6		3.3	8.1	7.7	4.3
USNM 337551 ♀	Nicaragua	33.8	20.6	20.4		3.5	8.0	7.6	4.2
KU 102370 ♂	Chiapas	33.4	19.7	18.8		2.9	7.9	6.9	4.2
AMNH 172778 ♂	Oaxaca	32.6	19.3	18.8		3.0	8.3	6.7	4.0
AMNH 172779 ♂	Oaxaca	33.1	18.9	18.2		2.9	8.0	6.7	3.9
AMNH 208869 ♂	Oaxaca	32.3	19.2	18.5		2.9	8.3	6.4	4.0
		Choeroniscus inca							
AMNH 140471 ♀	Guyana	37.3	24.5	24.1		3.8	8.5	8.3	4.7
BMNH 12.9.5.2 ♀	Perú	33.1				3.8	8.5	7.6	4.5
		Choeroniscus intermedius							
TTU 5319 ♀	Trinidad	34.2	23.1	22.8		3.8	8.5	7.8	4.6
TTU 5496 ♀	Trinidad	34.9	23.2	22.8		3.5	8.3	8.0	4.5
TTU 9006 ♀	Trinidad	34.8	22.6	22.5		3.5	8.4	8.1	4.4
TTU 9007 ♀	Trinidad	36.0	23.6	23.0		4.0	8.7	8.1	4.6
TTU 8994 ♂	Trinidad	34.1	22.8	21.8		3.3	8.8	7.6	4.3
TTU 8995 ♂	Trinidad	35.0	21.7	21.3		3.2	8.4	7.1	4.4
TTU 8998 ♂	Trinidad	35.4	21.2	20.7		3.2	8.2	7.5	4.2
TTU 8999 ♂	Trinidad	35.7	22.4	21.9		3.6	8.2	7.8	4.7
		Choeroniscus minor							
AMNH 69152 ♀	Guyana	36.0	22.7	21.6		3.7	8.2	7.7	4.2
USMN 361573 ♀	Brazil	33.7	23.2	22.5		3.6	8.2	8.6	4.6
USNM 361574 ♀	Brazil	35.7	22.7	22.2		3.4	8.3	8.3	4.4
USMN 460100 ♀	Brazil	35.7	23.6	22.8		3.6	8.7	8.2	4.5
		Choeroniscus periosus							
AMNH 217038 ♀	Colombia	40.4	30.0	29.2		4.8	9.3	10.5	5.0
USNM 344918 ♀	Colombia	41.2	30.2	29.5		4.9	9.8	10.9	5.3

APPENDIX 1.—*Continued.*

		Choeronycteris mexicana							
TTU 6288 ♀	Sonora	45.8	30.8	29.8		4.0	9.9	11.4	5.6
TTU 6360 ♀	Sonora	46.3	29.8	28.6		3.9	10.0	11.0	5.9
TTU 6447 ♀	Sonora	42.4	29.7	28.8		4.2	10.0	11.5	5.6
TTU 10122 ♀	Tamaulipas	45.9	29.4	28.5		4.0	9.6	11.0	5.7
KU 31863 ♂	Jalisco	45.6	30.3	29.0		4.1	9.6	11.5	5.6
KU 38250 ♂	Jalisco	45.3	29.5	28.6		4.0	9.4	11.3	5.3
KU 107192 ♂	Jalisco	43.0	29.4	28.5		3.7	9.4	11.0	5.2
KU 107194 ♂	Jalisco	43.6	30.1	28.9		3.8	9.7	11.6	5.5
		Glossophaga alticola							
KU 70624 ♀	Nicaragua	38.3	21.0	19.4	9.6	4.5	8.9	7.0	5.6
KU 70628 ♀	Nicaragua	38.1	20.4	18.8	9.7	4.5	8.9	7.0	5.7
KU 105966 ♀	Nicaragua	37.3	21.2	19.6	9.8	4.6	8.8	7.1	5.4
KU 114819 ♀	Nicaragua	36.8	20.9	19.3	9.5	4.4	8.6	7.1	5.6
KU 105964 ♂	Nicaragua	34.0	20.0	18.7	9.4	4.3	8.5	6.8	5.4
KU 105967 ♂	Nicaragua	35.8	20.1	18.4	9.4	4.6	8.9	6.9	5.3
KU 114820 ♂	Nicaragua	36.6	19.8	18.3	9.3	4.4	8.7	6.7	5.2
KU 114822 ♂	Nicaragua	36.3	20.7	19.0	9.8	4.5	9.0	7.1	5.8
		Glossophaga commissarisi							
KU 105972 ♀	Nicaragua	32.4	19.8	18.4	9.3	4.4	8.3	6.8	5.3
KU 105975 ♀	Nicaragua	32.7	20.2	18.8	9.6	4.5	8.2	6.9	5.5
KU 110770 ♀	Nicaragua	33.3	20.3	18.8	9.6	4.5	8.4	6.9	5.4
KU 110775 ♀	Nicaragua	34.5	20.4	19.0	9.3	4.3	8.1	7.1	5.4
KU 110730 ♂	Nicaragua	33.9	20.8	19.3	9.8	4.7	8.4	7.0	5.6
KU 110733 ♂	Nicaragua	31.1	20.6	18.8	9.9	4.7	8.9	6.9	5.3
KU 110734 ♂	Nicaragua	34.6	20.3	18.8	9.9	4.5	8.4	6.7	5.5
KU 110767 ♂	Nicaragua	35.6	20.7	19.1	9.4	4.4	8.5	6.7	5.1
		Glossophaga longirostris							
TTU 9338 ♀	Grenada	38.6	23.1	21.5	9.4	4.7	8.6	7.9	5.8
KU 118105 ♀	Venezuela	38.0	22.8	21.4	10.1	4.4	8.8	8.0	5.5
KU 118117 ♀	Venezuela	38.6	23.3	21.6	10.1	4.6	8.8	8.1	5.9
KU 118123 ♀	Venezuela	39.5	23.3	22.0	9.9	4.5	8.8	8.2	6.0
KU 110073 ♂	Grenada	37.5	23.1	21.5	10.2	4.5	8.6	7.9	5.7
KU 118114 ♂	Venezuela	36.4	22.2	21.1	9.8	4.5	8.8	7.6	5.9
KU 118115 ♂	Venezuela	37.6	23.0	21.2	9.8	4.4	8.8	7.7	5.8
KU 118116 ♂	Venezuela	36.3	22.8	21.4	10.1	4.7	9.4	8.0	5.8
		Glossophaga soricina							
KU 106015 ♀	Nicaragua	36.5	21.0	19.7	9.1	4.6	8.2	7.3	5.4
KU 106018 ♀	Nicaragua	36.7	21.4	19.9	9.3	4.5	8.6	6.9	5.2
KU 106019 ♀	Nicaragua	36.5	21.5	19.9	9.6	4.6	8.5	7.2	5.3
KU 106020 ♀	Nicaragua	36.0	21.9	20.6	10.0	4.9	8.9	7.7	5.7
KU 106008 ♂	Nicaragua	36.7	21.4	19.7	9.7	4.6	8.8	7.0	5.5
KU 106016 ♂	Nicaragua	35.0	20.9	19.2	9.2	4.7	8.5	7.0	5.3
KU 106021 ♂	Nicaragua	34.5	21.1	19.3	9.4	4.5	8.4	7.0	5.3
KU 106022 ♂	Nicaragua	36.8	21.7	20.1	9.7	4.5	8.6	7.3	5.4
		Hylonycteris underwoodi							
KU 108603 ♀	Jalisco	36.3	20.6	20.0		4.0	8.1	7.2	4.2
KU 108605 ♀	Jalisco	33.0	20.6	20.0		3.9	8.1	7.0	4.2
KU 98140 ♀	Oaxaca	33.9	23.0	22.0		4.5	8.8	8.2	4.9
TTU 13142 ♀	Costa Rica	32.2	21.9	21.2		4.0	8.1	7.6	4.5
KU 108604 ♂	Jalisco	31.6	20.0	19.0		4.1	8.1	6.7	4.0
KU 108606 ♂	Jalisco	32.5	20.3	19.5		3.8	8.0	7.0	4.2
KU 23709 ♂	Veracruz	33.1	21.6	20.8		4.1	8.6	7.4	4.6
KU 98139 ♂	Oaxaca	33.5	21.5	20.8		4.2	8.2	7.5	4.6
		Leptonycteris curasoae							
USNM 444799 ♀	Venezuela	53.7	28.1	26.8	11.2	5.2	9.8	9.6	7.0
USNM 444800 ♀	Venezuela	53.2	27.9	26.5	10.9	5.0	10.2	9.4	7.2
USNM 444802 ♀	Venezuela	54.4	27.5	26.7	11.0	4.7	9.6	9.3	7.3

APPENDIX 1.—*Continued.*

USNM 444803 ♀	Venezuela	54.0	27.8	26.9	10.8	4.8	9.9	9.5	6.9
USNM 444734 ♂	Venezuela	50.6	27.4	26.1	11.3	4.9	10.0	9.4	7.2
USNM 444736 ♂	Venezuela	52.6	27.1	26.1	11.2	4.7	10.1	9.1	7.0
USNM 444739 ♂	Venezuela	53.3	27.4	26.5	11.1	5.1	9.9	9.1	7.0
USNM 444740 ♂	Venezuela	53.8	27.9	26.6	11.2	5.2	10.3	9.5	7.1
			Leptonycteris nivalis						
TTU 6565 ♀	Texas	58.2	27.8	27.1	11.5	5.3	11.0	9.6	7.1
KU 33068 ♀	Coahuila	52.0	28.9	27.5	11.2	5.2	11.0	9.6	7.0
KU 33070 ♀	Coahuila	50.6	27.5	26.8	11.3	5.5	10.7	9.2	7.1
KU 33071 ♀	Coahuila	52.9	29.1	27.5	11.4	5.6	11.0	9.4	6.7
TTU 9208 ♂	Texas	56.7	27.7	26.8	11.0	5.5	10.6	9.0	6.7
KU 98378 ♂	Nuevo Leon	56.3	28.1	27.1	11.4	5.3	10.7	9.0	6.6
KU 98379 ♂	Nuevo Leon	54.8	28.4	26.8	11.4	5.5	10.9	9.0	7.0
KU 98413 ♂	Nuevo Leon	56.8	27.5	26.3	11.0	4.9	10.5	8.9	7.0
			Leptonycteris sanborni						
TTU 6564 ♀	Sonora	53.4	27.1	25.9	10.6	4.8	10.0	8.9	6.9
TTU 10603 ♀	Sonora	54.8	27.5	26.6	10.6	4.8	9.9	9.1	6.8
TTU 10604 ♀	Sonora	50.9	26.7	25.6	10.4	4.7	9.8	9.0	6.6
TTU 10605 ♀	Sonora	50.0	26.1	25.5	10.3	4.6	9.8	8.4	6.5
KU 33349 ♂	Jalisco	51.3	25.9	25.0	10.7	4.4	9.5	8.3	6.1
KU 34148 ♂	Jalisco	53.1	26.4	25.3	10.6	4.3	9.6	9.0	6.6
KU 34149 ♂	Jalisco	51.6	26.4	25.8	11.0	4.7	9.9	8.7	6.5
KU 34222 ♂	Jalisco	51.8	27.1	26.0	10.8	5.0	9.9	9.0	6.6
			Lichonycteris degener						
AMNH 95118 ♀	Brazil		18.4	17.9		4.3	8.4	6.0	4.4
AMNH 95485 ♀	Brazil	32.4							
USNM 239520 ♀	Brazil		18.8	18.2		3.8	7.9	6.0	4.2
			Lichonycteris obscura						
TTU 13124 ♀	Nicaragua	31.7	19.2	18.0		4.1	8.0	6.2	4.4
TTU 13125 ♀	Nicaragua	32.2	18.4	17.6		4.0	8.1	5.9	4.4
TTU 13126 ♀	Nicaragua	32.6	18.8	18.2		4.0	7.7	6.3	4.4
TTU 13128 ♀	Nicaragua	33.0	18.8	17.9		4.2	7.9	6.0	4.4
KU 110785 ♂	Nicaragua	30.7	18.2	17.0		3.9	7.9	5.7	4.3
TTU 13117 ♂	Nicaragua	30.3	18.0	16.8		3.9	8.1	5.5	4.2
TTU 13127 ♂	Nicaragua	32.1	18.5	17.3		4.0	8.2	5.8	4.1
TTU 18967 ♂	Nicaragua	31.9	17.9	16.9		3.9	7.9	5.5	4.5
			Lionycteris spurrelli						
USNM 385702 ♀	Venezuela	37.1	19.5	17.7		3.8	7.9	5.9	5.0
USNM 385704 ♀	Venezuela	36.8	20.3	18.8		4.2	7.9	6.4	5.3
USNM 385705 ♀	Venezuela	35.3	20.7	19.0		4.0	8.1	6.3	5.1
USNM 385706 ♀	Venezuela	34.8	19.5	17.5		4.1	7.5	6.2	5.1
BMNH 13.8.10.1 ♂	Colombia	32.5	18.9	17.1		3.7	8.0	5.9	4.6
USNM 385698 ♂	Venezuela	33.4	19.3	17.8		4.0	8.2	6.0	4.9
USNM 385699 ♂	Venezuela	35.2	19.5	18.0		4.0	7.9	6.0	4.7
USNM 239477 ♂	Brazil	35.2	19.5	18.0		4.2	8.0	6.0	5.1
			Lonchophylla concava						
TCWC 9826 ♀	Costa Rica	33.7	23.0	21.5		4.4	8.7	7.4	5.1
TCWC 9827 ♀	Costa Rica	33.7	22.8	21.5		4.6	9.1	7.6	5.3
TCWC 22528 ♀	Costa Rica	33.5	22.5	20.9		4.3	8.8	7.7	5.0
USNM 309389 ♀	Panamá	34.4	23.6	22.0		4.5	8.9	7.9	5.4
TCWC 9828 ♂	Costa Rica	34.0	22.8	21.5		4.4	8.9	7.4	5.2
TCWC 22526 ♂	Costa Rica	34.4	23.3	21.6		4.4	8.8	7.6	5.2
TCWC 22527 ♂	Costa Rica	33.7	23.1	21.7		4.3	8.8	7.5	5.0
USNM 179621 ♂	Panamá	33.5	23.5	22.1		4.5	9.0	7.9	5.5
			Lonchophylla hesperia						
TCWC 11899 ♀	Perú	38.4	27.4	26.1		4.6	9.2	8.9	5.6
TCWC 23274 ♀	Perú	38.7	26.0	24.5		4.8	9.0	8.3	5.4
USNM 283177 ♂	Perú	36.0	25.5	24.5		4.8	9.1	8.6	5.8

APPENDIX 1.—*Continued.*

		Lonchophylla mordax							
BMNH 3.9.5.32 ♂	Brazil	34.6	23.1	21.5		4.3	8.3	7.7	5.1
BMNH 3.9.5.33 ♂	Brazil	34.6	23.7	22.2		4.3	8.5	8.3	5.3
BMNH 3.9.5.34 ♂	Brazil	34.3	23.8	21.7		4.3	9.1	8.0	5.3
USNM 283008 ♂	Brazil	33.7	22.7	20.4		4.0	8.2	7.6	4.8
		Lonchophylla robusta							
TCWC 18945 ♀	Nicaragua	41.8	26.4	24.9		5.4	10.2	9.7	6.5
USNM 305237 ♀	Panamá	42.4	26.9	25.1		5.4	10.5	9.7	6.9
USNM 483361 ♀	Colombia	44.3	26.9	24.8		5.1	10.1	9.4	7.0
TCWC 11879 ♀	Perú	45.0	27.4	25.6		5.1	10.4	9.9	6.3
TCWC 18944 ♂	Nicaragua	41.0	26.5	24.8		5.4	10.2	10.0	6.7
TTU 13137 ♂	Costa Rica	43.0	27.4	25.8		5.2	10.3	9.8	6.5
TTU 13138 ♂	Costa Rica	45.1	27.1	25.4		5.3	10.3	9.8	7.0
AMNH 230214 ♂	Perú	45.2	27.0	25.9		5.0	9.8	10.1	6.4
		Lonchophylla thomasi							
USNM 335180 ♀	Panamá	32.0	21.7	20.3		4.1	8.0	7.0	5.1
USNM 483363 ♀	Colombia	31.4	21.3	19.8		4.2	8.3	6.7	5.3
ROM 33112 ♀	Guyana	32.4	21.2	19.4		4.2	8.3	6.7	5.2
AMNH 210688 ♀	Bolivia	31.8	21.8	20.2		4.2	8.0	6.8	5.2
USNM 483359 ♂	Colombia	31.0	21.7	19.7		4.2	8.6	6.9	5.4
AMNH 16120 ♂	Venezuela	31.2	20.8	19.1		4.2	8.5	6.5	5.1
ROM 31607 ♂	Guyana	31.9	20.2	18.7		4.2	8.3	6.2	5.0
ROM 33986 ♂	Guyana	33.2	20.4	18.9		4.2	8.3	6.4	5.0
		Monophyllus plethodon							
TTU 20798 ♀	Guadeloupe	41.2	23.5	22.0	10.0	4.5	9.5	7.9	5.4
TTU 20799 ♀	Guadeloupe	41.7	23.5	21.6	10.0	4.6	9.5	8.2	5.6
KU 104771 ♀	Dominica	40.2	22.8	21.2	9.6	4.4	9.2	7.8	5.2
KU 110088 ♀	St. Vincent	41.4	23.0	21.5	9.4	4.6	9.3	8.0	5.4
TTU 20795 ♂	Guadeloupe	40.1	23.5	21.4	10.3	4.5	9.5	7.8	5.5
TTU 20796 ♂	Guadeloupe	42.8	23.7	21.9	10.4	4.8	9.6	8.0	5.5
TTU 20800 ♂	Guadeloupe	41.8	23.3	21.7	10.2	4.6	9.3	7.9	5.6
TTU 9337 ♂	Dominica	40.9	23.3	21.5	10.4	4.5	9.7	7.7	5.6
		Monophyllus redmani							
TTU 22544 ♀	Haiti	39.6	22.0	20.7	8.8	4.2	8.8	7.9	5.1
TTU 22545 ♀	Haiti	40.0	21.7	20.2	9.1	4.3	9.0	7.8	5.0
TTU 22546 ♀	Haiti	39.6	21.3	19.8	9.0	4.3	8.9	7.8	5.0
TTU 22547 ♀	Haiti	39.6	21.5	20.0	9.1	4.2	9.1	7.8	4.8
TTU 22537 ♂	Haiti	39.8	21.2	20.0	9.2	3.9	8.7	7.8	4.9
TTU 22548 ♂	Haiti	41.4	21.8	20.4	9.2	4.1	9.1	7.9	5.0
TTU 22549 ♂	Haiti	40.8	22.0	20.6	9.4	4.2	9.2	7.8	4.9
TTU 22552 ♂	Haiti	41.0	22.3	20.7	9.3	4.3	9.0	7.8	5.1
		Musonycteris harrisoni							
LACM 11487 ♀	Colima	41.8	32.0	30.8		4.4	9.2	12.5	4.9
LACM 11488 ♀	Colima	41.5	31.7	30.5		4.6	9.2	11.6	4.7
USNM 314689 ♀	Colima	42.7	32.2	31.0		4.0	9.0	12.2	4.8
USNM 324971 ♀	Colima	42.4	31.5	30.5		4.2	9.0	11.7	4.8
AMNH 235179 ♂	Colima	42.4	34.4	32.9		4.0	9.1	12.3	4.5
BMNH 61.1612 ♂	Colima	42.3	34.4	33.1		4.4	9.0	13.2	4.9
KU 98874 ♂	Colima	40.8	34.5	33.3		4.1	9.1	13.6	5.0
TTU 9307 ♂	Colima	42.2	33.3	32.2		4.0	8.2	12.8	4.8
		Platalina genovensium							
USNM 268765 ♀	Perú		32.7	30.2		5.1		10.3	5.5
BMNH 27.11.19.38 ♂	Perú	46.1	32.7	30.3		4.9	10.3	10.7	5.3
FMNH 24336 ♂	Perú	48.5	31.1	29.4		4.6	9.6	10.2	5.5
MCZ 34843 ♂	Perú	49.6	31.9	29.9		4.7	9.5	10.7	5.8
MCZ 32948 ♂	Perú	50.0	32.6	30.0		4.8	9.5	11.2	5.7

APPENDIX 1.—*Continued.*

		Scleronycteris ega						
BMNH 7.1.1.671 ♀	Brazil	34.7			4.3	8.7	7.5	4.8
USNM 407889 ♂	Venezuela	35.0	22.0	21.2	4.5	8.8	7.7	5.0
		Carolliinae						
		Carollia brevicauda						
KU 110866 ♀	Nicaragua	38.9	22.0	19.4	5.2	9.2	7.0	7.6
KU 110870 ♀	Nicaragua	41.9	22.3	19.7	5.5	9.4	7.0	8.0
KU 110875 ♀	Nicaragua	39.8	22.5	19.5	5.1	9.1	6.7	7.2
KU 110878 ♀	Nicaragua	39.7	22.6	19.6	5.5	9.3	7.2	7.7
KU 110873 ♂	Nicaragua	39.9	22.5	19.9	5.6	9.6	6.7	7.6
KU 110874 ♂	Nicaragua	41.3	23.4	20.4	5.2	9.5	7.7	8.1
KU 110876 ♂	Nicaragua	39.0	22.7	20.2	5.7	9.5	7.1	8.1
KU 110877 ♂	Nicaragua	38.6	21.6	18.9	5.2	9.5	6.8	7.5
		Carollia castanea						
KU 110890 ♀	Nicaragua	36.5	19.0	17.0	5.2	8.5	6.0	6.9
KU 114871 ♀	Nicaragua	35.8	19.4	17.1	5.2	8.6	6.3	7.1
KU 114873 ♀	Nicaragua	35.8	19.4	17.0	5.2	8.9	6.3	6.9
KU 114880 ♀	Nicaragua	35.2	19.5	17.0	5.1	9.0	6.1	6.7
KU 110889 ♂	Nicaragua	35.2	19.4	17.0	5.2	8.9	6.0	6.5
KU 110892 ♂	Nicaragua	35.5	19.7	17.2	5.1	8.6	6.0	6.9
KU 114872 ♂	Nicaragua	35.9	19.9	17.4	5.1	8.8	6.3	6.8
KU 114881 ♂	Nicaragua	36.3	19.7	17.0	5.2	8.6	6.3	7.0
		Carollia perspicillata						
KU 97645 ♀	Nicaragua	42.3	23.7	20.7	5.4	9.6	7.7	7.8
KU 110791 ♀	Nicaragua	44.2	24.3	21.3	5.6	9.7	7.8	7.8
KU 114895 ♀	Nicaragua	42.7	23.4	20.5	5.3	9.5	7.5	7.7
KU 114896 ♀	Nicaragua	44.8	23.6	21.3	5.5	9.6	7.8	8.2
KU 110793 ♂	Nicaragua	44.8	24.4	21.4	5.7	9.7	8.0	8.2
KU 110805 ♂	Nicaragua	43.8	24.0	21.2	6.0	10.1	7.6	7.8
KU 110806 ♂	Nicaragua	43.0	23.9	20.7	5.3	9.6	7.8	7.8
KU 114897 ♂	Nicaragua	44.2	24.4	21.5	5.8	9.9	7.7	8.5
		Carollia subrufa						
KU 114906 ♀	Nicaragua	37.1	21.3	18.9	5.3	9.2	6.7	7.7
KU 114908 ♀	Nicaragua	39.5	21.1	18.8	5.1	9.0	6.7	7.5
KU 114915 ♀	Nicaragua	38.4	21.0	18.5	5.0	8.9	6.6	7.5
KU 114916 ♀	Nicaragua	38.9	20.8	18.4	5.2	9.0	6.6	7.4
KU 114905 ♂	Nicaragua	39.5	21.5	19.0	5.3	9.4	6.9	7.5
KU 114912 ♂	Nicaragua	38.1	21.5	19.2	5.3	9.3	6.9	7.7
KU 114913 ♂	Nicaragua	38.0	21.7	19.3	5.3	9.2	6.7	7.7
KU 114914 ♂	Nicaragua	38.7	21.6	19.1	5.3	9.0	6.6	7.5
		Rhinophylla alethina						
USNM 483445 ♀	Colombia	36.1	20.4	17.8	5.4	8.8	5.2	7.1
USNM 483446 ♀	Colombia	35.4	20.4	17.9	5.5	8.9	4.9	6.8
USNM 483447 ♀	Colombia	33.5	19.0	16.7	5.3	8.8	4.7	6.8
USNM 483449 ♀	Colombia	37.5	21.3	18.4	5.4	9.0	5.1	6.5
USNM 324988 ♂	Colombia	35.7	19.9	17.3	5.3	8.9	4.9	6.7
USNM 483448 ♂	Colombia	34.5	20.0	17.4	5.4	9.1	4.8	6.5
		Rhinophylla fischerae						
AMNH 94557 ♀	Brazil	30.5	16.8	14.6	4.8	7.8	4.5	5.9
TCWC 12102 ♀	Peru	30.0	17.0	14.7	5.1	7.9	4.3	6.1
USNM 364385 ♀	Perú	30.5	17.0	14.8	5.3	7.9	4.2	6.3
USNM 364386 ♀	Perú	30.0	17.0	14.7	5.1	7.6	4.3	6.2
AMNH 94555 ♂	Brazil	30.6	16.8	14.7	4.7	7.4	4.4	6.1
TCWC 12096 ♂	Perú	29.0	16.2	14.1	4.8	7.9	4.2	5.7
TCWC 12097 ♂	Perú	29.8	16.8	14.5	5.0	8.1	4.3	5.9

APPENDIX 1.—*Continued.*

		Rhinophylla pumilio							
USNM 386528 ♀	Venezuela	34.0	18.7	16.5		5.7	8.3	4.9	6.4
USNM 386530 ♀	Venezuela	34.5	19.2	17.1		5.5	8.5	5.2	6.5
USNM 386531 ♀	Venezuela	34.8	19.4	17.4		5.5	8.2	5.4	6.6
USNM 386532 ♀	Venezuela	34.4	19.8	17.6		5.6	8.7	5.3	6.8
USNM 386539 ♂	Venezuela	34.3	19.4	17.5		5.6	8.2	5.2	6.3
USNM 386551 ♂	Venezuela	32.4	19.1	16.8		5.5	8.4	5.1	6.5
USNM 393674 ♂	Brazil	32.3	19.3	16.9		5.5	8.2	5.1	6.5
USNM 393676 ♂	Brazil	33.6	18.9	16.9		5.4	8.2	4.8	6.3
		Stenoderminae							
		Ametrida centurio							
TTU 8814 ♀	Trinidad	32.9	16.4	13.7	11.4	4.1	8.7	4.9	8.1
TTU 8815 ♀	Trinidad	31.1	16.0	13.5	10.8	4.0	8.4	4.7	7.7
TTU 8816 ♀	Trinidad	31.7	16.5	13.6	11.2	4.4	8.2	4.9	7.9
TTU 8817 ♀	Trinidad	33.1	16.7	13.8	11.4	4.4	8.7	4.8	8.1
TTU 5215 ♂	Trinidad	25.2	15.1	12.2	10.3	4.5	8.3	4.0	7.0
TTU 8888 ♂	Trinidad	25.5	15.4	12.1	10.6	4.0	8.4	4.1	7.3
TTU 9545 ♂	Trinidad	26.0	14.9	11.7	10.4	4.0	8.4	4.2	7.3
TTU 9548 ♂	Trinidad	24.7	14.9	11.3	10.7	3.8	8.6	4.0	7.1
		Ardops nichollsi							
TTU 20802 ♀	Guadeloupe	49.3	23.5	19.9	15.0	5.6	10.2	7.4	10.0
TTU 20820 ♀	Guadeloupe	48.8	23.2	20.2	15.0	5.8	10.5	7.5	10.1
TTU 20821 ♀	Guadeloupe	50.8	23.4	20.2	15.3	5.8	10.7	7.5	10.3
TTU 20822 ♀	Guadeloupe	51.4	24.4	20.8	15.8	5.7	10.6	7.8	10.4
TTU 20806 ♂	Guadeloupe	47.9	22.3	18.7	14.9	5.9	10.6	6.8	9.7
TTU 20808 ♂	Guadeloupe	47.3	22.6	19.3	15.0	5.7	10.7	7.1	9.8
TTU 20809 ♂	Guadeloupe	47.4	22.3	19.4	15.0	5.8	10.4	7.0	9.6
TTU 20824 ♂	Guadeloupe	49.6	22.4	19.4	14.7	5.6	10.4	7.1	9.8
		Ariteus flavescens							
TTU 21721 ♀	Jamaica	42.7	20.6	17.3	14.2	4.9	9.8	5.9	9.1
TTU 21773 ♀	Jamaica	41.3	19.8	17.1	13.9	4.7	9.6	5.9	8.9
TTU 21777 ♀	Jamaica	43.0	21.3	17.9	14.5	5.2	10.3	6.2	9.3
TTU 21782 ♀	Jamaica	43.1	20.4	17.4	14.4	4.7	9.8	5.9	8.9
TTU 21763 ♂	Jamaica	37.8	18.5	15.2	12.9	4.5	9.4	5.4	8.2
TTU 21769 ♂	Jamaica	38.7	19.3	15.5	13.2	4.7	9.7	5.5	8.5
TTU 21774 ♂	Jamaica	39.8	18.6	15.7	13.0	4.6	9.2	5.3	8.2
TTU 21781 ♂	Jamaica	38.1	19.2	16.0	13.6	4.7	9.5	5.4	8.4
		Artibeus aztecus							
TTU 12907 ♀	Costa Rica	48.0	23.2	20.6	13.8	5.5	10.3	7.5	10.6
TTU 12911 ♀	Costa Rica	46.6	22.9	20.3	13.8	5.5	10.0	7.5	10.5
TTU 12913 ♀	Costa Rica	44.6	22.3	19.7	12.9	5.1	9.8	7.3	10.1
TTU 12914 ♀	Costa Rica	45.3	23.1	20.7	13.8	5.3	10.4	7.6	10.6
KU 94141 ♂	Sinaloa	42.9	22.0	19.6	13.3	5.9	9.8	7.0	9.3
KU 94142 ♂	Sinaloa	44.2	22.0	19.7	12.7	5.4	9.8	7.0	9.0
TTU 12908 ♂	Costa Rica	46.5	22.6	20.1	13.3	5.4	10.2	7.3	10.7
TTU 12910 ♂	Costa Rica	42.1	21.8	19.0	12.8	5.0	9.7	7.2	9.8
		Artibeus cinereus							
TTU 5335 ♀	Trinidad	37.6	20.3	18.2	11.3	4.6	9.0	6.5	8.2
TTU 5352 ♀	Trinidad	39.2	20.0	18.1	12.2	5.0	8.6	6.3	8.4
TTU 5769 ♀	Trinidad	40.6	21.2	18.8	12.2	4.7	9.2	6.8	8.5
TTU 5859 ♀	Trinidad	40.2	20.5	18.3	12.1	4.9	8.5	6.5	8.6
TTU 5229 ♂	Trinidad	39.4	20.4	18.5	11.2	4.8	8.9	6.6	8.8
TTU 5230 ♂	Trinidad	38.2	20.9	18.5	11.8	4.9	9.0	6.8	8.6
TTU 5541 ♂	Trinidad	41.8	21.1	19.2	12.3	5.0	9.0	6.8	9.0
TTU 9015 ♂	Trinidad	40.4	20.8	18.5	11.6	5.1	8.9	6.5	8.7
		Artibeus concolor							
ROM 36827 ♀	Guyana	48.2	21.7	18.9	13.5	5.6	9.9	6.7	9.5
ROM 36830 ♀	Guyana	47.4	22.0	19.5	13.1	5.1	10.0	7.3	9.4

APPENDIX 1.—*Continued.*

ROM 36847 ♀	Guyana	46.3	22.5	19.7	13.6	5.4	10.0	7.0	9.5
ROM 60446 ♀	Guyana	48.8	22.4	19.8	13.0	5.3	9.4	7.0	9.4
ROM 57444 ♂	Guyana	46.1	20.6	17.8	12.6	5.5	9.4	6.8	9.1
ROM 59925 ♂	Guyana	48.4	21.5	18.8	13.1	5.3	10.0	6.8	9.1
ROM 66581 ♂	Guyana	49.4	21.5	19.0	13.0	5.4	9.1	7.2	9.5
ROM 67478 ♂	Guyana	45.0	21.3	18.4	12.8	5.3	9.6	6.8	9.2
			Artibeus glaucus						
AMNH 214361 ♀	Perú	38.1	20.0	17.9	11.6	5.0	9.1	6.2	8.4
AMNH 233750 ♀	Perú	40.8	20.6	18.4	11.5	5.4	9.1	6.5	8.4
AMNH 233751 ♀	Perú	41.5	20.1	17.7	11.5	5.4	8.9	6.3	8.1
AMNH 233775 ♀	Perú	40.1	19.6	17.2	11.2	4.7	8.9	6.1	8.1
AMNH 214363 ♂	Perú	37.5	19.0	17.4	10.8	4.7	8.6	6.2	8.2
AMNH 233755 ♂	Perú	41.1	20.5	18.1	11.7	5.2	9.3	6.5	8.4
AMNH 233763 ♂	Perú	40.7	20.2	17.7	11.7	5.0	9.1	6.3	8.6
AMNH 233771 ♂	Perú	41.0	20.3	17.9	11.7	5.0	9.3	6.3	8.5
			Artibeus hirsutus						
TTU 8700 ♀	Jalisco	56.0	27.8	24.5	16.8	6.8	11.7	10.0	12.2
TTU 8701 ♀	Jalisco	55.0	26.8	23.4	16.8	6.5	11.9	9.4	11.6
TTU 8703 ♀	Jalisco	55.2	27.6	24.4	17.3	6.8	12.3	9.7	11.9
TTU 8704 ♀	Jalisco	56.9	27.3	23.9	16.8	6.7	11.8	9.6	11.6
TTU 8702 ♂	Jalisco	56.0	27.1	23.6	17.0	6.9	12.2	9.5	11.8
TTU 10592 ♂	Jalisco	55.2	26.7	23.7	16.5	6.8	12.3	9.8	11.4
TTU 10593 ♂	Jalisco	53.0	27.0	23.8	16.4	6.9	12.0	9.7	11.6
TTU 10596 ♂	Jalisco	57.3	26.3	23.0	15.7	6.7	12.0	9.8	11.3
			Artibeus inopinatus						
TCWC 9517 ♀	Honduras	52.8	26.1	22.2	16.2	5.6	11.6	9.0	10.9
TTU 7685 ♀	Honduras	50.3	25.7	21.9	15.8	5.4	11.2	8.6	10.4
TTU 7686 ♀	Honduras	52.0	25.8	22.2	15.6	5.4	11.4	8.8	10.7
TTU 12915 ♀	Nicaragua	51.1	25.3	21.7	15.4	5.4	11.2	8.6	10.6
TTU 7688 ♂	Honduras	50.0	25.9	22.4	15.6	5.4	11.7	8.9	10.7
TTU 7689 ♂	Honduras	50.0	25.2	21.5	15.7	5.3	11.3	8.7	10.6
TTU 7690 ♂	Honduras	50.2	25.2	21.8	15.6	5.6	11.4	8.8	10.7
TTU 12916 ♂	Nicaragua	50.0	25.6	21.7	15.5	5.4	11.4	8.6	10.6
			Artibeus jamaicensis						
AS 5234 ♀	Jamaica	61.4	29.5	26.1	17.1	7.2	12.8	10.4	13.0
AS 5236 ♀	Jamaica	57.0	28.3	24.7	17.0	7.1	12.1	9.5	12.4
KU 97801 ♀	Nicaragua	60.1	29.3	25.7	17.4	6.9	12.7	9.8	12.0
KU 97802 ♀	Nicaragua	56.4	27.9	24.3	17.0	7.2	12.2	9.5	12.1
COLU 316 ♂	Jamaica	59.2	28.7	24.8	17.3	7.2	12.6	10.0	12.8
COLU 323 ♂	Jamaica	57.3	27.8	24.5	16.8	6.7	12.0	9.6	12.1
AMNH 28335 ♂	Nicaragua	56.4	29.4	25.7	16.9	7.0	12.4	10.4	12.5
KU 115030 ♂	Nicaragua	58.8	28.8	24.9	17.7	7.3	12.9	9.7	12.9
			Artibeus lituratus						
KU 115967 ♀	Nicaragua	67.3	31.7	27.7	19.2	6.4	13.2	10.4	12.9
KU 115068 ♀	Nicaragua	72.6	31.9	28.8	19.1	6.6	13.7	11.1	13.6
KU 115069 ♀	Nicaragua	70.5	31.1	27.3	18.9	6.3	13.9	10.4	13.5
KU 115072 ♀	Nicaragua	71.1	32.1	28.3	19.9	6.5	14.3	11.2	13.8
KU 115062 ♂	Nicaragua	69.3	31.7	27.8	19.5	7.0	14.2	10.9	13.0
KU 115065 ♂	Nicaragua	72.8	31.1	27.1	19.0	6.7	14.0	10.1	12.9
KU 115070 ♂	Nicaragua	73.0	31.9	27.9	19.6	6.4	14.0	11.1	13.6
KU 115071 ♂	Nicaragua	69.3	31.0	27.2	18.9	6.6	13.6	11.0	13.0
			Artibeus phaeotis						
KU 106145 ♀	Nicaragua	35.1	18.3	15.9	10.6	4.5	8.6	5.6	7.7
KU 106146 ♀	Nicaragua	34.2	18.3	16.0	11.3	4.8	8.5	5.7	7.5
KU 106153 ♀	Nicaragua	35.7	19.4	17.2	11.8	4.7	9.0	5.8	7.7
KU 106155 ♀	Nicaragua	34.9	18.5	16.1	11.1	4.8	8.9	5.6	7.7
KU 106147 ♂	Nicaragua	34.9	18.3	15.8	11.1	4.8	9.0	5.6	7.5
KU 106148 ♂	Nicaragua	37.2	18.1	15.7	10.9	4.5	8.4	5.6	7.7

APPENDIX 1.—*Continued.*

KU 105149 ♂	Nicaragua	36.9	18.3	16.0	10.8	4.3	8.8	5.7	7.4
KU 106150 ♂	Nicaragua	36.3	19.0	17.0	11.5	4.5	8.7	5.8	7.7
		Artibeus toltecus							
TTU 73519	Tamaulipas	39.4	20.5	17.9	12.2	4.7	9.2	6.6	8.9
TTU 7354 ♀	Tamaulipas	37.5	20.8	18.1	12.5	5.1	9.3	6.6	8.9
TTU 7355 ♀	Tamaulipas	39.7	21.5	18.7	12.5	4.9	9.4	6.7	9.0
TTU 12930 ♀	Honduras	40.3	21.4	19.4	12.7	5.7	9.7	6.9	8.7
TTU 8163 ♂	San Luis Potosi	36.9	19.5	17.2	12.6	5.0	9.4	6.4	8.9
TTU 12929 ♂	Honduras	40.6	21.0	18.7	12.0	5.6	9.3	6.9	8.8
TTU 12931 ♂	El Salvador	39.0	20.3	17.9	11.7	5.0	9.2	6.7	9.0
TTU 12932 ♂	El Salvador	40.2	19.7	17.4	11.5	4.8	9.2	6.2	8.7
		Artibeus watsoni							
KU 82102 ♀	Guatemala	37.8	19.7	17.8	11.2	4.6	8.8	6.4	8.2
TTU 12964 ♀	Honduras	36.3	19.0	16.3	11.2	4.7	8.7	5.8	8.4
TTU 12967 ♀	Honduras	38.8	19.8	17.3	12.1	5.0	8.9	6.1	8.6
KU 111171 ♀	Nicaragua	38.5	19.9	17.6	11.5	4.9	8.7	6.6	8.4
TTU 12962 ♂	Honduras	37.5	19.1	16.6	11.7	4.7	9.0	6.0	8.5
TTU 12963 ♂	Honduras	37.6	19.8	17.1	11.8	4.8	8.8	6.0	8.5
TTU 12934 ♂	Nicaragua	39.3	20.0	17.7	11.3	4.9	8.5	6.2	8.0
TTU 12948 ♂	Nicaragua	37.9	19.5	17.4	11.4	4.8	8.6	6.2	8.3
		Centurio senex							
FHKSC 9813 ♀	Chiapas	45.7	18.5	15.1	15.0	5.8	10.4	4.8	10.7
TTU 13076 ♀	Honduras	42.6	18.9	14.5	14.9	5.7	9.3	4.8	10.6
KU 115113 ♀	Nicaragua	42.6	19.0	14.8	14.9	5.9	9.8	5.0	10.6
KU 115114 ♀	Nicaragua	43.5	18.9	15.0	15.0	6.0	10.0	4.7	10.6
FHKSC 9812 ♂	Chiapas	42.0	18.7	14.5	14.8	5.5	10.0	4.7	10.5
KU 115108 ♂	Nicaragua	41.6	18.7	14.6	14.5	5.6	10.6	4.6	10.3
KU 115111 ♂	Nicaragua	42.7	19.0	14.5	15.0	5.7	10.8	4.6	10.4
TTU 5221 ♂	Trinidad	44.1	19.8	15.2	15.8	6.1	10.5	5.1	11.1
		Chiroderma doriae							
BMNH 9.11.19.15 ♀	Brazil	53.7	28.0	25.9	17.8	6.1	11.2	10.3	13.6
TTU 30707 ♂	Brazil		28.1	25.8	17.6	6.4	12.0	10.0	13.0
TTU 30708 ♂	Brazil		28.8	26.3	17.9	6.2	12.0	10.2	13.4
TTU 30709 ♀	Brazil		29.0	26.4	18.1	6.3	12.5	10.2	13.5
		Chiroderma improvisum							
TTU 19900 ♂	Guadeloupe	57.5	29.9	27.7	18.9	6.5	12.2	10.7	7.2
		Chiroderma salvini							
USNM 338711 ♀	Colima	46.1	24.2	22.0	15.2	6.2	10.6	8.6	11.4
TCWC 17499 ♀	Guatemala	47.8	26.4	23.8	16.1	6.0	11.0	9.2	11.5
TTU 12809 ♀	Honduras	51.8	27.6	24.8	16.9	6.1	11.2	9.5	12.1
AMNH 142484 ♀	Costa Rica	51.5	27.6	24.8	17.5	6.3	11.6	10.1	13.0
TTU 6123 ♂	Colima	43.6	24.5	21.9	15.0	5.8	10.5	8.4	11.1
TTU 12800 ♂	Honduras	48.0	26.6	24.1	16.2	6.2	11.0	9.4	11.7
TTU 12801 ♂	Honduras	45.6	26.0	23.6	16.0	5.7	11.0	9.1	11.8
TTU 12802 ♂	Honduras	49.4	26.6	24.2	16.6	6.2	11.2	9.3	12.2
		Chiroderma trinitatum							
TTU 5223 ♀	Trinidad	41.5	22.7	19.8	13.4	5.4	9.5	7.8	10.6
TTU 5224 ♀	Trinidad	38.0	22.5	20.0	13.3	5.3	9.4	7.5	10.1
TTU 5336 ♀	Trinidad	40.3	22.4	19.7	13.8	5.4	9.5	7.5	10.1
TTU 5382 ♀	Trinidad	38.8	22.5	19.6	13.7	5.4	9.6	7.4	10.2
TTU 5487 ♂	Trinidad	39.0	22.4	19.8	13.5	5.5	9.7	7.4	10.3
TTU 5675 ♂	Trinidad	38.7	22.5	19.8	13.8	5.2	9.5	7.4	9.6
TTU 8989 ♂	Trinidad	39.5	22.3	19.8	13.6	5.3	9.6	7.5	9.7
TTU 9014 ♂	Trinidad	39.1	22.2	19.5	13.5	5.5	9.4	7.4	10.0
		Chiroderma villosum							
TTU 5289 ♀	Trinidad	46.5	26.0	23.4	16.4	5.7	10.8	9.1	11.6
TTU 5321 ♀	Trinidad	45.3	25.0	22.4	16.0	5.6	11.0	8.7	11.5

APPENDIX 1.—*Continued.*

TTU 5353 ♀	Trinidad	47.9	26.6	23.6	16.5	5.8	11.0	9.1	12.0
TTU 5354 ♀	Trinidad	47.2	26.2	23.4	17.0	6.2	10.4	9.0	12.0
TTU 5262 ♂	Trinidad	45.9	26.4	23.3	16.4	6.2	11.3	9.1	11.5
TTU 5276 ♂	Trinidad	46.0	25.3	22.4	15.7	5.9	10.5	8.5	11.4
TTU 5668 ♂	Trinidad	44.3	26.0	22.9	15.7	6.1	10.8	9.0	11.6
TTU 9016 ♂	Trinidad	46.8	26.5	22.8	15.1	5.8	10.6	8.6	10.9
			Ectophylla alba						
KU 88025 ♀	Costa Rica	28.1	16.4	15.1	9.8	4.0	7.3	6.0	7.4
USNM 335318 ♀	Panamá	29.1	16.4	15.5	10.0	4.2	7.5	6.0	7.2
USNM 335320 ♀	Panamá	28.9	16.7	15.5	10.0	4.0	7.7	6.0	7.3
USNM 335322 ♀	Panamá	29.4	16.3	15.2	10.3	4.3	8.0	6.0	7.6
TCWC 19372 ♂	Honduras	28.4	17.1	15.7	10.1	4.2	7.9	6.1	7.3
TCWC 19373 ♂	Honduras	28.5	17.1	15.7	10.3	4.2	7.8	6.3	7.4
USNM 315563 ♂	Panamá	28.4	16.9	15.4	10.3	4.3	7.8	6.1	7.5
USNM 319426 ♂	Panamá	28.7	16.5	15.4	9.9	4.2	7.5	6.0	7.2
			Enchisthenes hartii						
AMNH 206872 ♀	Oaxaca	40.1	21.1	19.1	13.0	6.1	9.5	6.8	9.0
KU 102600 ♀	Chiapas	39.5	20.7	18.7	12.2	5.9	9.3	6.6	8.5
TTU 5371 ♀	Trinidad	38.6	20.5	18.3	12.0	5.7	9.4	6.8	8.7
AMNH 233798 ♀	Perú	36.7	20.3	18.6	12.4	5.9	9.6	7.0	8.6
KU 97039 ♂	Jalisco	39.8	21.0	18.9	12.9	5.9	9.8	6.7	8.9
AMNH 126239 ♂	Honduras	36.5	20.9	18.6	11.3	5.4	9.4	7.1	8.6
BMNH 92.9.7.8 ♂	Trinidad	37.1	20.4	18.5	12.0	6.1	9.1	7.2	8.4
AMNH 233599 ♂	Perú	39.6	20.9	18.9	12.1	5.7	9.6	6.7	8.0
			Mesophylla macconnelli						
TTU 5359 ♀	Trinidad	32.6	18.6	16.6	10.7	4.6	8.2	6.2	7.6
TTU 5475 ♀	Trinidad	31.5	18.2	16.3	10.4	4.5	7.8	6.3	7.4
TTU 9786 ♀	Trinidad	33.5	19.0	16.7	10.8	4.8	8.3	6.5	7.7
BMNH 1.6.4.64 ♀	Guyana	30.0	17.7	15.5	10.1	4.4	7.8	6.0	7.0
TTU 5211 ♂	Trinidad	32.0	18.5	16.5	10.6	4.7	8.2	6.1	7.5
TTU 5212 ♂	Trinidad	31.5	18.5	16.3	10.8	4.5	8.3	6.2	7.5
TTU 5213 ♂	Trinidad	32.3	18.7	16.6	11.0	4.6	8.2	6.2	7.7
BMNH 70.1008 ♂	Brazil	29.5	17.7	15.4	9.8	4.2	7.7	5.8	7.0
			Phyllops falcatus						
AMNH 176190 ♀	Cuba	44.0	20.9	18.9	14.2	5.6	10.0	6.0	8.7
USNM 143844 ♀	Cuba	43.3	20.8	18.7	14.1	5.3	10.0	6.2	8.5
BMNH ♂	Cuba	42.9				5.3		5.8	8.1
			Phyllops haitiensis						
TTU 22675 ♀	Haiti	41.8	20.3	18.3	13.7	5.7	10.0	5.9	8.2
TTU 22676 ♀	Haiti	43.8	20.7	18.3	13.6	5.4	10.1	6.2	8.5
TTU 22677 ♀	Haiti	44.0	20.4	18.4	13.8	5.7	10.3	6.1	8.4
TTU 22678 ♀	Haiti	42.8	20.5	18.3	13.2	5.5	9.9	6.1	8.3
TTU 22697 ♂	Haiti	39.0	19.4	17.2	12.5	5.2	9.6	5.5	7.8
TTU 22698 ♂	Haiti	40.2	19.4	17.5	12.9	5.3	9.6	5.6	7.9
TTU 22699 ♂	Haiti	40.9	19.5	17.4	13.2	5.7	9.9	5.8	7.9
TTU 22700 ♂	Haiti	42.1	19.7	17.4	13.3	5.4	9.9	5.6	8.1
			Phyllops vetus						
AMNH 41001 ?	Cuba			18.1	13.5	5.4		5.9	7.9
AMNH 41002 ?	Cuba		19.5	17.3	13.0	5.2	9.7	5.4	7.3
AMNH 41003?	Cuba		20.1	18.0		5.3	10.0	5.5	7.5
AMNH 41005 ?	Cuba			17.0		5.0	10.0	5.3	7.3
			Pygoderma bilabiatum						
AMNH 234288 ♀	Paraguay	38.9	20.5	17.5	14.0	7.4	9.9	6.0	8.0
AMNH 234290 ♀	Paraguay	37.6	20.9	17.5	14.3	8.0	10.1	5.7	8.0
AMNH 234292 ♀	Paraguay	39.8	21.0	17.9	14.7	7.7	10.3	6.1	8.4
KU 92656 ♀	Paraguay	39.5	20.2	17.4	14.1	7.4	10.1	6.0	7.9
AMNH 234291 ♂	Paraguay	36.4	20.1	16.5	13.2	7.2	10.0	5.4	7.1

APPENDIX 1.—*Continued.*

AMNH 234294 ♂	Paraguay	36.6	20.0	16.8	13.4	7.3	10.0	5.3	7.2
AMNH 234297 ♂	Paraguay	36.2	20.5	17.2	13.7	7.7	10.4	5.5	7.5
AMNH 234298 ♂	Paraguay	37.0	19.9	17.0	13.7	7.5	10.3	5.4	7.3
		Sphaeronycteris toxophyllum							
TCWC 28252 ♀	Venezuela	39.5	17.2	14.2	12.1	5.6	9.5	4.7	7.9
USNM 370848 ♀	Venezuela	40.0	17.4	14.5	12.2	5.7	9.4	4.6	7.9
USNM 370849 ♀	Venezuela	40.1	17.2	14.5	12.3	5.7	9.2	4.7	7.8
AMNH 209704 ♀	Bolivia	39.6	17.5	14.6	12.1	5.6	9.0	4.4	8.0
TTU 10227 ♂	Colombia	36.6	16.1	13.8	11.7	5.5	8.9	4.4	7.2
USNM 405688 ♂	Venezuela	37.0	16.8	13.9	12.2	5.6	9.5	4.3	7.3
USNM 409233 ♂	Venezuela	37.3	16.5	13.4	11.9	5.6	8.9	4.4	7.4
AMNH 209741 ♂	Bolivia	38.7	16.9	13.8	12.4	5.7	9.0	4.2	7.6
		Stenoderma rufum							
TTU 8876 ♀	Puerto Rico	49.0	23.0	19.4	15.5	5.7	11.4	7.2	10.1
TTU 8879 ♀	Puerto Rico	49.0	22.5	19.1	15.2	5.7	10.6	6.8	9.7
TTU 8880 ♀	Puerto Rico	51.2	23.5	19.8	15.8	5.7	11.4	7.0	10.2
TTU 8884 ♀	Puerto Rico	50.3	22.9	19.4	15.3	5.7	10.7	7.0	10.0
TTU 8860 ♂	Puerto Rico	46.5	22.2	18.5	15.0	5.5	10.5	6.6	9.7
TTU 8861 ♂	Puerto Rico	47.1	22.5	19.0	14.9	5.6	10.6	6.6	9.7
TTU 8864 ♂	Puerto Rico	46.1	22.0	18.0	14.4	5.2	10.2	6.2	9.7
TTU 8865 ♂	Puerto Rico	48.5	22.5	18.7	14.9	5.4	10.7	6.3	9.5
		Sturnira aratathomasi							
ROM 70874 ♀	Colombia	58.0	29.1	25.4	17.2	7.5	12.9	7.6	10.2
USNM 501064 ♀	Colombia	57.5	28.5	25.5	16.9	6.9	12.5	7.7	10.1
USNM 501066 ♀	Colombia	56.8	28.8	25.0	16.7	7.2	12.5	7.4	9.7
ROM 46349 ♀	Ecuador	60.5	29.7	26.2	17.5	7.2	12.8	8.1	10.5
ROM 70875 ♂	Colombia	57.7	29.4	26.5	16.7	7.2	12.8	7.8	10.4
ROM 70876 ♂	Colombia	54.8	28.8	25.2	16.8	7.0	12.7	7.6	10.2
USNM 395158 ♂	Colombia	57.1	29.4	26.5	17.5	7.3	13.0	7.9	10.1
USNM 501065 ♂	Colombia	57.5	28.8	25.9	16.5	6.9	12.3	7.7	10.0
		Sturnira bidens							
USNM 386557 ♀	Venezuela	39.3	21.2	18.9	11.7	5.5	9.4	6.0	6.8
USNM 386558 ♀	Venezuela	40.2	21.6	19.7	11.7	5.3	9.7	6.0	6.8
USNM 386560 ♀	Venezuela	39.7	22.1	19.6	12.0	5.5	9.8	6.1	7.1
USNM 386562 ♀	Venezuela	40.8	21.7	19.5	12.0	5.5	9.6	6.0	6.9
USNM 386559 ♂	Venezuela	39.7	21.2	19.0	11.9	5.4	9.6	5.7	6.9
USNM 386567 ♂	Venezuela	39.7	21.3	18.7	11.7	5.4	9.5	5.9	7.0
USNM 386570 ♂	Venezuela	39.5	21.0	18.7	11.7	5.3	9.6	5.9	6.6
AMNH 214349 ♂	Perú	41.2	21.3	18.7	11.7	5.4	9.7	5.9	6.7
		Sturnira erythromos							
ROM 67254 ♀	Colombia	39.3	21.3	18.6	12.7	5.7	10.0	6.0	8.0
ROM 67267 ♀	Colombia	41.1	20.7	18.3	12.0	5.3	9.5	5.9	7.5
USNM 483451 ♀	Colombia	40.6	21.5	19.0	12.7	6.0	9.9	5.8	7.5
USNM 483452 ♀	Colombia	40.6	21.0	18.9	12.5	6.1	9.7	6.0	7.4
ROM 67270 ♂	Colombia	41.6	21.4	19.2	12.1	6.0	9.6	5.9	7.4
BMNH 15.7.11.13 ♂	Ecuador	40.8	22.0	19.4	12.9	6.0	10.4	6.3	8.0
		Sturnira lilium							
TTU 5367 ♀	Trinidad	42.5	23.4	20.4	13.6	6.0	10.3	6.4	8.4
TTU 5407 ♀	Trinidad	43.9	22.9	20.2	13.7	5.8	10.5	6.4	8.2
TTU 5669 ♀	Trinidad	42.4	22.7	19.9	13.4	5.6	10.1	6.5	8.0
TTU 5670 ♀	Trinidad	41.4	22.8	19.9	13.6	6.2	10.4	6.3	8.0
TTU 5408 ♂	Trinidad	43.2	23.1	20.4	13.8	6.0	10.4	6.6	8.2
TTU 5415 ♂	Trinidad	41.9	23.2	20.3	13.7	6.3	10.5	6.3	7.9
TTU 5775 ♂	Trinidad	41.3	22.9	20.4	13.6	6.4	10.5	6.8	8.5
TTU 5776 ♂	Trinidad	42.7	22.4	19.6	13.4	5.9	10.5	6.4	8.0

APPENDIX 1.—*Continued.*

		Sturnira ludovici							
TTU 15543 ♀	Hidalgo	44.1	24.0	20.8	13.0	6.1	10.3	6.5	8.0
TTU 15546 ♀	Hidalgo	43.2	24.0	20.8	13.5	6.1	10.2	6.5	8.0
TCWC 14359 ♀	Guatemala	45.1	23.2	20.1	13.2	5.6	10.3	6.3	8.0
TCWC 14360 ♀	Guatemala	46.9	24.4	21.6	13.9	6.1	10.6	6.6	8.3
TTU 7341 ♂	Tamaulipas	42.5	23.9	21.0	13.6	6.0	10.6	6.4	8.3
TTU 6124 ♂	Jalisco	44.3	23.4	20.3	13.9	6.1	10.0	6.2	7.9
TTU 6125 ♂	Jalisco	43.2	23.2	20.1	12.7	6.0	10.1	6.2	7.8
KU 97689 ♂	Nicaragua	45.1	24.0	21.4	14.2	6.2	10.4	6.5	8.3
		Sturnira magna							
AMNH 214347 ♀	Perú	59.2	29.0	25.3	16.7	6.9	12.0	7.1	9.0
TCWC 27474 ♀	Perú	57.7	27.9	24.7	16.4	7.0	11.8	7.2	8.8
LSU 16518 ♀	Perú	57.7	29.1	25.6	17.2	7.0	12.5	7.4	9.9
LSU 19031 ♀	Perú	57.4	28.5	24.4	16.0	6.8	11.5	7.3	8.8
LSU 16517 ♂	Perú	57.0	29.5	25.6	17.2	7.0	11.9	7.4	9.3
LSU 19027 ♂	Perú	55.4	28.5	24.7	17.0	7.0	12.1	7.1	9.1
LSU 19028 ♂	Perú	56.0	28.8	24.9	16.9	6.9	12.2	7.5	9.3
		Sturnira mordax							
BMNH 69.1263 ♀	Costa Rica	46.2	25.8	22.4	13.1	5.9	10.6	6.7	7.8
TCWC 10034 ♂	Costa Rica	48.3	26.1	22.9	13.8	6.1	10.9	6.9	8.2
TCWC 10035 ♂	Costa Rica	46.1	25.5	22.0	13.3	5.9	11.0	6.7	7.9
TCWC 10041 ♂	Costa Rica	47.7	25.7	22.4	13.3	6.0	10.7	6.7	7.8
TCWC 10042 ♂	Costa Rica	48.3	26.3	23.1	13.7	6.2	10.9	6.9	8.0
		Sturnira nana							
AMNH 219138 ♀	Perú	34.7	18.8	16.6	10.2	4.6	8.2	4.8	5.8
LSU 16521 ♀	Perú	34.8	18.5	16.5	10.0	4.7	8.1	4.7	5.6
LSU 16522 ♀	Perú	33.7	18.9	16.6	9.8	4.8	8.3	4.8	5.7
LSU 16524 ♀	Perú	34.1	19.0	16.8	10.1	4.6	8.5	4.9	6.0
AMNH 219171 ♂	Perú	34.5	18.7	16.5	10.1	4.7	8.5	4.7	5.5
AMNH 219172 ♂	Perú	35.4	18.8	16.5	10.1	4.6	8.5	4.9	5.8
AMNH 219173 ♂	Perú	35.0	18.5	16.3	9.7	4.7	8.2	4.7	5.6
TCWC 28071 ♂	Perú	32.6	18.4	16.1	9.9	4.7	8.1	4.8	5.7
		Sturnira thomasi							
TTU 19904 ♀	Guadeloupe	45.9	25.3	23.3	12.1	5.7	9.8	7.0	8.1
TTU 19905 ♀	Guadeloupe	46.4	24.4	22.4	11.9	5.6	9.5	6.7	7.7
TTU 19906 ♀	Guadeloupe	46.1	24.9	22.9	12.2	5.5	9.8	6.9	8.0
TTU 19907 ♀	Guadeloupe	47.7	25.1	23.6	12.5	5.9	9.6	6.9	8.0
AMNH 234950 ♂	Guadeloupe	46.5	25.1	23.7	12.2	5.7	9.5	6.7	8.2
USNM 361883 ♂	Guadeloupe	48.1	26.2	24.7	12.7	6.0	9.9	7.7	8.2
		Sturnira tildae							
TTU 5406 ♀	Trinidad	44.0	23.6	21.1	14.6	6.0	10.7	6.8	8.1
TTU 5667 ♀	Trinidad	44.1	23.9	21.5	14.3	6.1	10.8	6.9	8.5
TTU 5786 ♀	Trinidad	44.7	24.3	21.8	14.3	5.7	10.6	7.1	8.3
TTU 5791 ♀	Trinidad	43.4	22.8	20.2	13.7	6.1	10.4	6.6	7.8
TTU 5337 ♂	Trinidad	44.7	23.9	21.1	14.2	6.3	10.7	7.1	8.5
TTU 5372 ♂	Trinidad	44.5	23.1	20.5	14.0	5.9	10.6	6.9	8.2
TTU 5402 ♂	Trinidad	46.3	24.4	22.2	14.7	6.6	10.7	7.4	8.6
TTU 5454 ♂	Trinidad	44.2	23.7	21.5	14.6	6.5	11.0	6.8	8.8
		Uroderma bilobatum							
KU 114985 ♀	Nicaragua	41.6	22.8	20.2	13.0	5.4	9.5	7.9	9.3
TTU 5327 ♀	Trinidad	42.1	23.6	20.8	12.8	4.6	9.5	8.2	9.4
TTU 5485 ♀	Trinidad	39.6	23.0	20.6	12.5	5.3	9.3	7.9	9.3
TTU 5813 ♀	Trinidad	42.4	23.6	21.4	13.0	5.6	9.4	8.5	9.9
KU 114986 ♂	Nicaragua	43.0	22.6	19.9	12.7	5.3	9.9	7.8	9.1
TTU 5254 ♂	Trinidad	43.1	24.7	22.1	13.4	5.7	9.9	8.6	9.9
TTU 5300 ♂	Trinidad	40.5	23.7	21.6	13.1	5.4	9.7	8.3	9.5
TTU 5301 ♂	Trinidad	41.4	24.0	21.0	12.8	5.5	9.4	7.9	8.9

APPENDIX 1.—*Continued.*

		Uroderma magnirostrum							
TTU 17111 ♀	El Salvador	42.3	23.0	20.8	12.7	5.7	9.7	7.6	8.9
KU 114987 ♀	Nicaragua	45.1	23.9	21.8	13.1	5.8	9.3	8.3	9.1
TTU 9080 ♀	Colombia	42.6	23.1	21.0	12.6	5.6	9.3	8.1	9.2
TTU 9517 ♀	Colombia	41.8	22.4	20.3	12.2	5.6	9.3	7.8	8.9
TCWC 17189 ♂	Honduras	41.0	22.5	20.5	12.6	5.6	9.5	7.6	8.6
KU 106109 ♂	Nicaragua	41.6	23.6	21.7	12.9	5.5	9.5	7.7	8.7
TTU 9054 ♂	Colombia	43.6	24.0	21.7	13.5	6.0	10.3	8.1	9.5
TTU 9056 ♂	Colombia	43.4	23.5	21.3	12.9	5.3	9.7	8.0	9.1
		Vampyressa bidens							
ROM 59895 ♀	Guyana	36.0	20.2	17.2	11.8	5.4	9.1	6.3	8.3
ROM 66587 ♀	Guyana	38.2	20.5	17.8	12.3	5.3	9.0	6.4	8.9
AMNH 208072 ♀	Perú	36.6	20.4	17.8	12.1	5.1	8.8	6.5	8.9
TCWC 27508 ♀	Perú	36.4	19.5	16.8	11.4	4.8	8.6	5.9	8.1
AMNH 98780 ♂	Perú	39.1	20.0	17.1	12.2	5.2	9.1	6.1	8.6
TCWC 27503 ♂	Perú	35.6	20.0	17.3	11.7	5.2	9.3	6.2	8.5
TCWC 27505 ♂	Perú	35.3	19.8	17.1	11.2	5.2	8.4	6.3	8.2
TCWC 27506 ♂	Perú	35.5	20.2	17.3	12.2	5.4	9.1	6.3	8.3
		Vampyressa brocki							
TTU 8827 ♀	Colombia	35.4	18.4	16.0	10.9	4.9	8.4	5.7	7.9
TTU 8832 ♀	Colombia	32.1	18.3	15.8	10.8	4.7	8.4	5.7	7.6
TTU 9047 ♀	Colombia	33.2	18.4	16.2	10.7	5.1	8.0	5.7	7.8
ROM 38515 ♀	Guyana	33.0	17.7	15.5	10.4	4.7	7.8	5.6	7.6
		Vampyressa melissa							
BMNH 26.5.3.4 ♀	Perú	37.1	21.5	19.6	12.8	5.0	9.0	6.8	9.6
LSU 16580 ♀	Perú	39.2	22.2	20.4	13.2	5.2	9.5	7.1	9.5
LSU 16583 ♀	Perú	38.2	21.8	20.1	12.9	5.1	8.9	6.7	9.2
LSU 19100 ♀	Perú	37.3	21.3	19.8	13.1	5.1	8.9	6.6	9.1
USNM 319283 ♂	Panamá	37.9	22.8	21.2	12.0	5.1	8.8	7.6	9.1
USNM 319284 ♂	Panamá	36.5	22.8	21.3	12.1	5.2	9.1	7.5	9.2
USNM 319285 ♂	Panamá	37.8	22.8	21.3	12.3	5.1	9.0	7.7	9.3
AMNH 233769 ♂	Perú	36.5	21.9	20.0	13.1	5.2	9.4	6.9	9.4
		Vampyressa nymphaea							
KU 115005 ♀	Nicaragua	36.2	21.1	18.4	12.3	4.7	9.2	7.0	8.6
TCWC 19368 ♀	Nicaragua	35.7	21.2	18.0	12.1	4.9	9.2	7.1	8.7
TTU 12611 ♀	Nicaragua	37.9	21.6	19.1	13.0	4.6	9.4	7.5	9.4
USNM 483687 ♀	Colombia	39.0	21.6	18.7	12.2	4.8	9.3	7.0	8.8
TCWC 19367 ♂	Nicaragua	38.2	21.7	18.7	12.4	4.5	9.3	7.1	8.8
TTU 12612 ♂	Nicaragua	37.4	22.0	19.0	12.8	5.0	9.5	7.5	9.1
AMNH 233189 ♂	Colombia	37.0	21.2	18.4	11.9	4.9	9.3	6.8	8.9
BMNH 9.7.17.40 ♂	Colombia	34.9	21.0	18.3	12.2	4.7	9.2	7.2	8.8
		Vampyressa pusilla							
KU 114082 ♀	Nicaragua	31.2	18.2	16.5	10.3	4.7	8.1	5.7	7.7
KU 114084 ♀	Nicaragua	30.0	17.9	16.2	10.2	4.7	8.5	5.5	7.8
KU 114085 ♀	Nicaragua	31.1	18.7	16.7	10.8	4.7	8.3	6.0	7.9
KU 114086 ♀	Nicaragua	30.1	18.2	16.5	10.6	4.6	7.8	6.0	7.8
TTU 12894 ♂	Honduras	29.9	18.0	15.9	10.5	4.9	8.2	5.8	8.0
KU 114083 ♂	Nicaragua	31.9	18.6	16.0	10.5	4.7	8.5	6.0	7.9
TTU 9431 ♂	Colombia	31.9	18.1	16.0	10.5	4.5	7.7	5.5	7.3
TTU 9480 ♂	Colombia	32.5	18.6	16.7	10.5	4.6	8.1	5.7	7.5
		Vampyrodes caraccioli							
KU 111033 ♀	Nicaragua	53.7	28.1	24.3	17.0	6.6	11.6	9.6	12.2
KU 111035 ♀	Nicaragua	53.9	28.3	24.8	17.8	6.9	11.8	9.9	12.4
TTU 5288 ♀	Trinidad	49.5	25.7	22.7	16.1	6.5	10.8	9.1	11.4
TTU 5355 ♀	Trinidad	49.5	26.3	22.6	16.2	6.1	11.0	9.1	11.4
KU 111034 ♂	Nicaragua	53.3	28.3	24.9	17.8	6.7	11.9	9.7	12.7
TTU 5366 ♂	Trinidad	46.8	25.9	22.5	16.0	6.2	10.9	9.0	11.2

APPENDIX 1.—*Continued.*

TTU 5373 ♂	Trinidad	47.2	25.8	22.4	16.2	6.2	10.8	8.6	11.3
TTU 5509 ♂	Trinidad	47.4	26.0	22.5	16.1	6.0	11.2	9.0	11.5
		Vampyrops aurarius							
USNM 387157 ♀	Venezuela	52.0	28.2	25.2	16.0	6.5	11.3	10.6	12.5
USNM 387159 ♀	Venezuela	51.9	28.8	25.5	17.0	6.6	11.6	10.8	13.0
USNM 387171 ♀	Venezuela	52.5	29.1	26.0	16.8	6.6	11.8	10.5	12.1
USNM 387172 ♀	Venezuela	53.4	29.9	27.0	17.8	6.6	11.9	11.0	13.0
USNM 387153 ♂	Venezuela	52.4	28.8	25.9	16.5	6.6	11.8	10.6	12.3
USNM 387154 ♂	Venezuela	51.1	29.5	26.9	16.8	6.8	11.8	11.0	12.8
USNM 387155 ♂	Venezuela	51.4	29.3	25.9	16.6	6.7	12.2	10.9	12.6
USNM 387161 ♂	Venezuela	50.4	28.4	25.9	16.8	6.6	11.4	10.5	12.4
		Vampyrops brachycephalus							
TCWC 29658 ♀	Brazil	37.2	20.8	18.1	11.8	5.1	9.0	6.8	8.2
AMNH 230639 ♀	Perú	36.7	21.2	18.5	12.5	5.4	9.3	7.0	8.8
TCWC 12184 ♀	Perú	37.8	20.8	18.4	12.2	5.1	9.2	7.0	8.6
TCWC 12185 ♀	Perú	36.9	20.1	18.4	12.5	5.4	9.5	7.0	8.9
TCWC 29657 ♂	Brazil	37.5	20.9	18.3	12.5	5.5	9.3	7.1	8.8
TCWC 12177 ♂	Perú	37.5	20.5	18.1	11.8	5.3	9.2	6.9	8.2
TCWC 12178 ♂	Perú	36.8	21.0	18.3	12.3	5.3	8.9	7.0	8.6
TCWC 12193 ♂	Perú	40.7	21.9	19.2	13.4	5.7	9.6	7.8	9.9
		Vampyrops dorsalis							
AMNH 235778 ♀	Colombia	49.1	28.3	25.2	16.8	6.5	11.7	10.6	11.5
AMNH 235779 ♀	Colombia	47.2	27.2	24.0	16.1	6.8	11.7	10.0	11.4
AMNH 233614 ♀	Perú	48.0	26.7	24.0	15.4	6.0	11.1	10.4	11.8
AMNH 233615 ♀	Perú	50.5	26.7	24.2	16.0	6.1	10.8	10.3	12.1
AMNH 233186 ♂	Colombia	50.7	29.2	25.9	17.6	6.5	12.3	11.6	11.9
AMNH 233187 ♂	Colombia	49.6	28.8	25.6	17.0	6.4	11.7	10.4	11.5
BMNH 99.12.5.1 ♂	Ecuador	48.2	27.4	25.2	15.3	6.3	10.8	10.6	11.5
AMNH 214356 ♂	Perú	49.3	28.0	25.0	17.0	7.0	11.4	10.5	13.0
		Vampyrops helleri							
KU 106131 ♀	Nicaragua	38.0	22.3	19.8	11.9	5.2	8.8	7.5	8.7
KU 106133 ♀	Nicaragua	36.3	21.8	19.5	12.1	5.2	9.2	7.9	9.0
KU 106134 ♀	Nicaragua	37.1	21.4	19.0	11.8	5.2	8.9	7.3	8.4
FHKSC 8839 ♀	Colombia	37.0	22.5	20.2	12.7	5.3	9.0	7.8	9.0
FHKSC 9734 ♂	Chiapas	38.6	22.8	20.5	13.0	5.5	9.3	7.9	9.3
KU 106129 ♂	Nicaragua	37.6	21.7	19.3	12.2	5.6	10.0	7.5	8.8
KU 106130 ♂	Nicaragua	38.5	21.2	18.8	12.1	5.2	8.9	7.4	8.4
KU 106131 ♂	Nicaragua	38.7	22.3	20.2	12.3	5.5	9.2	7.7	8.9
		Vampyrops infuscus							
AMNH 67661 ♀	Ecuador	55.9	30.6	27.4	18.3	6.3	12.4	10.9	13.8
AMNH 67664 ♀	Ecuador	55.0	29.9	26.2	17.6	6.5	12.0	11.1	13.4
AMNH 236131 ♀	Perú	54.9	30.5	27.3	17.8	6.5	12.3	11.5	13.1
AMNH 236132 ♀	Perú	55.0	30.1	26.9	17.6	6.4	12.2	11.3	12.8
TTU 9494 ♂	Colombia	53.4	29.5	26.7	17.5	6.8	11.7	11.6	13.8
AMNH 67662 ♂	Ecuador	55.5	30.5	27.3	17.8	7.0	12.2	11.3	13.8
AMNH 67663 ♂	Ecuador	54.6	30.9	27.2	18.1	6.8	12.1	12.0	13.7
AMNH 233729 ♂	Perú	56.9	30.5	27.3	18.6	6.8	12.4	11.6	13.8
		Vampyrops lineatus							
AMNH 37013 ♀	Brazil	48.5	25.5	22.5	14.3	6.3	10.7	9.1	10.5
AMNH 37015 ♀	Brazil	47.6	25.0	22.4	14.6	6.2	10.2	8.8	10.3
AMNH 37016 ♀	Brazil	46.2	24.3	21.8	14.1	6.3	10.4	8.3	10.2
AMNH 205185 ♀	Paraguay	47.0	25.4	22.5	14.3	6.4	10.4	8.8	10.2
AMNH 36995 ♂	Brazil	46.6	24.5	22.0	13.7	5.9	10.3	9.0	9.8
AMNH 148666 ♂	Paraguay	50.1	25.0	22.1	14.0	6.3	10.5	8.6	10.2
AMNH 205184 ♂	Paraguay	44.6	24.6	21.9	14.1	6.4	10.6	8.7	10.1
AMNH 234285 ♂	Paraguay	45.8	25.2	22.2	14.4	6.4	10.7	8.8	10.1

APPENDIX 1.—*Continued.*

		Vampyrops nigellus						
AMNH 233686 ♀	Perú	43.9	25.2	22.8	14.2	6.0	10.3	9.2	10.6
AMNH 233710 ♀	Perú	44.1	24.6	22.0	13.9	5.9	10.4	8.9	10.1
AMNH 233716 ♀	Perú	43.1	25.0	22.3	14.8	6.0	10.6	9.3	10.7
AMNH 236106 ♀	Perú	44.4	25.2	22.2	14.4	6.0	10.8	9.0	10.8
AMNH 214353 ♂	Perú	43.2	24.4	22.2	13.9	5.9	10.3	9.0	10.3
AMNH 233644 ♂	Perú	41.1	24.4	21.8	13.5	5.6	10.3	9.0	10.2
AMNH 233646 ♂	Perú	43.5	25.2	22.8	14.0	5.8	10.4	9.2	10.3
AMNH 236111 ♂	Perú	44.3	25.3	22.9	14.4	5.9	10.6	8.8	10.1
		Vampyrops recifinus						
BMNH 93.1.9.15 ♀	Brazil	42.1	23.7	21.5	14.0	5.7	10.2	8.7	10.2
BMNH 81.3.16.4 ♂	Brazil	40.6	24.0	21.3	14.0	5.7	10.2	8.7	10.4
		Vampyrops vittatus						
TTU 12891 ♀	Costa Rica	63.7	34.0	30.6	19.8	7.7	13.4	13.0	14.6
KU 93925 ♀	Panamá	60.1	32.7	29.6	19.1	7.6	13.5	12.7	14.0
TTU 9439 ♀	Colombia	64.3	33.4	31.1	19.9	7.6	12.8	13.6	15.2
AMNH 233725 ♀	Perú	57.1	32.9	30.1	20.0	7.4	13.5	13.2	14.8
TCWC 10051 ♂	Costa Rica	61.5	32.8	29.6	19.5	7.2	13.2	12.5	14.5
KU 99355 ♂	Panamá	57.8	32.4	28.6	18.8	7.4	13.0	12.5	14.3
AMNH 233718 ♂	Perú	59.5	32.8	29.6	20.7	7.3	13.3	12.7	15.5
AMNH 233728 ♂	Perú	57.6	31.6	28.6	19.0	6.6	12.9	12.9	14.7
		Brachyphyllinae						
		Brachyphylla cavernarum						
TTU 20972 ♀	Guadeloupe	66.4	32.1	28.7	17.9	6.3	13.1	11.2	12.3
TTU 20989 ♀	Guadeloupe	63.3	30.9	27.4	16.6	6.2	12.7	10.7	11.6
TTU 20991 ♀	Guadeloupe	64.2	32.3	28.8	17.3	6.3	13.0	11.0	12.1
TTU 20995 ♀	Guadeloupe	66.0	31.0	27.7	17.2	6.5	12.6	10.7	11.6
TTU 20970 ♂	Guadeloupe	63.5	31.1	27.9	17.2	6.5	12.6	11.0	11.7
TTU 20977 ♂	Guadeloupe	68.7	32.6	29.0	16.9	6.3	12.8	11.0	11.6
TTU 20980 ♂	Guadeloupe	66.4	31.8	28.2	17.6	6.5	12.4	10.7	12.1
TTU 20985 ♂	Guadeloupe	65.3	31.1	27.1	16.6	6.6	12.5	11.2	11.7
		Brachyphylla nana						
AMNH 19085 ♀	Cuba	58.1	28.0	24.7	15.0	6.0	11.5	9.0	10.0
AMNH 19090 ♀	Cuba	59.1	28.9	25.8	14.7	6.2	11.4	9.8	10.5
TTU 22762 ♀	Haiti	58.8	28.1	25.3	14.9	6.3	11.7	9.4	9.9
TTU 22764 ♀	Haiti	58.3	28.1	24.8	14.6	6.4	11.9	9.5	10.1
AMNH 214390 ♂	Dominican Republic	56.7	28.2	25.2	14.6	6.5	11.3	9.5	9.8
AMNH 214393 ♂	Dominican Republic	57.9	28.6	25.1	14.5	6.5	11.8	9.4	9.6
TTU 22760 ♂	Haiti	58.0	28.4	25.1	15.5	6.3	11.7	9.5	10.1
TTU 22761 ♂	Haiti	58.8	28.2	25.0	14.7	6.2	11.2	9.5	9.4
		Erophylla bombifrons						
AMNH 97591 ♀	Dominican Republic	47.7	23.8	21.7	11.3	4.6	10.0	7.7	6.4
AMNH 212998 ♀	Dominican Republic	46.6	23.6	21.5	11.1	4.5	9.7	7.5	6.4
ROM 45709 ♀	Dominican Republic	47.1	24.0	22.1	10.8	4.5	9.6	7.6	6.1
TTU 22767 ♀	Haiti	46.8	24.4	22.5	11.7	4.5	10.2	8.1	6.7
ROM 45710 ♂	Dominican Republic	45.9	24.3	21.9	11.5	4.5	10.0	7.5	6.7
ROM 72710 ♂	Dominican Republic	49.7	24.5	22.3	11.2	4.6	10.1	8.1	6.4
AMNH 39339 ♂	Puerto Rico	48.8	24.7	22.4	11.6	4.6	10.2	7.8	6.5
AMNH 39340 ♂	Puerto Rico	48.8	24.8	22.5	11.8	4.5	10.3	7.9	6.7
		Erophylla sezekorni						
AS 5814 ♀	Jamaica	47.9	24.5	22.6	11.5	4.7	9.7	8.0	6.6
AS 5815 ♀	Jamaica	47.9	24.7	22.5	11.0	4.1	9.7	8.2	6.3
AS 5816 ♀	Jamaica	46.5	24.0	22.1	11.0	4.4	9.5	8.0	6.5
AS 5817 ♀	Jamaica	49.1	24.8	22.7	11.0	4.7	9.7	8.1	6.6
AMNH 45178 ♂	Jamaica	45.4	25.7	23.3	11.8	4.7	10.1	8.2	6.8
AMNH 45179 ♂	Jamaica	47.8	25.5	22.6	11.3	4.5	10.0	8.0	6.6

APPENDIX 1.—*Continued.*

AMNH 45181 ♂	Jamaica	45.5	25.3	22.9	11.4	4.5	10.0	8.2	6.6
AMNH 45182 ♂	Jamaica	45.4	24.1	22.9	11.2	4.5	9.7	7.8	6.2
		Phyllonycteris aphylla							
TTU 21907 ♀	Jamaica	46.0	24.6	22.4		4.9	9.7	7.5	6.7
TTU 21908 ♀	Jamaica	45.3	24.9	22.6		5.0	9.9	7.8	6.8
TTU 21913 ♀	Jamaica	45.4	24.4	22.4		5.1	9.8	7.8	6.8
TTU 21914 ♀	Jamaica	44.8	23.9	21.8		5.0	9.5	7.6	6.8
TTU 21905 ♂	Jamaica	48.3	25.8	23.5		4.7	10.0	8.0	7.0
TTU 21906 ♂	Jamaica	44.3	25.2	22.8		4.8	10.2	7.9	6.9
TTU 21909 ♂	Jamaica	47.6	24.7	22.7		5.2	9.9	7.9	7.0
TTU 21915 ♂	Jamaica	46.0	25.1	23.1		5.2	10.1	7.9	6.9
		Phyllonycteris major							
AMNH 40925 ?	Puerto Rico		26.3	24.6		5.7	11.4	8.4	8.1
AMNH 40926 ?	Puerto Rico		26.8	25.1		5.9	11.1	8.7	7.9
AMNH 40927 ?	Puerto Rico		27.0	25.2		5.6	11.0	8.5	7.8
AMNH 40928 ?	Puerto Rico			25.9		5.8		8.8	8.3
		Phyllonycteris poeyi							
USNM 103548 ♀	Cuba	47.6	24.5	22.5		5.4	10.0	7.7	6.9
USNM 103588 ♀	Cuba	46.5	23.9	21.5		5.2	10.5	7.4	6.8
USNM 103589 ♀	Cuba	46.2	23.7	21.6		5.3	10.7	7.0	6.8
USNM 103592 ♀	Cuba	46.6	24.3	22.2		5.3	10.0	7.5	6.9
USNM 103537 ♂	Cuba	46.9	25.3	23.0		5.7	10.6	7.8	7.3
USNM 103586 ♂	Cuba	46.5	24.8	22.5		5.4	10.8	7.3	6.8
USNM 103597 ♂	Cuba	46.9	25.7	23.9		5.3	10.3	7.9	7.4
USNM 103600 ♂	Cuba	47.1	24.8	22.6		5.4	10.4	7.6	7.2
		Phyllonycteris poeyi obtusa							
TTU 22783 ♀	Haiti	49.8	24.2	22.1		5.5	10.2	7.1	7.1
TTU 22792 ♀	Haiti	46.4	23.9	21.6		5.7	10.9	7.4	6.9
TTU 22793 ♀	Haiti	47.2	24.0	22.1		5.5	10.8	7.2	7.0
TTU 22794 ♀	Haiti	47.7	23.7	22.0		5.6	10.0	7.4	7.2
TTU 22772 ♂	Haiti	47.8	25.2	22.6		5.5	10.5	7.5	7.2
TTU 22773 ♂	Haiti	47.5	24.8	22.4		5.5	10.4	7.6	6.7
TTU 22782 ♂	Haiti	48.7	25.4	22.9		5.4	10.5	7.4	7.4
TTU 22783 ♂	Haiti	48.7	24.7	22.4		5.5	10.2	7.3	6.9
		Desmodontinae							
		Desmodus rotundus							
TTU 8228 ♀	Tamaulipas	60.2	24.8	21.4	11.7	5.1	11.6	3.5	6.1
TTU 8170 ♀	San Luis Potosi	60.1	25.0	21.5	11.9	5.2	11.9	3.3	6.0
KU 111209 ♀	Nicaragua	62.2	25.2	21.3	12.4	5.6	12.3	3.1	6.1
KU 111210 ♀	Nicaragua	60.1	25.0	21.0	12.1	5.4	11.7	3.4	6.5
TTU 9927 ♂	San Luis Potosi	56.9	24.2	20.8	11.4	5.5	11.8	3.4	5.7
KU 111204 ♂	Nicaragua	58.6	24.2	20.8	11.8	5.3	12.0	3.4	6.2
TTU 5426 ♂	Trinidad	55.3	23.9	20.3	11.5	5.2	11.9	3.5	5.8
TTU 5894 ♂	Trinidad	55.5	23.5	20.3	11.7	5.2	11.8	3.5	5.7
		Diaemus youngii							
USNM 409368 ♀	Venezuela	53.4	25.3	21.7	13.8	6.1	13.2	3.4	6.0
USNM 409374 ♀	Venezuela	54.5	26.0	21.7	14.1	6.1	13.2	3.4	6.2
USNM 409375 ♀	Venezuela	53.5	24.8	21.1	14.1	6.5	12.6	3.8	6.4
TTU 5232 ♀	Trinidad	51.0	24.1	20.4	13.6	6.2	13.0	3.2	6.0
USNM 405767 ♂	Venezuela	51.0	24.3	20.2	13.5	6.4	12.9	3.4	5.8
TTU 5233 ♂	Trinidad	51.3	25.4	21.5	14.3	6.1	13.1	3.3	5.8
TTU 5411 ♂	Trinidad	49.5	24.7	20.7	13.4	6.0	13.0	3.1	5.9
TTU 5428 ♂	Trinidad	50.1	25.1	21.2	14.4	6.0	13.5	3.3	6.0
		Diphylla ecaudata							
TTU 5658 ♀	Texas	53.7	23.5	20.5	13.0	7.6	11.8	3.3	5.9
TTU 10171 ♀	Tamaulipas	55.3	23.5	19.6	13.0	7.2	11.7	3.4	6.2

APPENDIX 1.—*Continued.*

TTU 10157 ♀	Veracruz	55.8	24.0	20.1	12.9	7.6	11.6	3.6	6.2
KU 115131 ♀	Nicaragua	56.1	23.0	20.0	12.6	7.0	11.1	3.6	5.9
TTU 10000 ♂	Veracruz	54.0	23.5	19.9	12.8	7.3	11.8	3.5	5.7
KU 97854 ♂	Nicaragua	56.1	23.8	20.6	13.0	7.4	11.6	3.6	6.1
KU 115129 ♂	Nicaragua	55.4	23.1	19.7	12.7	7.2	11.2	3.5	5.8
KU 115132 ♂	Nicaragua	54.7	23.1	20.5	13.1	7.4	11.4	3.5	6.1

* Measurements as given by Gardner and Patton (1972).
** Measurements as given by Starrett (1969).

KARYOLOGY

ROBERT J. BAKER

This chapter is in memory of Dr. Claude M. Ward, who introduced me to the world of bats and whose premature death robbed me of a good friend and the world of a dedicated educator.

The systematics of the New World leaf-nosed bats are based primarily on classical morphological features such as shoulder articulation, dentition, and other cranial features. The available fossil record is inadequate and probably will always be too poor to determine much about the evolutionary relationships of subfamilies and genera (Smith, 1976). As an adjunct to the data based on classical morphological features, data from chromosomal and electrophoretic studies are being generated (see also Straney *et al.*, this volume). Hopefully, a synthesis of the data from these and other works will result in a reasonably complete understanding of the systematics and genetic strategies of members of the family Phyllostomatidae. Data derived from bat chromosomes also serve to verify, refute or modify the proposed models of chromosomal evolution (Wilson *et al.*, 1975; Bush, 1975).

In 1966 when I first began working with the chromosomes of this family, I assumed that chromosomal divergence in the standard karyotypes of species, genera, subfamilies, and the like generally would reflect their taxonomic status and the evolutionary time that any two lineages had been separated. However, some taxa (for instance, *Glossophaga* and *Erophylla*) that obviously have been separated long enough to evolve morphological distinctness deserving of generic and subfamilial status had indistinguishable karyotypes, whereas other species (such as *Uroderma bilobatum* and *Choeroniscus intermedius*, see also *Rhogeessa*, Bickham and Baker, 1977) contained considerable intraspecific chromosomal divergence. If evolutionary relationships were based solely on standard karyotypic data, one would produce a considerably different classification than that currently derived from classical osteological and exomorphological studies. Therefore, I began to question the value of chromosomal divergence as a taxonomic indicator. I presently am opposed to placing too much emphasis on degree of gross karyotypic divergence as a justification for taxonomic status (with the possible exception of specific distinctness). Of course, the longer two lineages have been separated, the more probable it is that events have occurred that result in karyotypic divergence. However, karyotypic changes become established in a species at such irregular intervals that one cannot depend on the rate of their establishment to indicate taxonomic position.

John Bickham and I are preparing a manuscript in which we propose that the rate and magnitude of chromosomal change is primarily a function of the degree to which the karyotype is adaptive to the adaptive zone occupied by the organism.

If this model proves accurate then, at times, organisms would undergo relatively rapid chromosomal evolution and at other times there would be long periods of reduced rates of chromosomal change.

The fact that karyotypic changes do not evolve at a constant rate is not too startling if one realizes it is a well documented fact that morphological features also evolve at different rates. In a given taxon, some features can become highly derived from the ancestral condition, whereas others remain indistinguishable from the primitive condition. Meanwhile, in a closely related taxon, a different suite of characters can become derived whereas all other characters remain near the primitive. If greater emphasis is placed on the derived characters, the systematics would result in greater taxonomic distance than if the classification were based only on the characteristics that remained in the primitive condition. A similar case might be made for the degree of morphological divergence—it does not necessarily reflect the evolutionary history. Certainly, parallelism and convergence can result in incorrect "lumping," and yet, emphasis on most rapidly evolving features may result in oversplitting. However, the fossil record reveals that generally there is agreement between total morphological divergence and evolutionary history. In light of data from the fossil record, I believe that in the majority of cases an overview of classical morphological data gives a more reasonable and accurate reflection of the evolutionary history than does degree of chromosomal divergence.

On the other hand, there are cases where karyotypic data can be more valuable than general morphology. To a much greater extent than general morphological information, G-band chromosomal data are applicable to the cladistic methodologies of Hennig (1966). The likelihood of extensive convergence of G-banding patterns is sufficiently low to warrant placing considerable confidence in the data. The typical mammalian genome is arranged in such a manner that there are enough chromosomal arms (linkage groups) to provide an adequate number of data points to determine the relationships within complex taxa. Additionally, G-band chromosomal characteristics are independent of exomorphological, cranial, or osteological features and, therefore, serve as an independent data source. A synthesis of findings from all of the aforementioned, plus those of a biochemical nature (such as electrophoretic, immunological, and DNA hybridization), should give the most accurate interpretation of the phylogeny and systematics of a taxon. Also, data from these three sources (general morphology, karyology, and biochemical) will be necessary to understand the evolutionary strategy of major taxa.

Of the 137 phyllostomatid species recognized by Jones and Carter (1976), basic karyotypic data are available for 105 (Table 1). In addition, Gardner (1977) reported karyotypic data for two additional taxa, *Artibeus fuliginosus* and *A. planirostris*, which were not recognized by Jones and Carter (1976). Representative standard karyotypes for 60 species are presented in Plates 1 through 60, which follow the literature cited. I have attempted to illustrate the major chromosomal complements found in the Phyllostomatidae. Plates are arranged alphabetically by generic and species names within subfamilies: Phyllostomatinae,

TABLE 1.—*Chromosomal data for phyllostomatid bats. Subfamilies are arranged in the order followed by Jones and Carter (1976). Genera and species are in alphabetical order. Symbols are* 2n, *diploid number; FN, Fundamental Number; M, metacentric; SM, submetacentric; ST, subtelocentric; A, acrocentric. Two species names not recognized by Jones and Carter (1976) are identified by an asterisk.* Mesophylla *is recognized as distinct from* Ectophylla.

Taxon	2n	FN	X	Y	Y_2	Authority	Number of specimens
PHYLLOSTOMATINAE							
Chrotopterus auritus	28	52	SM	A		Yonenaga, 1968;	1
	28	52	SM	A		Yonenaga *et al.*, 1969	1
Lonchorhina aurita	32		M	A		Baker and Hsu, 1970	2
	32	60	M	A		Baker, 1973	
Lonchorhina orinocensis	No information						
Macrophyllum macrophyllum	No information						
Macrotus californicus	40					Kniazeff *et al.*, 1967	
	40	60	SM	SM		Nelson-Rees *et al.*, 1968	10
	40	60				Davis and Baker, 1974	155
	40	60				Greenbaum and Baker, 1976	100
Macrotus waterhousii	46	60	SM	A		Baker, 1967; Hsu *et al.*, 1968	5
	46	60	SM	A		Nelson-Rees *et al.*, 1968	7
	46	60	SM	A		Davis and Baker, 1974	44
	46	60				Nagorsen and Peterson, 1975	4
	46	60	M	A		Greenbaum and Baker, 1976	118
	46	60	SM	A		Patton, 1976	2
Micronycteris behni	No information						
Micronycteris brachyotis	32	60	SM			Patton, 1976	1
Micronycteris daviesi	No information						
Micronycteris hirsuta	28	32	A	A		Baker, 1973	
	30	32	A	A		Baker *et al.*, 1973	7
	28	32	A	A		Baker *et al.*, 1973	4
Micronycteris megalotis	40	68	ST	A		Baker, 1967; Hsu *et al.*, 1968	1
	40	68	SM	A		Patton, 1976	1
Micronycteris minuta	28	50	ST	A		Baker, 1973	
	28	50	SM			Patton, 1976	1
Micronycteris nicefori	28		M	A		Baker and Hsu, 1970	5
	28	52	SM			Patton, 1976	1
Micronycteris pusilla	No information						
Micronycteris schmidtorum	38	66	ST	A		Baker, 1973	
Micronycteris sylvestris	No information						
Mimon bennettii	No information						
Mimon cozumelae	34	56				Patton, 1976	1
Mimon crenulatum	32					Baker and Hsu, 1970	2
	32	60	M	M		Baker *et al.*, 1972*b*	20
	32	60	SM	A		Hsu and Benirschke, 1974	
	32	60	SM	A		Gardner, 1977	
	32	60	SM	M		Patton, 1976	1
Mimon koepckeae	32	60	SM	A		Gardner, 1977	
Phylloderma stenops	32	58				Baker and Hsu, 1970	1
	32	58	M	A		Baker, 1973	
Phyllostomus discolor	32	60	SM	A		Baker, 1967; Hsu *et al.*, 1968	4
	32		?	?		Yonenaga, 1968	1
	32	60	M	A		Kiblisky, 1969	4
	32		?	?		Yonenaga *et al.*, 1969	1
	32		SM	A		Baker and Hsu, 1970	2
	32	60	SM	A		Baker, 1970	1
	32	60	SM			Patton, 1976	1
Phyllostomus elongatus	32	58	SM	A		Baker, 1973	
Phyllostomus hastatus	32	58	SM	A		Yonenaga, 1968	5
	32	58	SM	A		Yonenaga *et al.*, 1969	5
	32	58	M	A		Kiblisky, 1969	7
	32		SM	A		Baker and Hsu, 1970	2
	32	58	SM	A		Patton, 1976	2

TABLE 1.—*Continued.*

Phyllostomus latifolius	No information						
Tonatia bidens	16	20	M	A		Baker and Hsu, 1970	3
	16	20	SM			Patton, 1976	2
Tonatia brasiliensis	30	56	ST	A		Gardner, 1977	
Tonatia carrikeri	26	46				Gardner, 1977	
Tonatia minuta	30		SM	A		Baker and Hsu, 1970	3
	30	56	SM	A		Baker, 1973	
	30	56	SM			Patton, 1976	1
Tonatia silvicola	34	60	SM	A		Gardner, 1977	
Tonatia venezuelae	30	56				This paper	1
Trachops cirrhosus	30	56	ST	A		Baker, 1967; Hsu *et al.*, 1968	4
Vampyrum spectrum	30	56				Baker and Hsu, 1970	1
	30	56	SM	A		Baker, 1973	
GLOSSOPHAGINAE							
Anoura brevirostrum	No information						
Anoura caudifer	30					Yonenaga, 1968	
	30	56	SM	A		Baker, 1973	
Anoura cultrata	30	56	SM	A		This paper	1
Anoura geoffroyi	30	56	SM	A		Baker, 1967; Hsu *et al.*, 1968	3
	30		SM	A		Baker and Hsu, 1970	3
			SM			Pathak and Stock, 1974	
Anoura werckleae	No information						
Choeroniscus godmani	19	32	SM	ST	A	Baker, 1967	5
	19					Hsu *et al.*, 1968	5
	19	32	SM	A	A	Baker, 1970*a*	1
	20	36	SM			Patton and Gardner, 1971	1
	20	36				This paper	2
Choeroniscus inca	No information						
Choeroniscus intermedius	20	36				Baker, 1970*a*	
	20					Baker, 1973	
			SM			Pathak and Stock, 1974	1
	20	36	SM	A		Stock, 1975	1
Choeroniscus minor	No information						
Choeroniscus periosus	No information						
Choeronycteris mexicana	16	24-26				Baker, 1967; Hsu *et al.*, 1968	1
	16	24	SM	SM		Baker, 1973	
Glossophaga alticola	32	60	M	A		Baker, 1967	4
Glossophaga commissarisi	32	60	M	A		Baker, 1967; Hsu *et al.*, 1968	5
Glossophaga longirostris	32	60	M	A		This paper	
Glossophaga soricina	32	60	M	A		Baker, 1967; Hsu *et al.*, 1968	14
	32		M	A		Baker and Hsu, 1970	4
	32	60	SM	A		Baker, 1970*a*	1
Hylonycteris underwoodi	16	24				Baker, 1973	
Leptonycteris curasoae	No information						
Leptonycteris sanborni	32	60	M	A		Baker, 1967; Hsu *et al.*, 1968	5
Leptonycteris nivalis	32	60				Baker, 1973	
Lichonycteris degener	No information						
Lichonycteris obscura	28	50	SM	A		Baker, 1973 (data incorrect)	1
	24	44				This paper	2
Lionycteris spurrelli	28	50	SM	A		This paper	1
Lonchophylla concava	No information						
Lonchophylla hesperia	No information						
Lonchophylla mordax	No information						
Lonchophylla robusta	28	50	SM	A		Baker, 1973	
Lonchophylla thomasi	30	34				Baker, 1973	
	32	38				Gardner, 1977	
Monophyllus plethodon	32	60	SM	A		This paper	3
Monophyllus redmani	32	60	SM	A		Baker and Lopez, 1970*b*	7
Musonycteris harrisoni	No information						
Platalina genovensium	No information						
Scleronycteris ega	No information						

TABLE 1.—*Continued.*

CAROLLIINAE							
Carollia brevicauda	20-21	36	ST	A	A	Patton and Gardner, 1971	4
	20-21	36				Stock, 1975	1
Carollia castanea	20-21	36	ST	A	A	Baker and Bleier, 1971	4
	22	38	SM	A		Patton and Gardner, 1971 (Perú)	5
	20-21	36	ST			Patton and Gardner, 1971 (Costa Rica)	1
	22	38	SM	A		Hsu and Bernischke, 1973	
	20-21	36	SM			Pathak and Stock, 1974	
	22	38	SM	A		Stock, 1975	1
	22	38	SM	A		Hsu *et al.*, 1975	1
Carollia perspicillata	20-21	36	ST	A	A	Baker, 1967	2
	21					Hsu *et al.*, 1968	2
	20-21	36	SM	A	A	Yonenaga, 1968	4
	20-21	36	ST	A	A	Kiblisky, 1969	3
	20-21	36	SM	A	A	Yonenaga *et al.*, 1969	4
	20	36	ST	A	A	Baker, 1970*a*, 1970*b*	1
	20-21	36	ST	A	A	Baker and Hsu, 1970	4
	20-21	36	SM	A	A	Baker and Bleier, 1971	5
	20-21	36	ST	A	A	Patton and Gardner, 1971	7
	20-21	36	SM	A	A	Pathak and Stock, 1974	
	20-21	36	SM	A	A	Hsu *et al.*, 1975	2
	20-21	36	ST	A	A	Stock, 1975	1
Carollia subrufa	20-21	36	ST	A	A	Baker, 1967	12
	20-21					Hsu *et al.*, 1968	11
	20	36	ST			Baker, 1970*a*, 1970*b*	1
	20-21	36	ST	A	A	Baker and Bleier, 1971	2
Rhinophylla alethina	No information						
Rhinophylla fischerae	34	56	SM	A		Baker and Bleier, 1971	1
Rhinophylla pumilio	36	62	M	A		Baker and Bleier, 1971	6
	36	62	M	SM		Hsu and Benirschke, 1973	
STENODERMINAE							
Ametrida centurio	30-31		ST	SM	M	Baker and Hsu, 1970	5
Ardops nichollsi	30-31	56	SM	ST	A	Greenbaum *et al.*, 1975	10
Ariteus flavescens	30-31	56	ST	ST	A	Greenbaum *et al.*, 1975	12
Artibeus aztecus	30-31	56	ST	A	A	Baker, 1973	
Artibeus cinereus	30-31	56	ST	SM	M	Baker and Hsu, 1970	4
Artibeus concolor	No information						
*Artibeus fuliginosus**	30-31	56	ST	A	A	Gardner, 1977	
Artibeus glaucus	30-31	56	ST	A	A	Gardner, 1977	
Artibeus hirsutus	30-31	56	ST	ST	A	Baker, 1973	
Artibeus inopinatus	30-31	56	ST	ST	A	This paper	5
Artibeus jamaicensis	30-31	56	ST	A	A	Baker, 1967	15
	30-31	56				Hsu *et al.*, 1968	9
	30-31	56	ST	A	A	Kiblisky, 1969	2
	30-31		ST	A	A	Baker and Hsu, 1970	3
	30-31	56	ST	A	A	Baker and Lopez, 1970*b*	5
Artibeus lituratus	30-31	56	ST	A	A	Baker, 1967	8
	30-31					Hsu *et al.*, 1968	8
	30-31	56	SM	A	A	Yonenaga, 1968	2
	30-31	56	SM	A	SM	Becak *et al.*, 1969	4
	30-31	56	ST	A	A	Kiblisky, 1969	3
	30-31	56	SM	A	A	Yonenaga *et al.*, 1969	2
	30-31		ST	ST	A	Baker and Hsu, 1970	2
			SM			Pathak and Stock, 1974	
Artibeus phaeotis	30	56	ST	SM		Baker, 1967	4
	30	56	ST	SM		Hsu *et al.*, 1968	2
*Artibeus planirostris**	30-31	56	ST	A	A	Gardner, 1977	
Artibeus toltecus	30-31	56	ST	A	A	Baker, 1967	4
	30-31	56	ST	A	A	Hsu *et al.*, 1968	4
Artibeus watsoni	30	56	ST	SM		Baker, 1973	

TABLE 1.—*Continued.*

Centurio senex	28	52				Baker, 1967; Hsu *et al.*, 1968	1
	28		ST	SM		Baker and Hsu, 1970	1
Chiroderma doriae	No information						
Chiroderma improvisum	26	48	ST	ST		Baker and Genoways, 1976	1
Chiroderma salvini	26	48	ST	SM		Baker, 1973	
Chiroderma trinitatum	26		ST	SM		Baker and Hsu, 1970	3
	26	48	ST	ST		Baker and Genoways, 1976	
	26	48				Gardner, 1977	
Chiroderma villosum	26	48	ST	SM		Baker, 1967; Hsu *et al.*, 1968	3
	26		ST	SM		Baker and Hsu, 1970	4
				SM		Pathak and Stock, 1974	
	26	48				Gardner, 1977	
Ectophylla alba	30	56	SM	A		Greenbaum *et al.*, 1975	1
	30	56				This paper	
Enchisthenes hartii	30	56				Baker, 1967; Hsu *et al.*, 1968	2
	30-31		ST	SM	A	Baker and Hsu, 1970	2
Mesophylla macconnelli	21-22		A			Baker and Hsu, 1970	16
	21					Baker and Hsu, 1970	1
	21-22	20	A			Hsu and Benirschke, 1971	
	21-22	20	A			Baker *et al.*, 1973	27
Phyllops falcatus	No information						
Phyllops haitiensis	30-31	56	ST	ST	A	Greenbaum *et al.*, 1975	8
	30	56				Nagorsen and Peterson, 1975	3
Pygoderma bilabiatum	No information						
Sphaeronycteris toxophyllum	28	52	ST	SM		Baker, 1973	
Stenoderma rufum	30-31	56	ST	A	A	Baker and Lopez, 1970*b*	16
	30-31	56	ST	A	A	Genoways and Baker, 1972	16
Sturnira aratathomasi	No information						
Sturnira bidens	30	56	ST	A		Gardner and O'Neill, 1969	2
Sturnira erythromos	30	56	ST	A		Gardner and O'Neill, 1969	6
Sturnira lilium	30	56	ST	SM		Baker, 1967; Hsu *et al.*, 1968	15
	30	56	ST	SM		Kiblisky, 1969	3
	30	56	ST	SM		Baker and Hsu, 1970	4
Sturnira ludovici	30	56	ST	SM		Baker, 1967; Hsu *et al.*, 1968	2
	30	56				Kiblisky, 1969	1
Sturnira magna	30	56	ST	A		Gardner, 1977	
Sturnira mordax	30	56				Baker, 1973	
Sturnira nana	30	56	ST	A		Gardner, 1977	
Sturnira thomasi	30	56				This paper	
Sturnira tildae	30		ST	SM		Baker and Hsu, 1970	3
Uroderma bilobatum	44	48	ST	SM		Baker, 1967; Hsu *et al.*, 1968	4
	42		ST	SM		Baker and Hsu, 1970	3
	38	44	ST	SM		Baker and Lopez, 1970*a*	5
	42	50	ST	SM		Baker and Lopez, 1970*a*	13
	42	50	SM	SM		Hsu and Benirschke, 1971	
	44 or 43	48	ST	SM	O	Baker and McDaniel, 1972	122
	38	44	SM	M		Baker *et al.*, 1972	
	39	45				Baker *et al.*, 1972	total of 144
	44 or 43	48	SM	M		Baker *et al.*, 1972	
	38					Baker *et al.*, 1975	88
	39					Baker *et al.*, 1975	4
	40					Baker *et al.*, 1975	1
	41					Baker *et al.*, 1975	1
	42					Baker *et al.*, 1975	1
	43					Baker *et al.*, 1975	14
	44					Baker *et al.*, 1975	82
Uroderma magnirostrum	36	62	ST	SM		Baker and Lopez, 1970*a*	11
	35	62	ST	SM		Baker and Lopez, 1970*a*	2
	36	60	SM	M		Hsu and Benirschke, 1971	
Vampyressa bidens	26	48				Gardner, 1977	
Vampyressa brocki	24	44				Baker and Genoways, 1972	3
	24	44				Baker *et al.*, 1973	3
	24	44	ST			Gardner, 1977	

TABLE 1.—*Continued.*

Vampyressa melissa	14	24	ST		Gardner, 1977	
Vampyressa nymphaea	26	48	ST	SM	Baker, 1973	
	26	48	ST	SM	Baker *et al.*, 1973	
	26	48	ST	A	Gardner, 1977	5
Vampyressa pusilla	23-24	22	ST		Baker, 1973	
	18	20	ST	SM	Baker, 1973	
	18	20	ST	ST	Baker *et al.*, 1973	13
	24-23	22			Baker *et al.*, 1973	9
	22-23	22	ST-A	SM	Gardner, 1977	
Vampyrodes caraccioli	30		ST	SM	Baker and Hsu, 1970	4
	30	56	ST	SM	Baker, 1973	
Vampyrops aurarius	No information					
Vampyrops brachycephalus	30	56	ST	SM	Baker, 1973	
Vampyrops dorsalis	30	56	ST	SM	Baker, 1973	
Vampyrops helleri	30	56	ST	SM	Baker, 1967; Hsu *et al.*, 1968	2
	30		ST	SM	Baker and Hsu, 1970	4
Vampyrops infuscus	30	56	ST	A	Gardner, 1977	
Vampyrops lineatus	No information					
Vampyrops nigellus	30	56	ST	A	Gardner, 1977	
Vampyrops recifinus	No information					
Vampyrops vittatus	30	56	ST	A	Baker, 1973	
BRACHYPHYLLINAE						
Brachyphylla cavernarum	32	60	SM	A	Baker and Lopez, 1970*b*	11
Brachyphylla nana	32	60	SM	A	This paper	3
Brachyphylla pumila	32	60	SM	A	Nagorsen and Peterson, 1975	4
Erophylla sezekorni	32	60			Baker and Lopez, 1970*b*	11
	32	60	SM	A	Nagorsen and Peterson, 1975	4
Phyllonycteris aphylla	32	60	SM	A	This paper	
Phyllonycteris major	No information					
Phyllonycteris obtusa	32	60	SM	A	Nagorsen and Peterson, 1975	1
	32	60	SM	A	This paper	
Phyllonycteris poeyi	No information					
DESMODONTINAE						
Desmodus rotundus	28	52	SM	A & ST	Forman *et al.*, 1968	13
	28	52			Yonenaga *et al.*, 1969	6
	28	52	SM	ST	Cadena and Baker, 1976	
Diaemus youngii	32	60	SM	A	Forman *et al.*, 1968	4
	32	60			Cadena and Baker, 1976	1
Diphylla ecaudata	28	52	SM	A	Baker, 1973 (data incorrect)	
	32	60			Cadena and Baker, 1976	2
	32	60			Gardner, 1977	

Plates 1 to 17; Glossophaginae, 18 to 29; Carolliinae, 30 to 32; Stenoderminae, 33 to 52; Phyllonycterinae, 53 to 57; Desmodontinae, 58 to 60.

DETERMINATION OF PRIMITIVE KARYOTYPE

One very important point of information relative to determining evolutionary events and their systematic implications is an understanding of the primitive versus the derived condition. Because there is no fossil record for karyotypes, primitive cytogenetic aspects are difficult to ascertain.

Prior to the availability of G-band data, two theories were developed as to the diploid and fundamental characteristics of the primitive karyotype for the family Phyllostomatidae. Baker (1967, 1973) proposed that the primitive karyotype for the Phyllostomatidae consisted of a diploid number ($2n$) of 30 or 32, with a fundamental number (FN) of 56 to 60. This theory was based on the

widespread occurrence of the $2n = 30$ or 32, FN = 56-60 karyotype among species from the different subfamilies; the alternative explanation was to assume the condition arose through convergent evolution. Gardner (1977), on the other hand, proposed that the primitive karyotype was $2n = 36$ to 40 with an FN near the minimum for this diploid number, 38 or slightly higher. The significant difference between the two theories centers around the types of chromosomal rearrangements required to derive the karyotypes found in extant species. The $2n = 30$ or 32, FN = 60, would require terminalization of centromeres by pericentric inversion or centric transpositions in addition to translocations (especially centric fusions) as the primary rearrangements, whereas the $2n = 36$-40, FN = 38, would require centralization of centromeres (by pericentric inversion or centric transpositions) in addition to some fusions.

It is of interest to note that when Gardner (1977:314-315) interpreted phylogenetic relationships within the family based on chromosomal evolution from a primitive karyotypic condition of a higher diploid number (about 40) and a lower fundamental number (about 38), his three "major deviations from more classical portrayals" were essentially those proposed earlier based on a primitive $2n = 32$, FN = 60, karyotype. Relative to Gardner's case 1, Baker and Lopez (1970*b*:471) pointed out the "possibility of a close phylogenetic relationship" of the phyllonycterine genera to *Monophyllus*. In Gardner's case 2, Baker (1967: 423), basing his remarks on karyotypes, not only suggested that *Sturnira* "must have evolved from the Stenoderminae complex," he also regarded the two subfamilies as synonymous, which is the systematic relationship followed by Jones and Carter (1976:20). In case 3, Greenbaum *et al.* (1975) suggested the recognition of *Mesophylla* as generically distinct from *Ectophylla*. The point is that even though a $2n = 40$, FN = 38, primitive karyotype theory might be a viable alternative to the $2n = 32$, FN = 60, theory in several examples, the systematic implications of the chromosomal data are the same.

With data from G-bands, it became possible to identify homologous segments between variant karyotypes even at the subfamilial level (Mascarello *et al.*, 1974), and G-band studies became the means for testing these two theories. It could be predicted that if the theory of $2n = 30$ or 32, FN = 56-60, were true, there should be considerable homology of banding patterns between the two arms of the supposed homologous elements of the $2n = 30$ or 32, FN = 56 or 60 karyotypes within the family, and although some elements in each karyotype may have been rearranged, the same pairs should not always be affected. On the other hand, if the $2n = 40$, FN = 38 (Gardner, 1977) karyotype proved primitive, G-banding patterns of biarmed elements of the $2n = 32$ karyotypes from separate subfamilies should show little homology between the subfamilies. Therefore, G-banding homology among these karyotypes with lower fundamental numbers from different subfamilies would be strong proof in favor of Gardner's theory.

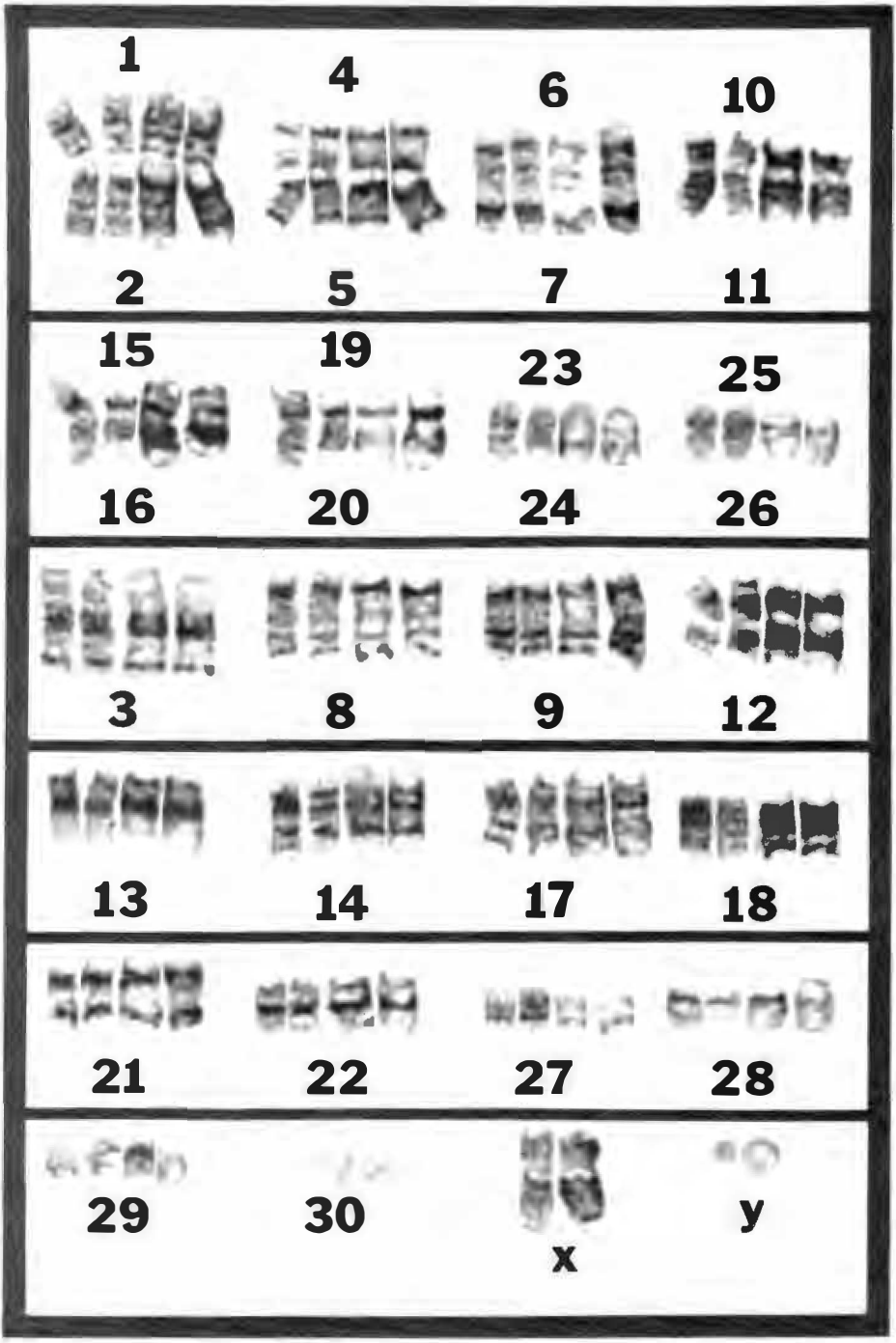
Patton (1976) examined G-banded chromosomes of five genera (involving 10 species) of the subfamily Phyllostomatinae as well as one species from the families Mormoopidae (*Pteronotus parnellii*) and Noctilionidae (*Noctilio albiventris*). His results indicated that the FN = 60 was primitive for the Phyl-

lostomatinae as well as for the Mormoopidae and Noctilionidae. *Macrotus* (as well as several other species of the Phyllostomatinae), *Pteronotus*, and *Noctilio* all have 30 pairs of autosomal arms. When the G-banded karyotypes of these three genera are compared, the thirty homologous arms found in the karyotype of each genus have a distinguishable counterpart in the karyotypes of the other two genera. The most logical interpretation of these data is that the number of autosomal arms in the karyotype of the common ancestor of *Macrotus*, *Pteronotus*, and *Noctilio* was 30 pairs (FN = 60), which have retained their respective G-banding patterns since their separation from a common ancestor. The alternative explanation, that the G-band similarity between the representatives of these three families is the result of the evolution of convergent G-banding patterns in the exact same number of pairs (30) of autosomal arms, is less plausible (Patton, 1976). Additionally, data from the G-banded karyotypes of other taxa thus far studied (by Patton, 1976, and unpublished data including representatives of the Desmodontinae, Glossophaginae, and Stenoderminae) support the conclusion that the FN = 60 was primitive for the Phyllostomatidae. Derivation of the various karyotypes of the taxa studied from any of the karyotypes with the more aberrant fundamental numbers (such as *Tonatia bidens* FN = 20 or *Micronycteris megalotis* FN = 68) would require many convergent chromosomal rearrangements in order to avoid concluding that *Macrotus* was more closely related to the mormoopids and noctilionids than to the other phyllostomatids.

The primitive diploid number for the Phyllostomatidae was believed to be $2n = 46$ (Patton, 1976). The following discussion, modified from Patton's thesis, points out the reasons for this conclusion.

A diploid number of 46 (with 16 biarmed autosomes, 28 acrocentric autosomes, plus two sex elements) is most probably like the primitive condition (Patton, 1976). Essentially, this is the karyotype of *Macrotus waterhousii* (Fig. 1). Data supporting this conclusion are the eight pairs of biarmed elements found in the karyotype of *Macrotus* that have corresponding biarmed elements in the karyotype of *Noctilio*. Seven of these eight pairs are present also in *Pteronotus*, *Tonatia minuta*, *Mimon crenulatum*, *Phyllostomus discolor*, and *Phyllostomus hastatus*. The majority of these eight pairs are identifiable in most of the karyotypes of other phyllostomatine species studied. Therefore, it is likely that these eight biarmed pairs were primitive for the phyllostomatoid karyotype. In addition to the eight biarmed pairs described as common for *Noctilio*, *Pteronotus*, and *Macrotus*, the karyotypes of most species examined include several other biarmed elements, the banding patterns of which suggest independent fusions of acrocentric elements.

An alternative hypothesis would be to propose a noctilionid-mormoopid-like karyotype as primitive. Such a primitive karyotype would, however, require additional events—fission would have to precede several independent fusions. As demonstrated by Mascarello *et al.* (1974) for rodents, the establishment of fission rearrangements is quite rare, whereas Robertsonian fusion products are the most common type of euchromatic variation observed between closely related taxa. Therefore, a fission-fusion mode not only would require additional events, it would also be less probable from a cytogenetic standpoint.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In the following paragraphs on the evolutionary relationships indicated by karyotypic data, it is assumed that the primitive karyotype for the Phyllostomatoidea was $2n = 46$, FN = 60 and with a morphology similar to that of *Macrotus waterhousii*. The discussion is essentially limited to G-band data because all other would be too speculative and G-band studies of most subfamilies will undoubtedly appear shortly. Proposed karyotypic relationships for some phyllostomatid taxa, based on standard karyotypes, are presented in Baker (1973), Greenbaum *et al.* (1975), and Gardner (1977).

Systematic Affinities

Familial Affinities

The first instance where the members of the Mormoopidae, Noctilionidae, and Phyllostomatidae were classified together, but distinct from all other bats, was Winge (1941). Smith (1972) drew similar conclusions—the Phyllostomatoidea consisted of the families Mormoopidae, Noctilionidae, and Phyllostomatidae. G-band chromosomal data strongly support this classification and suggest that *Pteronotus* and *Noctilio* shared a common evolutionary ancestor in which five Robertsonian fusions became established (Patton, 1976). These data indicate that the Noctilionidae and Mormoopidae are more closely related to each other than either is to the Phyllostomatidae. Smith (1972) came to the same conclusions based on morphological data. The most recent common ancestor of *Pteronotus* and *Noctilio* probably had a $2n = 36$ condition.

The degree of chromosomal divergence distinguishing *Noctilio* from *Pteronotus* is the least known to separate two mammalian families. Before someone jumps to the conclusion that the families Mormoopidae and Noctilionidae are confamilial, I would point out that prior to the study by Patton (1976), there had been considerable disagreement as to the evolutionary affinities of both families (Smith, 1972). In fact, there would be little agreement as to what family *Noctilio* should be placed in if it were not awarded familial status. Some classifications have included the mormoopids as a subfamily of the Phyllostomatidae (Miller, 1907; see also the review by Smith, 1972), and the chromosomal data merely indicate that if all lineages evolved from the most recent ancestor of the mormoopid-phyllostomatid line are to be included in the family Phyllostomatidae, then the Noctilionidae should also be reduced to a subfamily.

Chromosomal data from *Noctilio* and *Mormoops* further document the fact that karyotypic change is not a requirement for the evolution of a magnitude of morphological difference worth of recognition of a higher taxonomic category (Patton, 1976). It has been suggested by Wilson *et al.* (1975) that the large degree of morphological evolution in mammals is due to regulator gene alterations by

←

FIG. 1.—A composite of two G-banded karyotypes of *Macrotus waterhousii* prepared for use as standard reference in describing chromosomal events in the family Phyllostomatidae as proposed by Patton (1976). Both homologs from the two spreads are presented in order that minor variation can be observed. Figure courtesy of Rebecca A. Bass.

chromosomal mutations. However, few changes in primitive linkage groups are often characteristic of rather divergent taxa of bats and rodents (see also Mascarello *et al.*, 1974; Stock and Hsu, 1973), which leads one to conclude that at least some mammalian taxa have evolved primarily via point mutations and have conserved the primitive gene arrangements. A similar conclusion can be drawn for reptiles, based on chromosomal banding analysis of turtles (Stock, 1972; Bickham and Baker, 1976), and for birds (Stock *et al.*, 1974).

Subfamilial Affinities

There has been only one paper in which G and C-band data have been used to relate species from different subfamilies (Stock, 1975) and this work found essentially no G-band autosomal homologies between *Carollia* (subfamily Carolliinae) and *Choeroniscus* (subfamily Glossophaginae). From standard karyotypes, a close relationship between these two genera had been proposed (Baker, 1967). Stock noted that the X elements were essentially the same between the two genera but concluded that there were no data supporting a close common ancestor for *Carollia* and *Choeroniscus* and suggested that these two genera be placed in separate subfamilies. I have little doubt that a complete G-band study of the genera within all subfamilies will reveal the evolutionary relationships of most subfamilies. G and C-band studies on the Brachyphyllinae and Desmodontinae (by Rebecca A. Bass) and Stenoderminae (by Anette Johnson) are presently being conducted in my laboratory.

Relationships Within Subfamilies

Phyllostomatinae.—Relationships within the subfamily Phyllostomatinae were studied by Patton (1976), but his results were somewhat incomplete because only five of 11 genera (involving 10 of 33 species) were studied; these were arranged into three groups: 1) *Micronycteris,* 2) *Tonatia, Mimon,* and *Phyllostomus,* and 3) *Macrotus.*

The *Macrotus* group could have evolved from any lineage just as long as it became separated from the other stocks prior to the establishment of any chromosomal rearrangements. The karyotype of *Macrotus waterhousii* has been proposed as like that which was primitive for the family (see above). The karyotype of *M. californicus* ($2n = 40$, FN = 60) would then be derived by three centric fusions (Davis and Baker, 1974), which would have been independent events from fusions established in the other two lines discussed below.

Patton's (1976) *Micronycteris* group is characterized by the sharing of two derived arrangements. One is a terminal translocation of chromosome 13 onto pair 26/25 and the other is a Robertsonian fusion between acrocentric pairs 18 and 21. All other rearrangements within the *Micronycteris* cluster appear to have been achieved through independent events within the three subgenera (*Trinycteris, Micronycteris,* and *Lampronycteris*) studied by Patton. The hypothesized primitive karyotype for the subgenera *Trinycteris* and *Micronycteris* would be $2n = 42$, FN = 58. The fact that these species (*minuta, nicefori,* and

brachyotis) representing three subgenera, can be chromosomally related, strongly reinforces the natural status of at least portions of the genus. I have heard several people propose that this genus is a catchall with several species of questionable generic affinity. One species that cannot be related chromosomally to the other representatives of the genus thus far studied is *M. megalotis*, the type species of the genus.

The *Tonatia-Mimon-Phyllostomus* group is identified by five shared derived chromosomal events: four Robertsonian fusions (22/3, 8/9, 17/12, 29/27) and one inversion (4/5). These chromosomal characteristics are shared by *Tonatia minuta*, *Phyllostomus discolor*, *P. hastatus*, and *Mimon crenulatum*. The ancestral karyotype for the common ancestor probably had a $2n = 38$, FN = 60. A common ancestor for *Phyllostomus hastatus*, *P. discolor*, and *Mimon crenulatum* is suggested by three shared fusion events (18/13, 14a/21, 30/28). This would mean that the common ancestor for these three species had a karyotype with a $2n = 32$ or 34. As Robertsonian fusion products occurring independently in forms containing only two acrocentric linkage groups could only lead to the same fusion product, a $2n = 34$ divergence cannot be totally discounted (Patton, 1976). The possibility of a $2n = 34$ divergence is strengthened by *Mimon cozumelae* having a $2n = 34$, FN = 60 karyotype.

The karyotype of *Tonatia bidens* ($2n = 16$) is so derived from the *Macrotus* and *Tonatia minuta* karyotypes that it could not be related to those of other members of the subfamily. Again, this points out a case where most chromosome divergence has been limited to changes that can be traced by homology of G-bands, but during the evolution of *T. bidens* numerous chromosomal changes became established. If systematic position were based solely on chromosomal divergence, one would have to recognize *T. bidens* as generically distinct from other phyllostomatines possibly with subfamilial status, a ridiculous conclusion in my opinion.

Glossophaginae.—There are no G-band studies on the generic relationships within the Glossophaginae. The only published G-banded karyotype is of *Choeroniscus intermedius* (Stock, 1975), which is discussed above under subfamilial relationships.

Gardner (1977) presented a phylogeny of the Glossophaginae based on standard karyotypes and in most cases has followed the most parsimonious routes. However, I cannot accept that the similar karyotypes of *Choeronycteris* and *Hylonycteris* are the result of parallelism. This $2n = 16$ karyotype is undoubtedly derived, and I feel that it is explained best as being due to their common ancestor having a diploid number of 16. G-banding should be valuable in settling this difference in interpretation.

Carolliinae.—G-band data (Stock, 1975) have been published for one (*Carollia*, three species studied) of the two genera of the Carolliinae. *Carollia brevicauda* and *C. perspicillata* share two chromosomal features (an X-autosomal translocation and similar heterochromatin patterns) that distinguish these two species from at least some individuals of *C. castanea*. Pine (1972), in a study based on classical morphological features, concluded that *C. brevicauda* and *C. perspicillata*

FIG. 2.—G-banded karyotype of *Artibeus jamaicensis*. Figure courtesy of M. Anette Johnson.

were more closely related to each other than either is to *C. castanea*. *Carollia castanea* has two chromosomal races that are based on the presence of the X-autosomal translocation in specimens from Central America (Patton and Gardner, 1971) and Colombia (Baker and Bleier, 1970) and the absence of this translocation in Peruvian specimens (Patton and Gardner, 1971).

Patton and Gardner (1971) argued that the absence of the X-autosomal translocation in some populations of *C. castanea* is the result of the primitive condition being maintained. This would best explain the current taxonomic distribution of the X-autosomal translocation if the ancestor of all *Carollia* species was polymorphic for this translocation. In *C. perspicillata*, *C. subrufa*, and *C. brevicauda*, this translocation became fixed and characteristic of the species, whereas

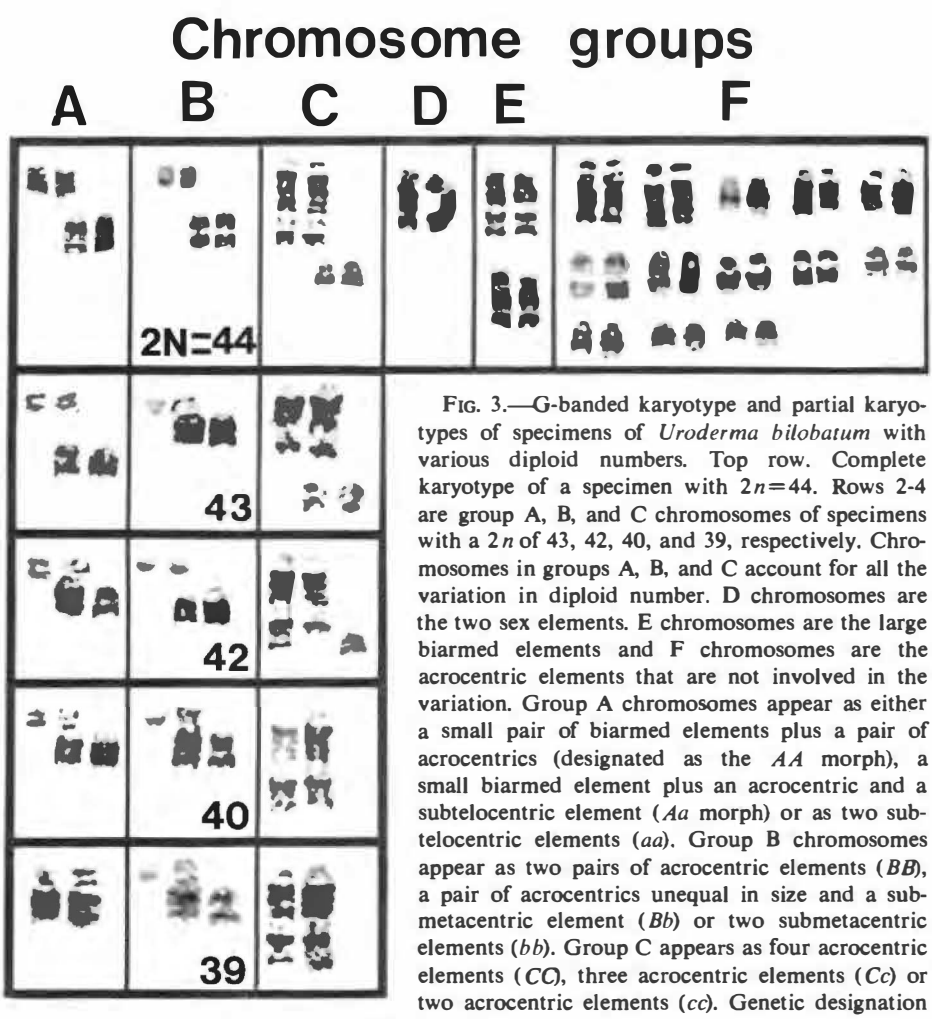

FIG. 3.—G-banded karyotype and partial karyotypes of specimens of *Uroderma bilobatum* with various diploid numbers. Top row. Complete karyotype of a specimen with $2n=44$. Rows 2-4 are group A, B, and C chromosomes of specimens with a $2n$ of 43, 42, 40, and 39, respectively. Chromosomes in groups A, B, and C account for all the variation in diploid number. D chromosomes are the two sex elements. E chromosomes are the large biarmed elements and F chromosomes are the acrocentric elements that are not involved in the variation. Group A chromosomes appear as either a small pair of biarmed elements plus a pair of acrocentrics (designated as the *AA* morph), a small biarmed element plus an acrocentric and a subtelocentric element (*Aa* morph) or as two subtelocentric elements (*aa*). Group B chromosomes appear as two pairs of acrocentric elements (*BB*), a pair of acrocentrics unequal in size and a submetacentric element (*Bb*) or two submetacentric elements (*bb*). Group C appears as four acrocentric elements (*CC*), three acrocentric elements (*Cc*) or two acrocentric elements (*cc*). Genetic designation for each karyotype: $2n$ of 44 is *AA BB CC*; $2n=43$ is *AA Bb CC*; $2n=42$ is *Aa BB Cc*; $2n=40$ is *Aa Bb cc*; and $2n=39$ is *aa Bb cc*.

in *C. castanea* some populations became fixed for both conditions. This explanation might be correct and I agree that it is the first choice; however, based on the limited data now available, an alternative explanation cannot be ruled out. It is possible that the absence of the X-autosomal translocation in some *C. castanea* is due to a fission of these elements and represents a condition more derived than that characteristic of *C. perspicillata*, *C. subrufa*, and *C. brevicauda*.

Stenoderminae.—G and C-band chromosomal data for *Sturnira lilium*, *Artibeus jamaicensis* (Fig. 2), *Enchisthenes harti*, and *Uroderma bilobatum* ($2n=44$ cytotype, Fig. 3) are described by Baker *et al.* (1979). The G-banding pattern for *Artibeus* and *Sturnira* revealed that the similarity in the gross karyotypes reflected homology with only one autosomal change (a pericentric

inversion) distinguishing their respective karyotypes. The karyotype of *Enchisthenes harti* could be derived from the *Artibeus* karyotype by a reciprocal translocation involving two autosomes. This translocation changes two submetacentric chromosomes in *Artibeus* to two subtelocentric chromosomes in *Enchisthenes.*

It was more difficult to show homology between *Artibeus* and the *Uroderma* $2n=44$ karyotype. Two pairs of *Artibeus* autosomes were homologous with elements in *Uroderma*; the other 12 pairs of *Artibeus* (85 per cent of the autosomal pairs) autosomes required rearrangement to derive the *Uroderma* karyotype. For some chromosomal segments, homologous elements could not be determined between the two karyotypes.

Artibeus has five (Baker *et al.*, 1979) pairs of biarmed chromosomes that are homologous with pairs found in *Macrotus.* The biarmed pairs homologous between *Artibeus* and *Macrotus* are thought to be primitive for the family (Patton, 1976). *Uroderma* and *Macrotus* have no homologous biarmed chromosomes; however, they share acrocentric chromosomal homologies.

Only two pairs of chromosomes (both biarmed) were shared by all four stenodermine genera studied. These two pairs are not found in any of the other subfamilies studied (Phyllostomatinae, Patton, 1976; Glossophaginae and Carolliinae, Stock, 1975) and are, therefore, potentially valuable indicators of a common ancestry for these and other stenodermine genera. Such marker elements should prove valuable in determing if *Brachyphylla* has evolutionary affinities with the Stenoderminae. The G-band data for *Sturnira* are interpreted as additional documentation that the genus *Sturnira* has a common ancestry with the Stenoderminae and should be recognized as a member of that subfamily (Baker *et al.*, 1978). G-banded karyotypes for *Uroderma bilobatum* are shown in Fig. 3 and are discussed below in the following section.

Desmodontinae and Brachyphyllinae.—No G-banded karyotypes have been published for the subfamilies Desmodontinae and Phyllonycterinae.

[*Note added in galley.*—G-band data are now available for several additional species so that the following important conclusions can be drawn. The glossophagine genera *Glossophaga* and *Monophyllus* have identical G-band chromosomal homologies with species of *Phyllonycteris, Erophylla,* and *Brachyphylla.* These data indicate that these five genera shared a common ancestor after separating from the other subfamilial lineages (with the possible exception of the Carolliinae) and that *Brachyphylla* is properly associated with the genera *Phyllonycteris* and *Erophylla* (Baker and Bass, 1979), as was suggested by Silva Taboada and Pine (1969). However, when the genus *Brachyphylla* is placed in this subfamily, Brachyphyllina Gray, 1866, becomes the oldest available family-group name for the subfamily (Phyllonycterinae was first proposed by Miller, 1907). The proper name of the subfamily then would be Brachyphyllinae.

In a manuscript recently submitted for publication by Rebecca A. Bass and the author, it was shown that the vampire bats (Desmodontinae) shared a common ancestry with the glossophagines and brachyphyllines, after this lineage separated from the remainder of the family.]

Variation within Species

From the standpoint of population biology, this is the level where chromosomal variation can be used to make the most significant studies. The role of various types of mechanisms of chromosomal evolution can be studied as an isolating mechanism, effective means of producing heterosis, supergenes, etc. Variation at this level can be due to populational polymorphisms or chromosomal races.

Polymorphisms

A widely distributed polymorphism has been described (Baker *et al.*, 1972*b*) for *Mimon crenulatum*. The polymorphism was found in samples from Perú, Trinidad, and Colombia and is believed to be restricted to the fifth largest pair of autosomes. Three morphs of this chromosome were identified from each of the three localities. For polymorphism to be maintained over such a wide geographic range, it must offer a selective advantage to the species greater than the expense of its maintenance.

Baker and Lopez, (1970*a*) demonstrated a polymorphism also for *Uroderma magnirostrum*. Eleven of thirteen specimens examined from Colombia had a diploid number of 36, whereas two had a diploid number of 35. Because the size of the additional biarmed element was greater than a fusion between any two acrocentrics, the polymorphic system may not be the result of a simple centric fusion.

Other cases of chromosomal variation at a single locality are based on the discovery of a single aberrant individual, which may represent a balanced polymorphic system or variation that originated within that individual.

A centric fusion was reported in a female *Mesophylla macconnelli* from Trinidad; nine other specimens from this locality did not possess the chromosome. An *Artibeus toltecus* from San Luis Potosí, México, had a $2n=32$ with what appeared to be a trisomy for a small autosome and one other male from this locality had a $2n=31$, which is normal for the species.

In a sample of 78 *Uroderma bilobatum* from near Choluteca, Honduras, one individual had a $2n=37$, which resulted from a fusion of two acrocentrics into a metacentric of the same general size range as the subtelocentric autosomes. Chromosomal variation at this locality is common as a result of hybridization between two cytotypes (see the discussion on *Uroderma* below); however, this centric fusion is easily identifiable from those events that separate the two cytotypes because the fusion product is a metacentric, and such an element has not been observed in 332 other specimens of *Uroderma bilobatum* from Central America.

Chromosomal Races

Chromosomal races are known for three species of phyllostomatid bats. What originally was reported as chromosomal races in *Macrotus waterhousii* proved to be specific differences characteristic of two species: *M. waterhousii*, with

$2n=46$, and *M. californicus*, with $2n=40$ (Davis and Baker, 1974; Greenbaum and Baker, 1976). Two races are known for *Micronycteris hirsuta* (Baker *et al.*, 1973). One is a $2n=30$ cytotype from Middle America characterized by a single pair of submetacentric autosomes. Specimens from Trinidad, on the other hand, have a karyotype with a $2n=28$, FN = 32 and show two pairs of submetacentric autosomes and two less pairs of acrocentrics. The degree of divergence in cranial and forearm measurements in the specimens karyotyped is too low to suggest that the two chromosomal races represent distinct species (Baker *et al.*, 1973).

Two races of *Vampyressa pusilla* were described by Baker *et al.* (1973). One race has a $2n=18$, FN = 20 with two pairs of submetacentric autosomes and six acrocentric pairs. The X is a subtelocentric, and the Y is a small distinctly biarmed element. This race is known from Honduras, Nicaragua, and Costa Rica. The second race, found in Colombia, has a karyotype that consists of a $2n=24$ in females and a $2n=23$ in males, with an FN of 22. There are no submetacentric autosomes. To explain divergence between the two races requires at least three events. Even though the magnitude of variation is greater than that characteristic of most congeneric species of phyllostomatids, no exomorphological or cranial differences were found that could distinguish the races (Baker *et al.*, 1973). Data from *V. pusilla* documents another case of discordant rates of evolution between classical and karyotypic morphology.

Uroderma bilobatum, Peters' tent-making bat, is the third species of phyllostomatid bat known to have chromosomal races. The three chromosomal races reported for this species have been the object of considerable study (Baker and Lopez, 1970*a*; Baker *et al.*, 1972*a*; Baker and McDaniel, 1972; Baker *et al.*, 1975); one zone of contact between two races has been located. Information on the nature and dynamics of this zone could be valuable in understanding some aspects of the speciation process.

Elucidation of the processes by which one species becomes transformed into two or more is the key to understanding evolution. The genetic interactions involved between two diverging populations within a species dictate the evolutionary future of these populations. Although several theories have been postulated for such genetic interactions and their relationships to the process of speciation, actual measurements of the interaction are difficult to make and definitive data are lacking.

An important aspect involved in speciation is the chromosomal compatibility between diverging populations. One proposed model of speciation (stasipatric speciation by White, 1968) is based entirely on chromosomal divergence. The situation with *Uroderma bilobatum* (see details below) does not exactly fit the stasipatric model put forth by White; however, *Uroderma* offers a unique opportunity to examine the role of karyotypic diversity and the resulting interaction between two interbreeding populations. A detailed understanding of the mechanisms and events occurring at the contact zone between two chromosomally characterized populations of *Uroderma bilobatum* is important because we will be able to observe a stage of evolution that could result in the

formation of two species. It could provide insight into how chromosomal changes become fixed within a population.

The paucity of measurements on the genetic interactions resulting in speciation (especially in mammals) can be attributed to both the difficulties in obtaining such measurements and the inability of available techniques to identify appropriate biological situations for study. In order to attempt to measure the genic interactions that might produce speciation, it is first essential to locate a situation where populations have diverged. In addition, it is necessary to be able to identify within the population first generation crosses between the types (referred to as F_1s, although this does not imply specific status of the types) and backcross individuals.

Measurements of degree of exomorphological and cranial divergence have proven inadequate for such studies. By the point in time when organisms are sufficiently diverged to enable the recognition of F_1 and backcross individuals by these techniques, the stage at which the most significant interactions occur has passed. Numerous studies can be cited to document this problem (see Lidicker, 1962, for a review of the problems of subspecific evolution in mammals). Even when interpreted with the use of the most sophisticated multivariate techniques, measurements of exomorphological and cranial features cannot identify with any certainty the F_1 and backcross individuals or measure genetic interaction (see Baker *et al.*, 1975). The extent to which gene flow has been reduced when alloptric populations reestablish contact simply cannot be ascertained with any degree of accuracy from measurements of exomorphological and cranial features.

In cases where two interacting populations are characterized by chromosomal differences, F_1 individuals will have a predictable karyotype unique from that of both parental types. If the chromosomal differences are of sufficient magnitude, the first generation backcross individuals will have karyotypes distinguishable from the F_1 and parental karyotypes. Such biological situations provide an excellent case for detailed investigations into the genetic interactions of divergent populations and the process of speciation.

It should be pointed out, however, that anytime karyotypes are used to identify diverging populations, one is studying a special case because chromosomes are involved and chromosomes could be the primary isolating mechanism. There are many isolating mechanisms known, and it is possible that each represents a special case. It is also probable that no single isolating mechanism is involved in all cases of speciation. The aim of the detailed study of *Uroderma* in my laboratory is to investigate the role of chromosomal divergence in the evolutionary process as exemplified by these bats.

The classical systematics and distribution of *U. bilobatum* are as follows: *Uroderma bilobatum* occurs at lower elevations from southern México southward through parts of tropical South America. Based on variations in external and cranial measurements, karyology, and pelage color, six subspecies (*bilobatum*, *molaris*, *convexum*, *trinitatum*, *davisi*, and *thomasi*) are recognized (Davis, 1968; Baker and McDaniel, 1972). Extensive chromosomal investigations of the

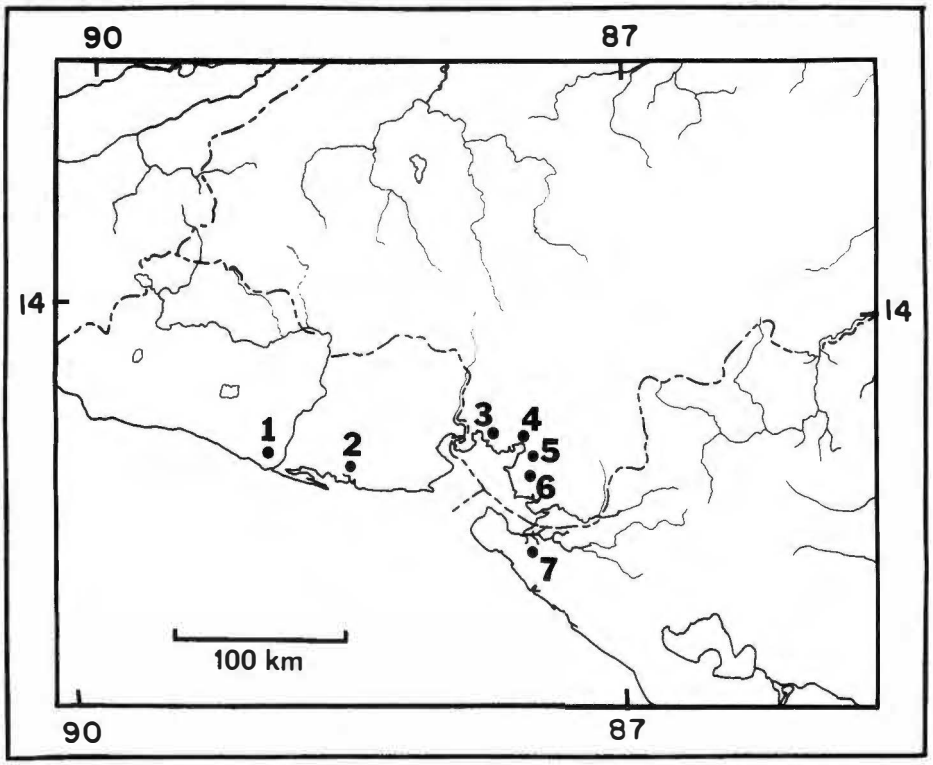

FIG. 4.—Geographic distribution of samples of *Uroderma bilobatum* within contact zone (see Table 2). Specific localities are 1) El Salvador: La Paz: 3.0 mi. NW La Herradura; 2) Usulatán: 3.0 mi. E Usulatán; 3) Honduras: Valle: 9 mi. SE Nacaome; 4) Valle: 10.0 mi. SSW Nacaome, 5) Choluteca: 10.2 mi. NW Choluteca, 6) Choluteca: 11.5 mi. SW Choluteca; 7) Nicaragua: Chinandega: 3.5 mi. NW and 1.5 mi. S Chinandega. The $2n=44$ parental cytotype occurs at localities 1-3, both parental cytotypes are present at locality 4, and the $2n=38$ parental cytotype occurs at localities 5-7.

Uroderma bilobatum complex have revealed chromosomal divergence greater than that reported for any other species of bat (Baker, 1967, 1970*a*, 1970*b*; Hsu *et al.*, 1968; Baker and Hsu, 1970; Capanna and Cibitelli, 1970).

Karyotypically, the *U. bilobatum* complex can be divided into the following groups: $2n=44$, *davisi* (central Honduras north to southern México; (Baker and McDaniel, 1972); $2n=38$, including *convexum* (central Honduras south to northern South America on the Pacific versant), and *molaris* (México to Nicaragua on Atlantic versant; as suggested by Davis, 1968); and $2n=42$, consisting of the nominal subspecies *trinitatum* and *bilobatum* (South American mainland). *Uroderma b. thomasi*, which has not been karyotyped, is known from western South America. *Uroderma b. convexum* ($2n=38$) and *U. b. davisi* ($2n=44$) have been found to form a contact zone over 200 kilometers in length (Fig. 4) that extends from southern El Salvador, across the Pacific coast of Honduras and northwestern Nicaragua (Baker *et al.*, 1975).

Conclusions concerning the nature of chromosomal variation in *Uroderma* between the $2n=38$ and $2n=44$ forms are based on G-band data (Fig. 3). The diploid number at the contact zone in Central America ranges from 38 to 44, with individuals of all intermediate diploid numbers being represented. Northwest of the contact zone the diploid number is 44 and to the southeast is 38 (Fig. 4). Intermediate individuals are not known from outside of the zone of contact. The differences between the two parental types (38 to 44) result from three separate events, each involving a translocation or fission, depending on direction of the event. The first change to be discussed (designated the *A* chromosomes) is shown in column A of Fig. 3. One morph (represented by a capital *A*) has a small biarmed element and an acrocentric element; the other morph (represented by a lower case a) has these two elements fused to form a subtelocentric chromosome. Where only a standard karyotype is available, the number of large *A*'s in the karyotype will be reflected by the number of small biarmed autosomes present in the complement.

The second event (designated the *B* chromosomes) involves a centric fusion-fission in which morph *B* (column B, Fig. 3) appears as two acrocentrics (the smallest acrocentric in the $2n=44$ karyotype and one of the medium-sized acrocentric elements). Morph *b* is a subtelocentric element representing a fusion of the two acrocentric elements in *B*. This variation can be recognized in a standard karyotype because each *b* is reflected by a decrease of one in the diploid number and an increase of one in the number of large biarmed elements, without effecting a decrease in the number of small biarmed autosomes.

The third change (designated the *C* chromosomes), as shown in column C of Fig. 3, is a terminal translocation in which a small acrocentric element is translocated to the end of the long arm of the longest acrocentric element in the karyotype. For each morph *C*, there will be two acrocentrics in the karyotype, whereas each morph *c* is a single large acrocentric in which the segments homologous to the two *C* acrocentrics are fused. Production of the *c* morph reduces the diploid number by one and reduces the number of acrocentrics by one but does not alter the number of biarmed elements (either small or large) in the karyotype.

Although the exact nature of these changes can be identified only by the G-band patterns, the three changes produce distinct morphological differences in the chromosomes that allows one to determine the chromosomal phenotype from a standard karyotype for the *A*, *B*, and *C* chromosomes of any individual. Using the *ABC* designation for the chromosomal variation enables the characterization of all of the individuals involved in the contact zone. An animal with *AABBCC* would be a $2n=44$ parental type and an animal with *aabbcc* would be a $2n=38$ parental type. Each capital letter in the phenotype will raise the diploid number above 38 by one. For example, an animal with a phenotype of *aaBbCC* or *AaBbCc* would have a diploid number of 41 and an animal with *AABbCC* would have a diploid number of 43. I have determined the chromosomal phenotype for 333 specimens from the zone of contact.

C-banding patterns are important because they identify segments of the chromosomes that are believed to be heterochromatic in nature. Variation in

the amount of C-band material between karyotypes is not thought to interfere with meiosis as does variation in euchromatin. It is important, therefore, to know the amount and placement of C-band positive material within the three chromosomal variants. The karyotype of *Uroderma bilobatum* contains very little C-band positive material. Most biarmed elements have a small amount near the centromere and one medium-sized acrocentric (not one of the *A*, *B*, or *C* chromosomes) has a C-band proximal to the centromere. Although all of the *A*, *B*, and *C* chromosomes have a small amount of centromeric C-band material, none of the major segments involved in the variation is C-band positive. The small biarmed pair involved in the *Aa* variation, however, has heterochromatin incorporated into part of one arm. All of the C-bands identified in this small biarmed element (of the *A* morph) are present in the subtelocentric *a* morph fusion product and the *a* morph subtelocentric has about as much C-band material as do the two elements of the *A* morph.

Although the break and alteration may have occurred in this C-band positive area, no major addition or deletion of C-band material seems to have occurred. Variations in the C-banding patterns do not seem to be involved in the genetic strategy of *Uroderma*. This constitutes a major difference between chromosomal evolution in this species and that seen in some rodents, for example, *Peromyscus* (Duffey, 1972; Pathak *et al.*, 1973).

The zone of contact between the cytotypes of *Uroderma* is about 200 kilometers in length but its width is not known. Because *Uroderma* is ecologically restricted to the relatively low lands of the coast, the zone cannot be over 100 kilometers wide at many places and must be considerably narrower at some. The two parental cytotypes occur sympatrically at a single locality in my sample (Fig. 4), and the area of overlap of parental cytotypes is probably not much longer than 30 kilometers. At the locality where the two parental cytotypes occur sympatrically, most individuals have a hybrid karyotype (for instance, within a sample size of 15, one bat had $2n=38$, one had $2n=39$, two had $2n=40$, five had $2n=41$, one had $2n=41$, one had $2n=42$, three had $2n=43$, and two had $2n=44$). Intensive hybridization occurs in the central part of the zone between Nacome and Choluteca, Honduras. Away from this area, parental cytotypes probably do not come into direct contact, and hybrid karyotypes are found much less frequently; I suggest that these are primarily the result of the survival and successful reproduction of backcross individuals.

Different types of chromosomal rearrangements produce different meiotic aberrations and, therefore, the percentage of sterile gametes in a heterozygote will be a function of the nature of the rearrangement. If the rate of production of sterile gametes is the only factor regulating the penetration of a chromosomal morph of one parental type into a population of the other parental form, an increase of sterile gametes should result in a decrease in successful penetration into the other cytotype. Furthermore, across the zone of contact the frequency of the penetrating chromosomal morphs should produce a symmetrical bell-shaped curve reflecting the greater number of F_1 backcross individuals near the zone and the decrease in such individuals with distance away from the area of primary

contact. The width of this symmetrical curve for a given chromosomal aberration would be a function of the severity of meiotic selection against heterozygotes of that type of aberration.

If factors other than meiotic mechanisms play a role in the penetration of one chromosomal morph into populations of the other, there is no reason to assume that selection on both sides of the zone should be the same and the frequency of F_1 and heterozygous individuals across the zone would not be symmetrical.

The frequencies (p and q-values) of the various chromosomal morphs from 333 specimens of *Uroderma bilobatum* from the contact zone are shown in Table 2. The two northernmost localities (La Herradura and Usulatán) have similar chromosomal frequencies. Notably, the *b* morph of the *B* chromosomes has been the most successful in surviving in these populations, whereas the *c* morph was not found to be present in any of the 133 specimens from these two localities. This might be predicted based on the type of segregation that would result in a heterozygote for the respective *B* and *C* chromosomes. Centric fusions and fissions (origin of the *B* chromosomal system) are not believed to interfere greatly with the meiotic process, especially if preferential segregation occurs. Proper segregation probably would not be affected, and therefore natural selection at the meiotic level would be ineffective in eliminating such variation from the population. On the other hand, such translocations as might have given rise to the *C* chromosomal variation should result in loss of about 25 per cent of the gametes in the heterozygote if there has been crossing over in the portion homologous to the large acrocentric. It would appear that, in the absence of other factors, the variation in the *B* chromosomes would be more common in all populations than would variation in the *C* chromosome. In samples from the southeastern part of the contact zone, survival of the *B* chromosome is less frequent than *C*; *C* actually accounts for about 4.5 per cent of the *C* chromosomes at the Choluteca locality (Table 2, Fig. 4). Two of 86 individuals were heterozygous (*Cc*) at the Chinandega locality. The per cent variation resulting from each chromosomal change is not the same northwest and southeast of the central part of the zone (Table 2), which suggests that successful reproduction of hybrid and backcross individuals is not explained totally by meiotic problems, but that possibly fitness of the adult varies as well.

It also should be noted that although Chinandega is closer to the central part of the contact zone than is La Herradura, less total chromosomal variation is found at Chinandega (4.6 per cent of the individuals had hybrid karyotypes) than at La Herradura (14 per cent had hybrid karyotypes).

Baker *et al.* (1975) concluded that the chromosomal data pointed to considerable chromosomal flow between the cytotypes. At that time it was not possible to identify patterns in exchange and survival of the different morphs. From the above data (Table 2), there is clearly a pattern of selective chromosomal flow between cytotypes. If the variation in the *C* chromosomes is used to estimate chromosomal flow (and implied gene exchange) of the $2n = 38$ chromosomes into the $2n = 44$ populations, the data strongly suggest no exchange (the one individual at Nacome that was heterozygous, *Cc*, was a presumed F_1). On the other hand, if

TABLE 2.—*Frequency of the chromosomal morphs at localities in the zone of hybridization. Numbers preceding localities identify geographic samples in Fig. 4, where exact localities are given. The 2n = 44 parental type occurs at localities 1-3. Both parental cytotypes occur at locality 4. At localities 5-7, the 2n = 38 parental type is present.*

	1. La Herradura	2. Usulatán	3. Nacáome	4. Hybrid locality	5. San Lorenzo	6. Choluteca	7. Chinandega
Sample size	50	83	9	15	12	78	86
Chromosomal morphs							
A	p= 98; q=02	p= 99; q=01	p=94; q=06	p=60; q=40	p=42; q=58	p=05; q=95	p=01; q= 99
B	p= 95; q=05	p= 95; q=05	p=78; q=22	p=53; q=47	p=29; q=71	p=01; q=99	p=00; q=100
C	p=100; q=00	p=100; q=00	p=94; q=06	p=57; q=43	p=33; q=67	p=04; q=96	p=01; q= 99

the *B* chromosomes are used, the implications are different. Chromosomal data fit the pattern of introgression in which some chromosomes are allowed to enter the "chromosome pool" of another type by hybridization and backcrossing, but other chromosomes are selected against.

The pattern of chromosomal morphs across this contact zone closely fits the tension zone (White, 1973; Key, 1974) characteristic of stasipatric speciation. In evaluating my data in light of White's model, several points need to be made. First, at this time it is impossible to determine if this zone is the result of primary or secondary contact. White's model requires that the zone be the product of primary contact. Second, stasipatric tension zones have been described for several species (Bush, 1975), and a suite of the biological characteristics of these species do not fit those of *Uroderma*. In species with low vagility, the tension zone is usually not more than a few hundred meters wide; in *Uroderma*, species with high vagility, the zone is more than 200 kilometers in breadth. Third, *Uroderma* is K-selected, whereas other species with tension zones are R-selected.

My data point out the fact that tension zones need not be composed of species characterized by low vagility and R-selection. Although the zone of interaction between the two *Uroderma* cytotypes might or might not be in equilibrium, it will eventually proceed to one of several endpoints. One possibility is that the two cytotypes could develop additional isolating mechanisms, such as behavioral or postmating, and evolve into two species. Another possibility is the replacement of one parental type by the other via the mechanisms of competition or genetic swamping. A less likely outcome could be the survival of some intermediate cytotype with, say, 42 chromosomes (for instance, *AABBcc*). At any rate, this type of chromosomal variation undoubtedly offers a unique set of possibilities on which evolution can act. The unique nature of these biological circumstances certainly offers a rare chance to observe evolution in action.

Electrophoretic data would be extremely valuable in shedding some light on the history of *Uroderma* populations that have produced this tension zone. Electrophoretic data indicate that when two species have been derived by the classical allopatric model, the level of similarity of allozymes is usually about 85 per cent or less (Avise, 1974). If these chromosomal differences accumulated during a long allopatric period, it could be predicted that these two chromosomal races should have accumulated a significant number of fixed allelic

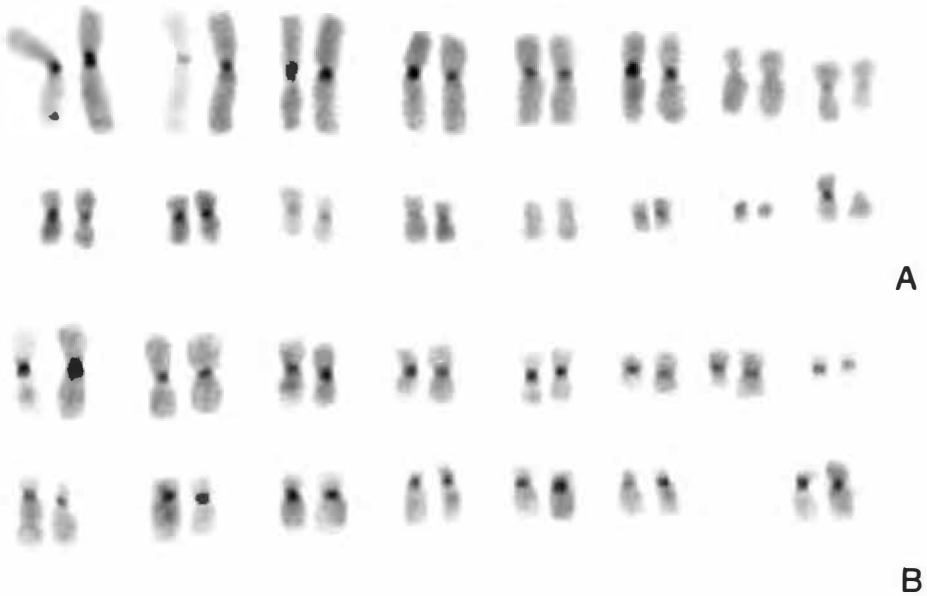

FIG. 5.—Sample patterns of C-bands of phyllostomatid bats: A, *Phyllostomus elongatus*; B, *Enchisthenes hartii*.

differences; however, if the process that gave rise to the current condition has been like that proposed by White (1968, 1973), very few electrophoretic differences should be detectable. This situation is currently under study by Ira F. Greenbaum.

MISCELLANEOUS CYTOGENETIC STUDIES

In addition to the more systematically oriented papers discussed above, there have been a few more detailed studies on biochemical aspects involving karyotypic data for phyllostomatid bats.

C-bands.—C-band material for phyllostomatid bats is described in enough species that general trends can be predicted (Stock, 1975; Patton, 1976; Baker *et al.*, 1978). In general, phyllostomatid bats have C-band material restricted to the centromeric region. The amount found is small, similar to that shown in Fig. 5 for *Phyllostomus* and *Enchisthenes*, respectively. However, in some species (*Carollia perspicillata* and *Choeroniscus intermedius*) there are additional portions of the karyotype carrying C-band positive material (Stock, 1975). Also, see the discussion on C-band material in *Uroderma* under the section on chromosomal races.

Nucleolar organizer regions.—Two papers, both dealing with *Carollia perspicillata* and *C. castenea*, have reported studies of nucleolar organizer regions (NOR) in phyllostomatids (Hsu *et al.*, 1975; Goodpasture and Bloom, 1975). Hsu *et al.* (1975) used DNA/rRNA (ribosomal RNA) hybridization to reveal NOR's. In the karyotype of *C. perspicillata*, the only NOR was located on the X chromosome; their studies of *C. castanea* were made on a transformed culture. Hsu *et al.* concluded that the origin of the NOR on the *Carollia* X/auto-

somal chromosome was from the X and not the translocated autosomal portion. Because DNA-RNA hybridization is difficult and expensive, Goodpasture and Bloom (1975) tested the feasibility of using ammoniacal silver to reveal NOR's. Their methods localized NOR's at the same points as did the methods of Hsu *et al.* The same individuals were studied from *in vitro* cultures. Goodpasture and Bloom (1975) present theories on the cytological basis for silver NOR staining.

Cesium chloride buoyant densities.—Arrighi *et al.* (1968, 1972) reported on cesium chloride buoyancy in phyllostomatid bats. Findings are summarized in the latter paper. Ten species of phyllostomatid bats (*Anoura geoffroyi, Artibeus fallax*=*A. lituratus* in Jones and Carter, 1976, *Artibeus lituratus, Carollia perspicillata, Chiroderma villosum, Choeroniscus intermedius, Sturnira erythromos, Sturnira lilium, Sturnira magna,* and *Uroderma bilobatum*) were studied and values ranged from 1.6982 for *Carollia perspicillata* to 1.7005 for *Anoura geoffroyi* and *Sturnira erythromos.* These values fall within those given for other Microchiroptera (1.696 to 1.702) from the families Rhinolophidae, Molossidae, and Vespertilionidae, but only slightly overlap the values reported for Megachiroptera (1.694 to 1.697). Of the families of Microchiroptera, Phyllostomatidae had values nearest those for the Megachiroptera. Although the magnitude of difference between the suborders is small, it is the greatest found between suborders of mammals and is interpreted as supporting relatively ancient lineages for the two suborders (Arrighi *et al.*, 1972).

X chromosomes.—G-banded X chromosomes for a variety of mammals (including eight species of phyllostomatids) were studied by Pathak and Stock (1974). They found that X chromosomes always have two dark staining, trypsin resistant bands regardless of the centromere placement. They interpreted these data as supporting Ohno's (1967) hypothesis that the mammalian X chromosome is extremely conservative in genetic constitution.

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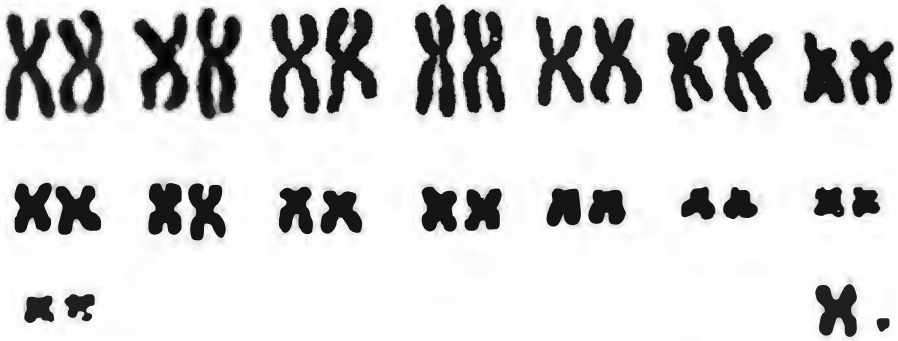

PLATE 1.—Karyotype of a male *Lonchorhina aurita* from Trinidad.

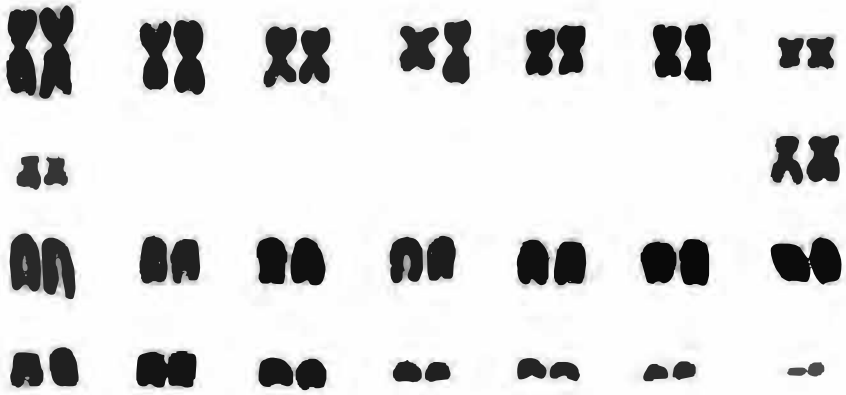

PLATE 2.—Karyotype of a female *Macrotus waterhousii* from Haiti.

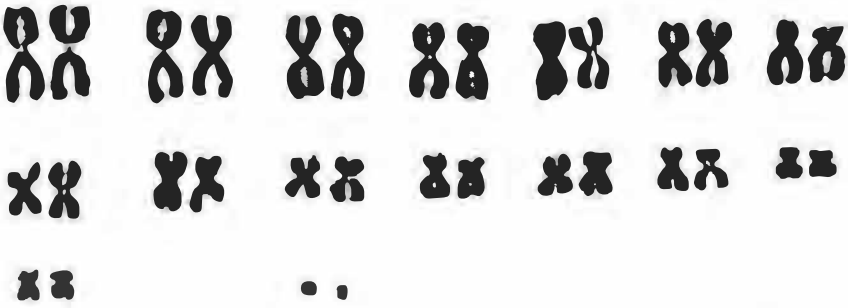

PLATE 3.—Karyotype of a female *Micronycteris brachyotis* from Trinidad.

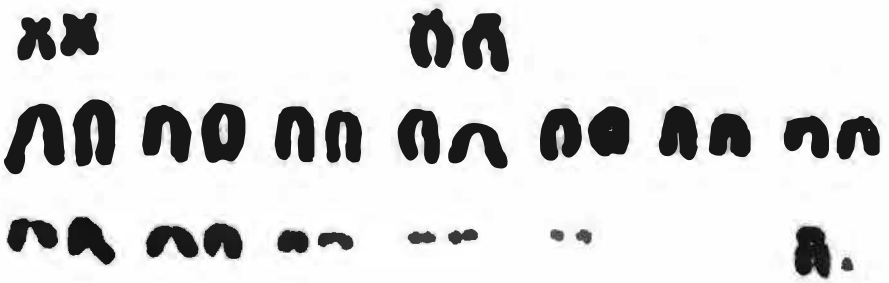

PLATE 4.—Karyotype of a male *Micronycteris hirsuta* from Nicaragua.

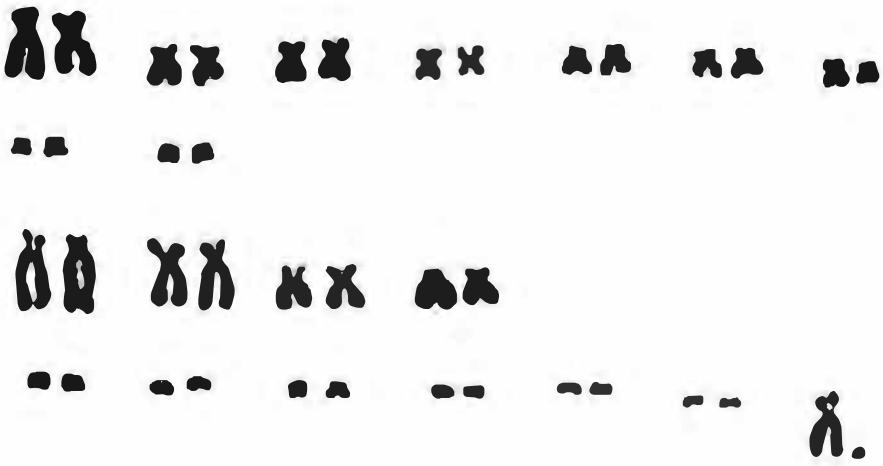

PLATE 5.—Karyotype of a male *Micronycteris megalotis* from Trinidad.

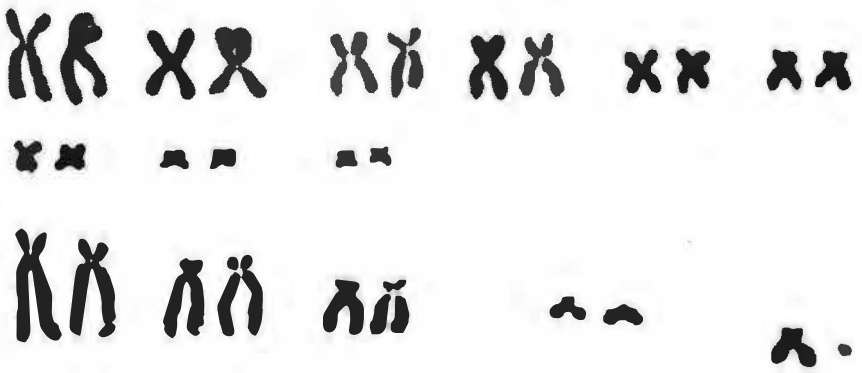

PLATE 6.—Karyotype of a male *Micronycteris minuta* from Trinidad.

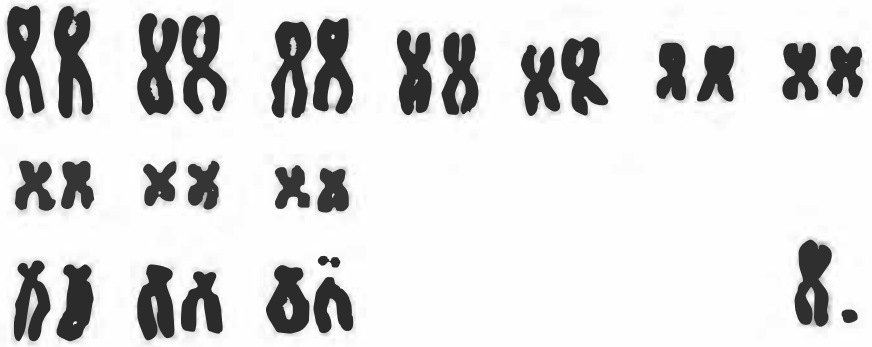

PLATE 7.—Karyotype of a male *Micronycteris nicefori* from Trinidad.

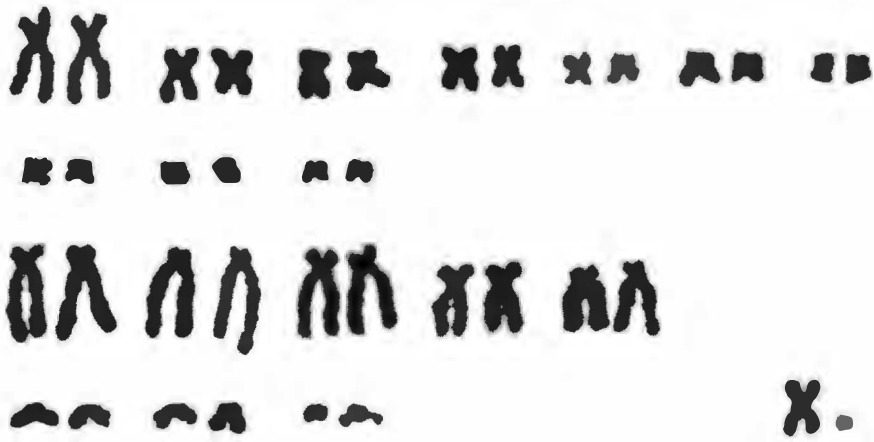

PLATE 8.—Karyotype of a male *Micronycteris schmidtorum* from Costa Rica.

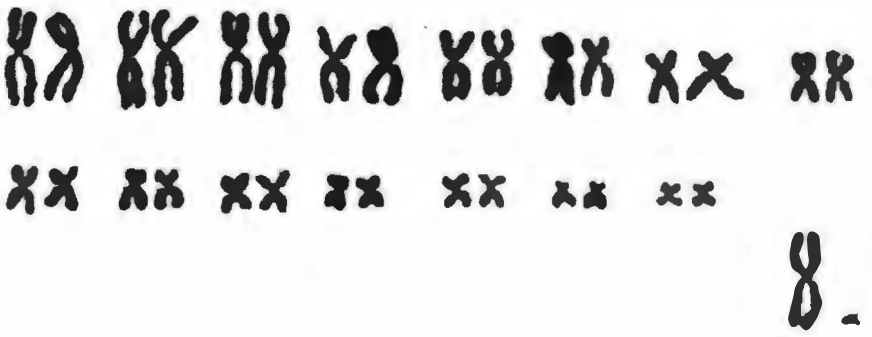

PLATE 9.—Karyotype of a male *Mimon crenulatum* from Colombia.

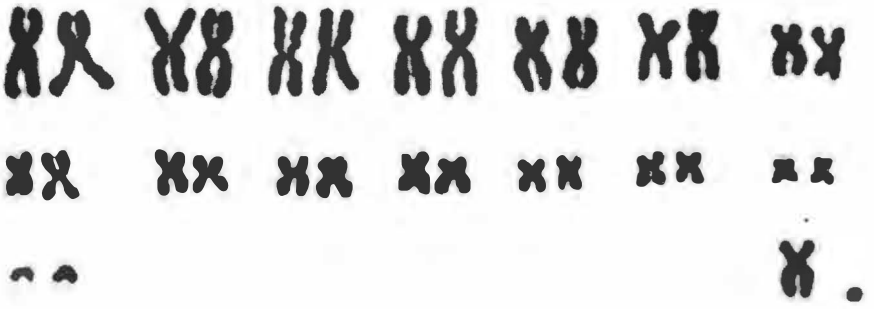

PLATE 10.—Karyotype of a male *Phylloderma stenops* from Colombia.

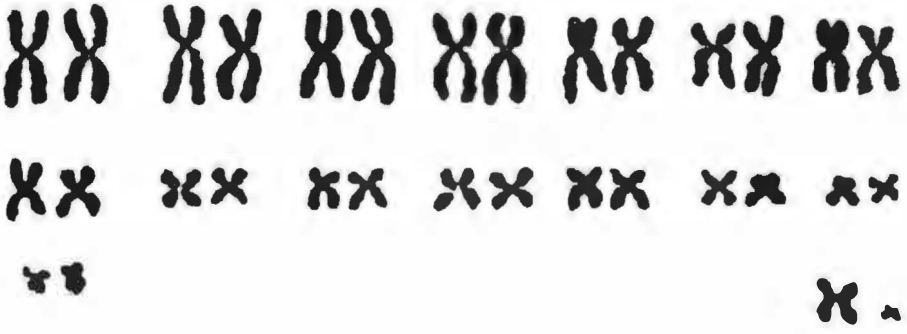

PLATE 11.—Karyotype of a male *Phyllostomus discolor* from Trinidad.

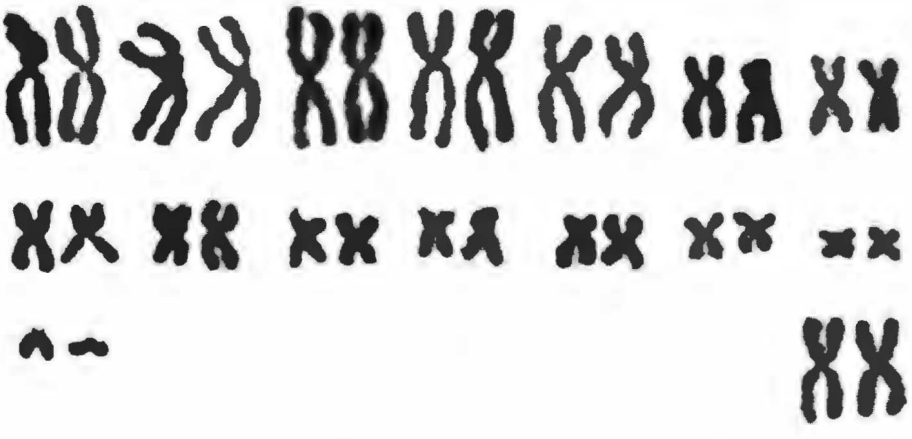

PLATE 12.—Karyotype of a female *Phyllostomus elongatus* from Colombia.

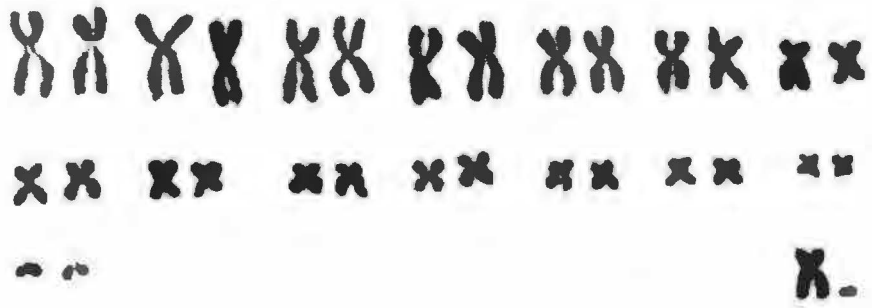

PLATE 13.—Karyotype of a male *Phyllostomus hastatus* from Trinidad.

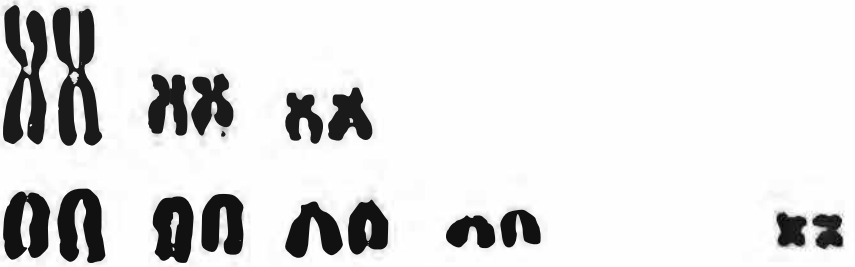

PLATE 14.—Karyotype of a female *Tonatia bidens* from Trinidad.

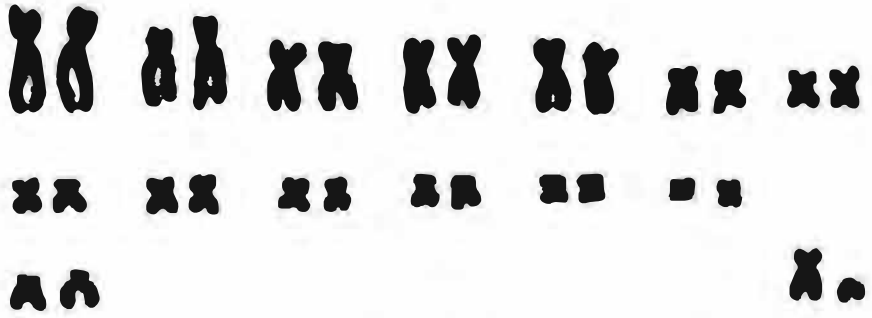

PLATE 15.—Karyotype of a male *Tonatia minuta* from Trinidad.

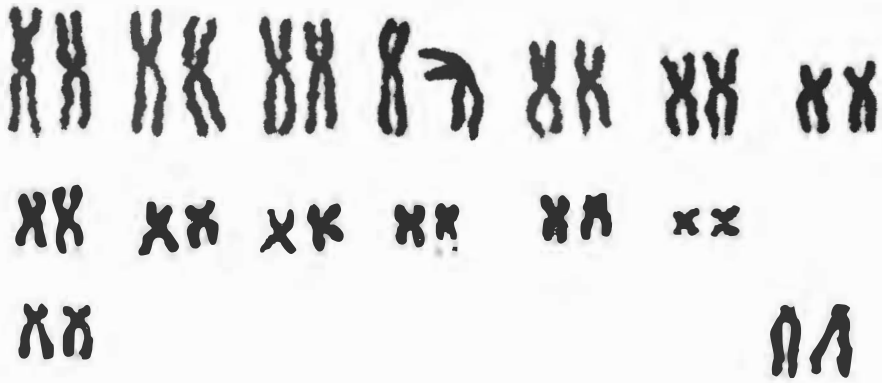

PLATE 16.—Karyotype of a female *Trachops cirrhosus* from Trinidad.

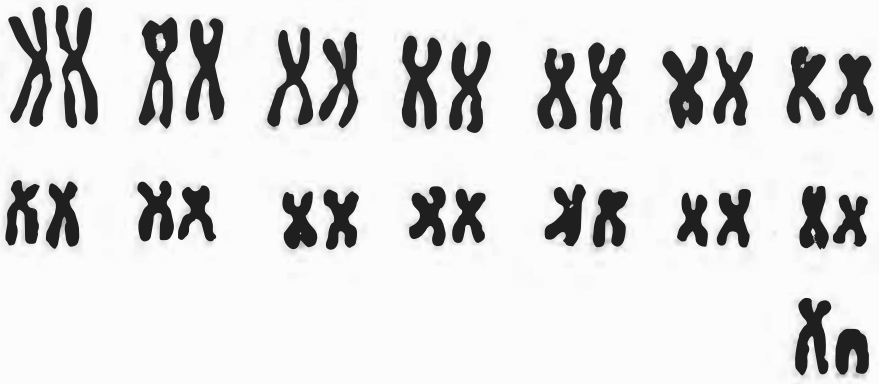

PLATE 17.—Karyotype of a male *Vampyrum spectrum* from Trinidad.

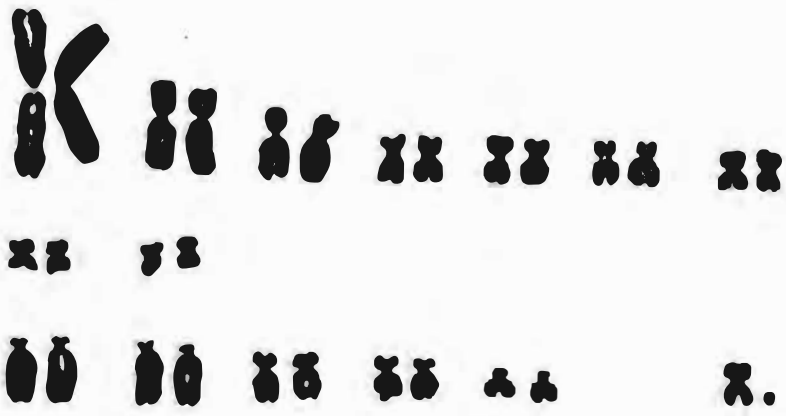

PLATE 18.—Karyotype of a male *Anoura caudifer* from Colombia.

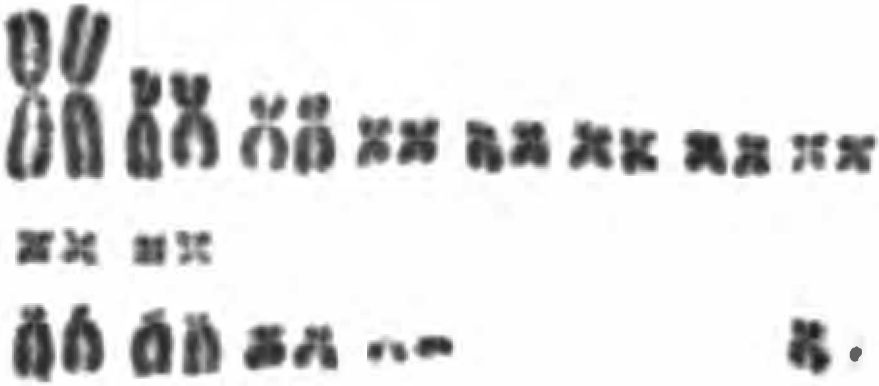

PLATE 19.—Karyotype of a male *Anoura cultrata* from Costa Rica.

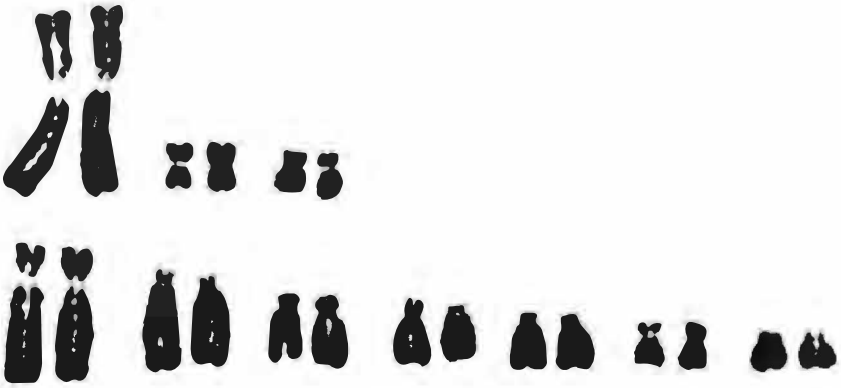

PLATE 20.—Karyotype of a female *Choeroniscus godmani* from Honduras.

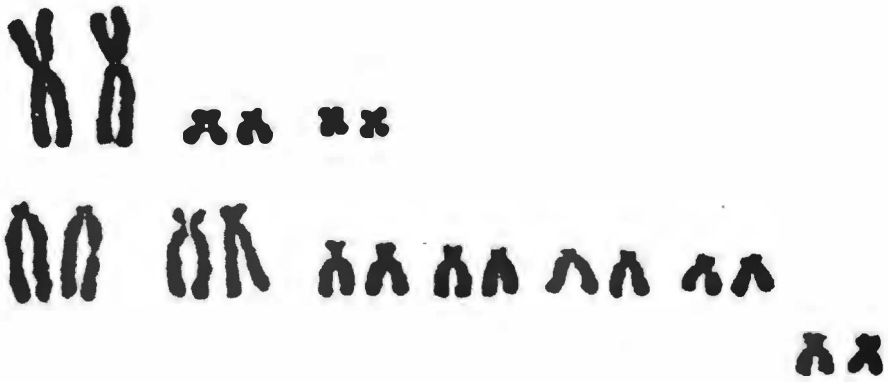

PLATE 21.—Karyotype of a female *Choeroniscus intermedius* from Trinidad.

PLATE 22.—Karyotype of a female *Choeronycteris mexicana* from Tamaulipas.

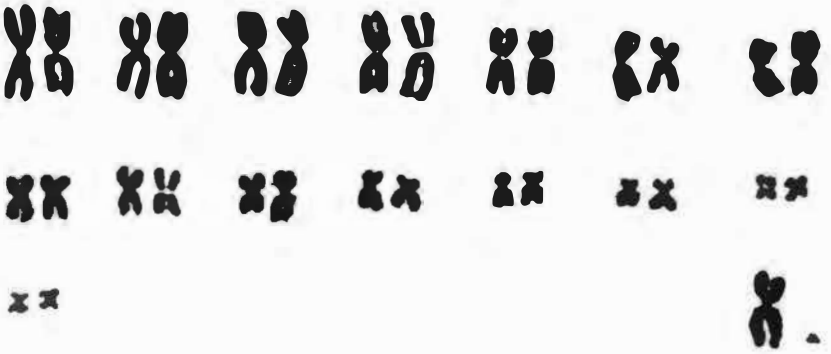

PLATE 23.—Karyotype of a male *Glossophaga soricina* from Colombia.

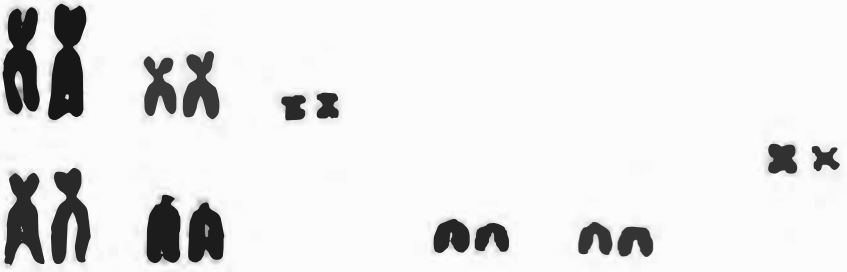

PLATE 24.—Karyotype of a female *Hylonycteris underwoodi* from Costa Rica.

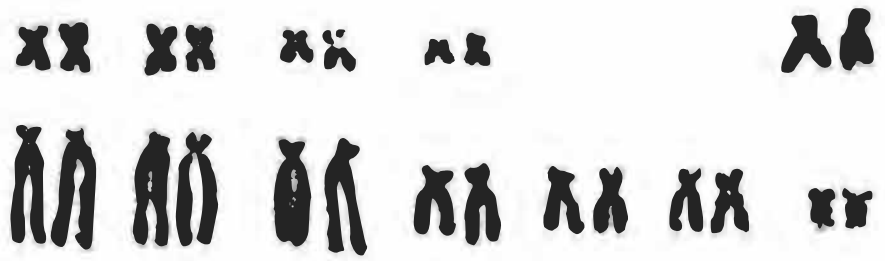

PLATE 25.—Karyotype of a female *Lichonycteris obscura* from Nicaragua.

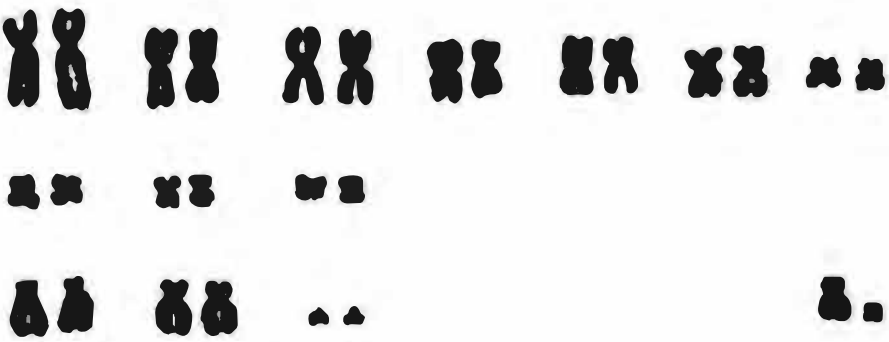

PLATE 26.—Karyotype of a male *Lionycteris spurrelli* from Colombia.

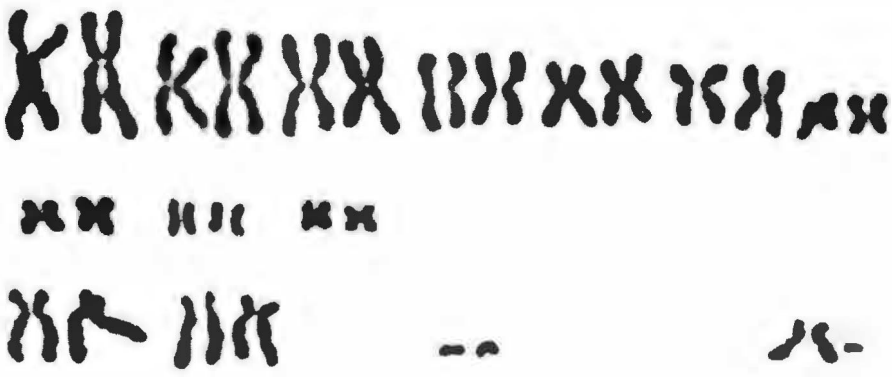

PLATE 27.—Karyotype of a male *Lonchophylla robusta* from Nicaragua.

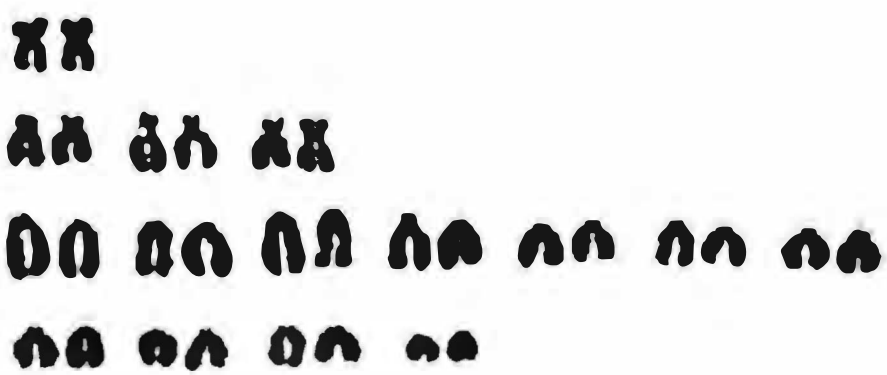

PLATE 28.—Karyotype of a female *Lonchophylla thomasi* from Colombia.

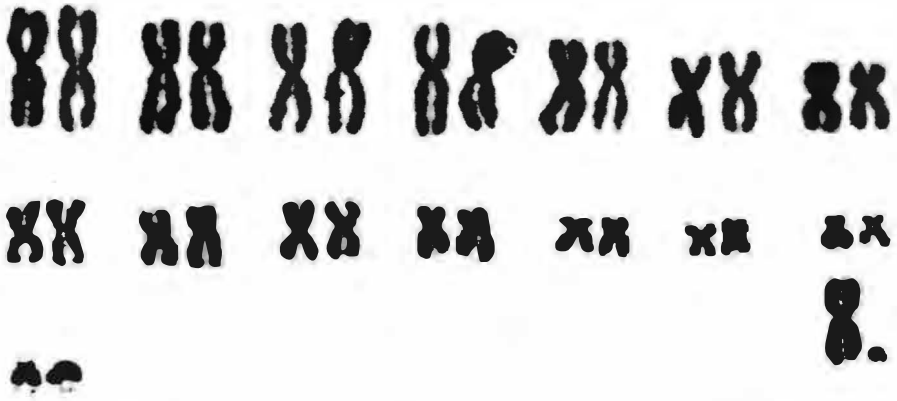

PLATE 29.—Karyotype of a male *Monophyllus redmani* from Puerto Rico.

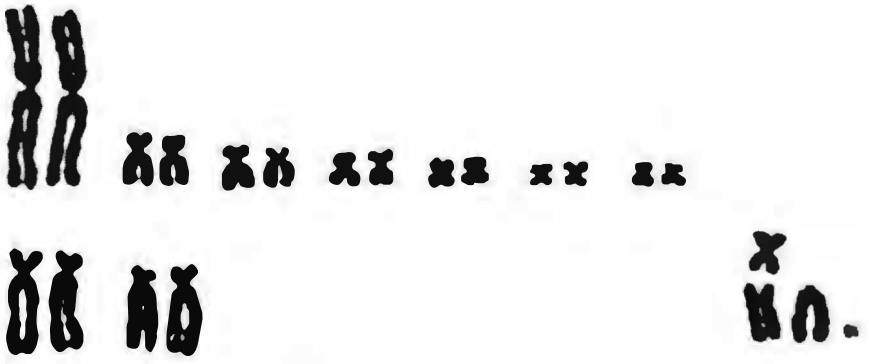

PLATE 30.—Karyotype of a male *Carollia perspicillata* from Colombia.

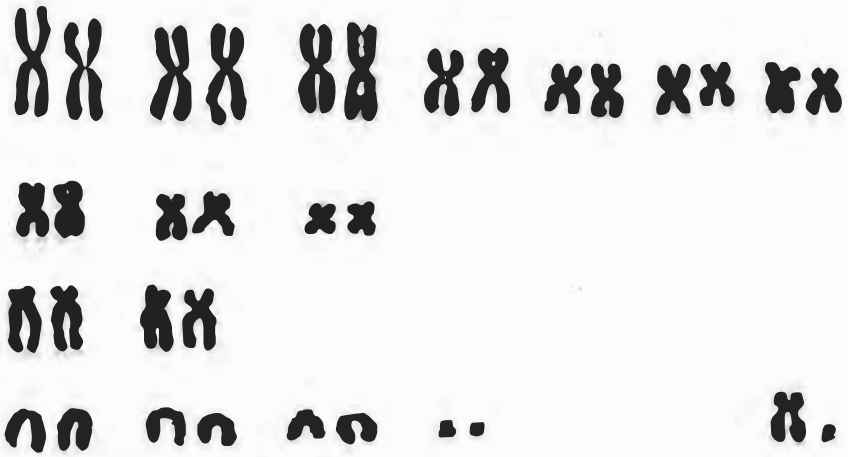

PLATE 31.—Karyotype of a male *Rhinophylla fischerae* from Colombia.

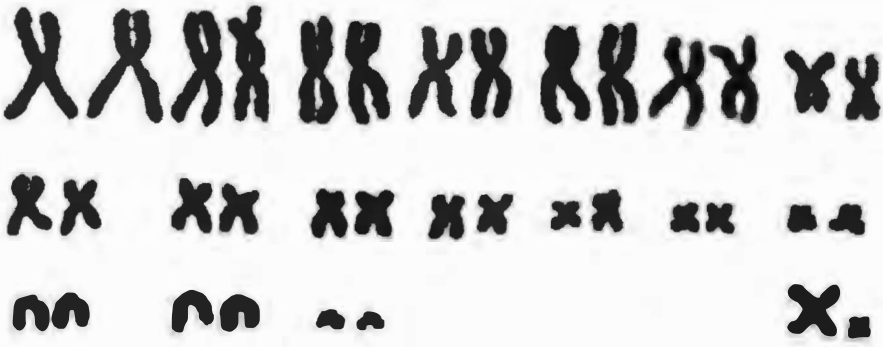

PLATE 32.—Karyotype of a male *Rhinophylla pumilio* from Colombia.

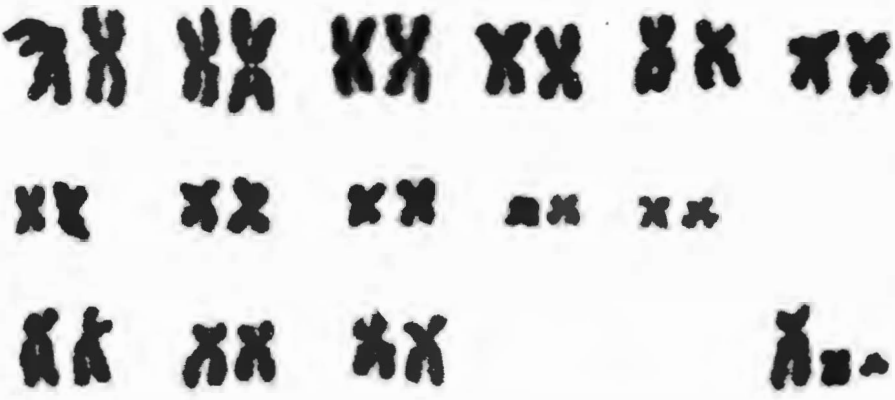

PLATE 33.—Karyotype of a male *Ametrida centurio* from Trinidad.

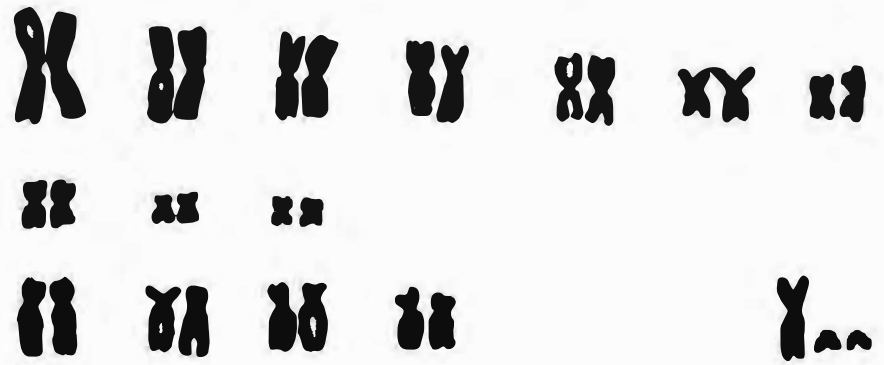

PLATE 34.—Karyotype of a male *Ardops nichollsi* from Guadeloupe.

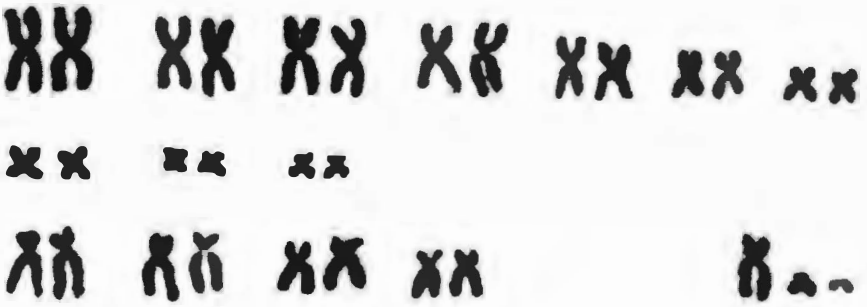

PLATE 35.—Karyotype of a male *Ariteus flavescens* from Jamaica.

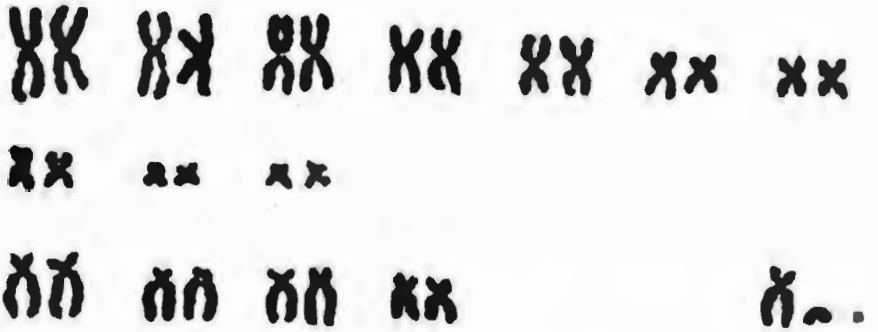

PLATE 36.—Karyotype of a male *Artibeus lituratus* from Colombia.

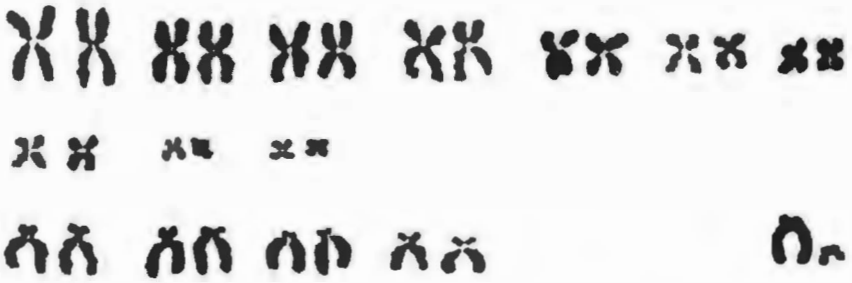

PLATE 37.—Karyotype of a male *Artibeus phaeotis* from Colombia.

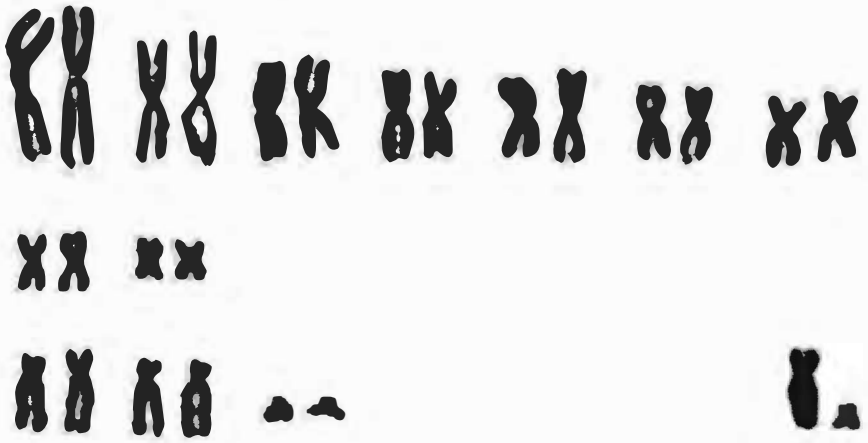

PLATE 38.—Karyotype of a male *Chiroderma improvisum* from Guadeloupe.

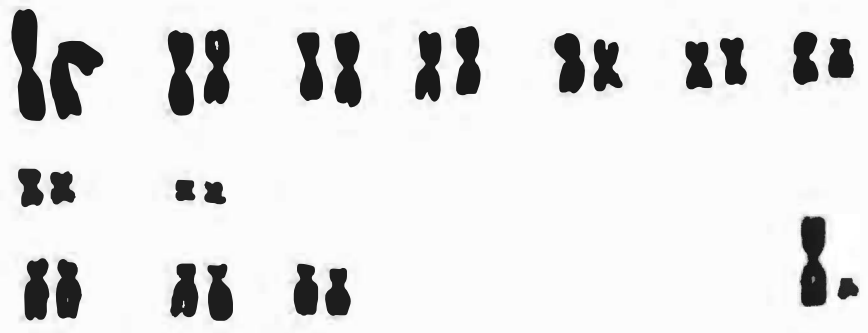

PLATE 39.—Karyotype of a male *Chiroderma salvini* from Honduras.

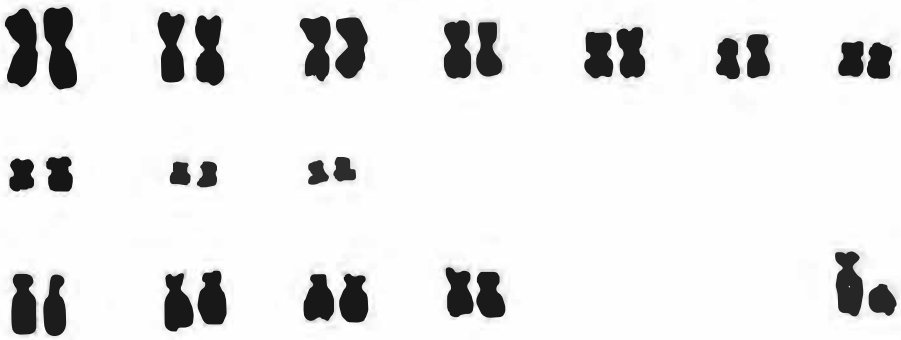

PLATE 40.—Karyotype of a male *Ectophylla alba* from Costa Rica.

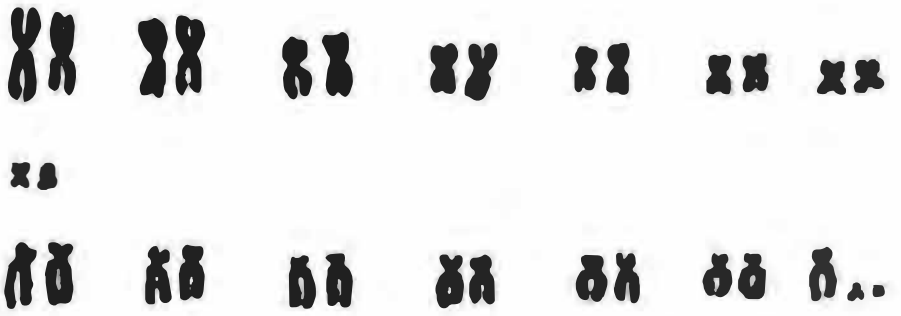

PLATE 41.—Karyotype of a male *Enchisthenes hartii* from Colombia.

PLATE 42.—Karyotype of a male *Mesophylla macconnelli* from Trinidad.

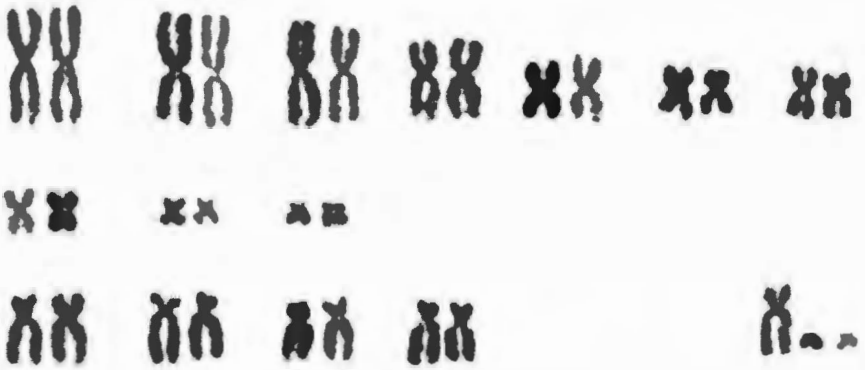

PLATE 43.—Karyotype of a male *Phyllops haitiensis* from Haiti.

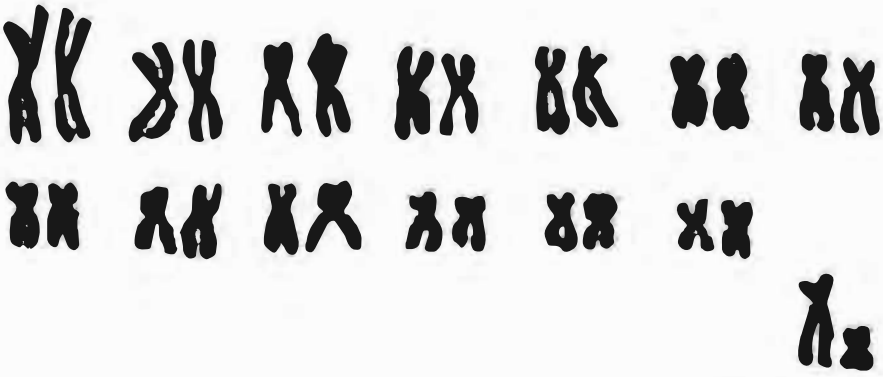

PLATE 44.—Karyotype of a male *Sphaeronycteris toxophyllum* from Colombia.

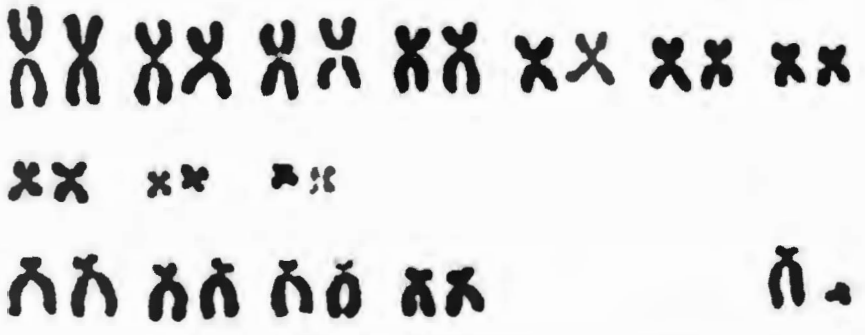

PLATE 45.—Karyotype of a male *Sturnira erythromos* from Colombia.

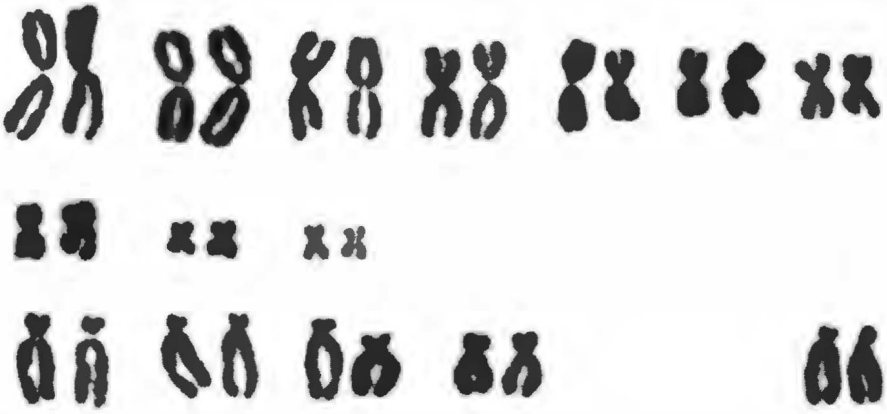

PLATE 46.—Karyotype of a female *Sturnira mordax* from Costa Rica.

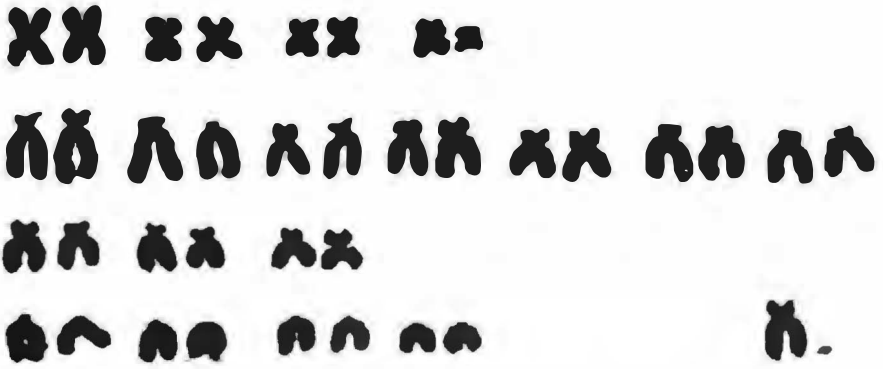

PLATE 47.—Karyotype of a male *Uroderma magnirostrum* from Colombia.

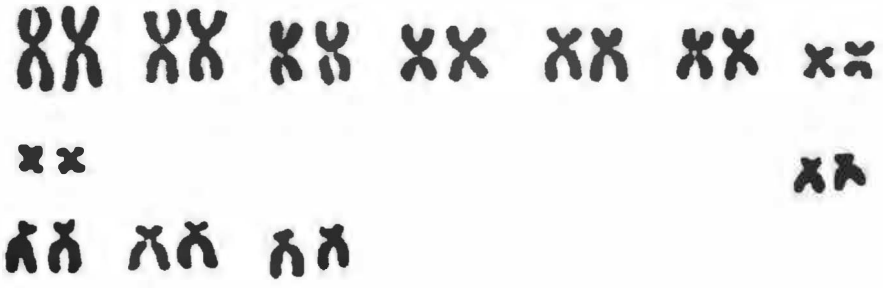

PLATE 48.—Karyotype of a female *Vampyressa brocki* from Colombia.

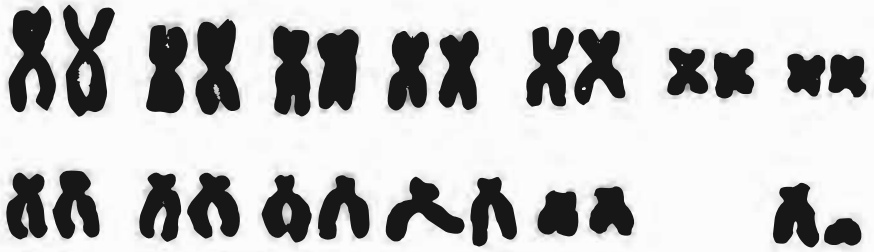

PLATE 49.—Karyotype of a male *Vampyressa nymphaea* from Honduras.

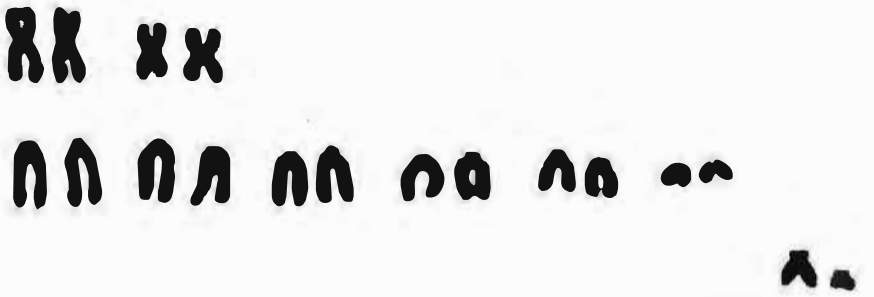

PLATE 50.—Karyotype of a male *Vampyressa pusilla* from Honduras.

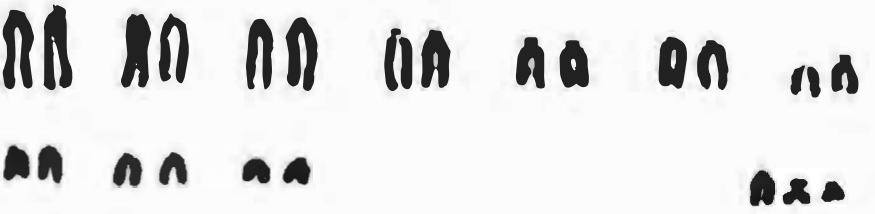

PLATE 51.—Karyotype of a male *Vampyressa pusilla* from Colombia.

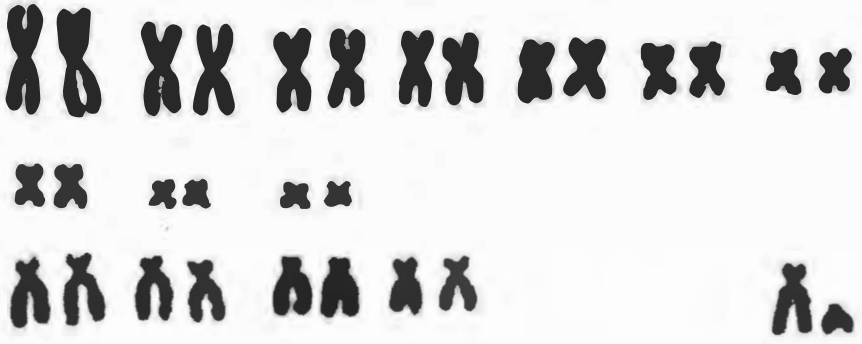

PLATE 52.—Karyotype of a male *Vampyrops vittatus* from Colombia.

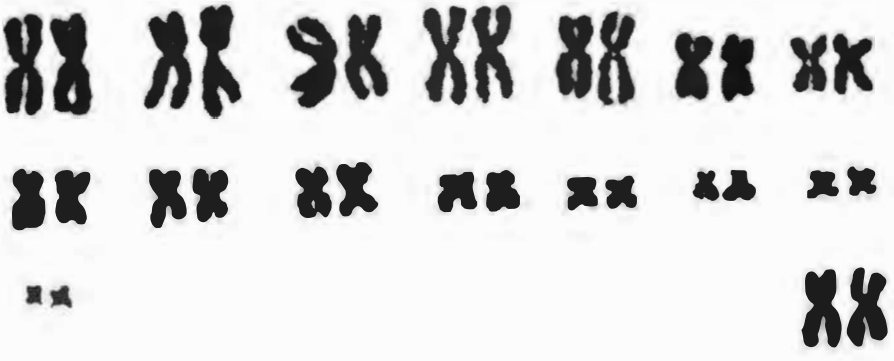

PLATE 53.—Karyotype of a female *Brachyphylla cavernarum* from Puerto Rico.

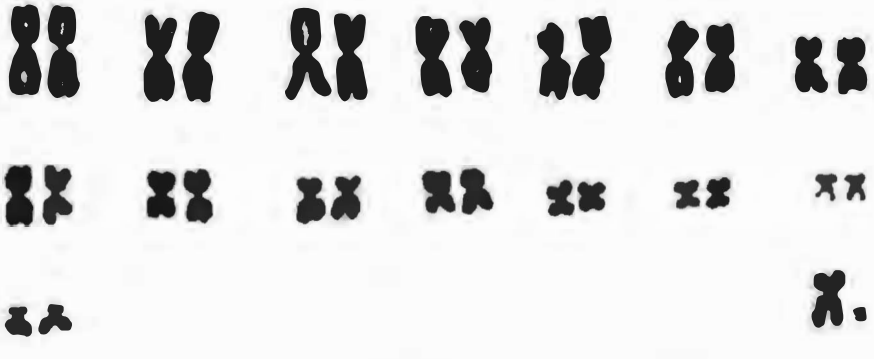

PLATE 54.—Karyotype of a male *Brachyphylla nana* from Haiti.

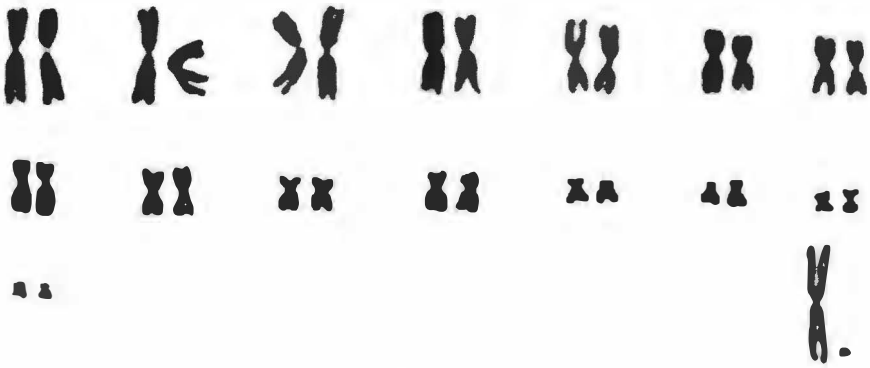

PLATE 55.—Karyotype of a male *Erophylla sezekorni* from Puerto Rico.

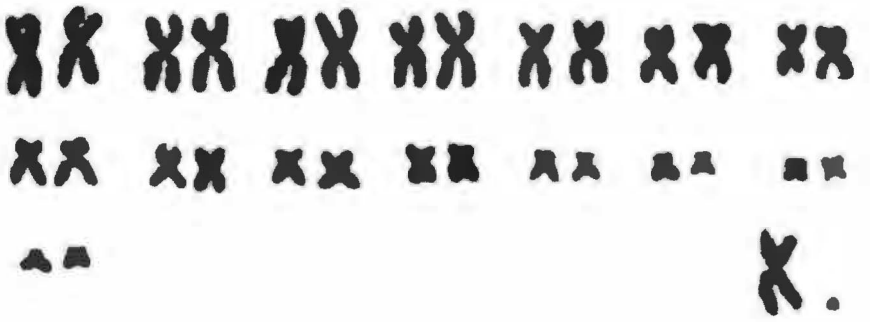

PLATE 56.—Karyotype of a male *Phyllonycteris aphylla* from Jamaica.

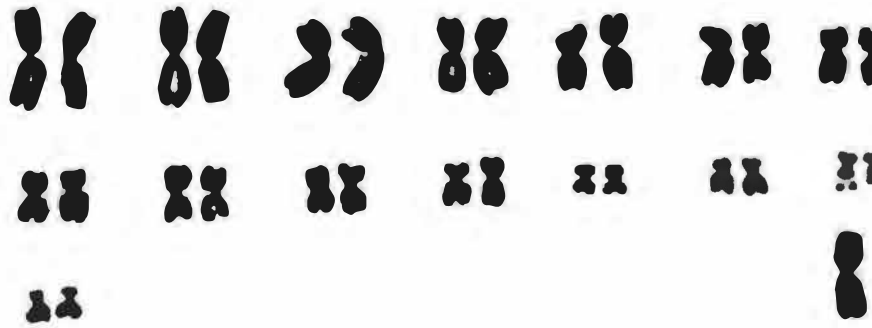

PLATE 57.—Karyotype of a male *Phyllonycteris poeyi* from Haiti.

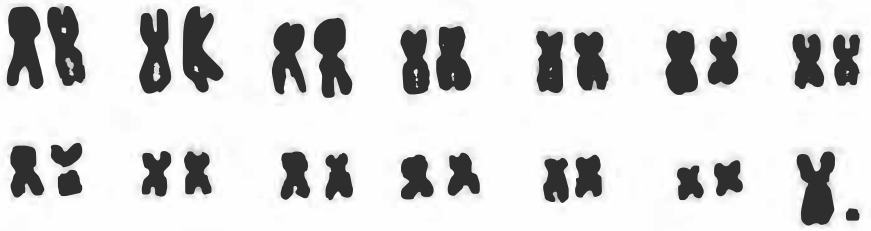

PLATE 58.—Karyotype of a male *Desmodus rotundus* from Veracruz.

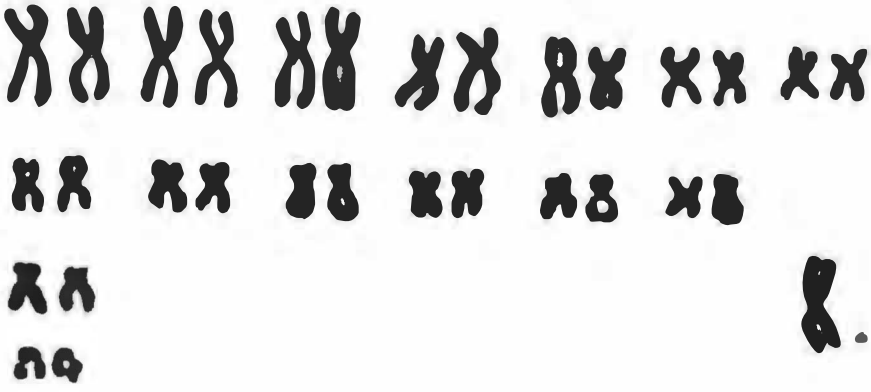

PLATE 59.—Karyotype of a male *Diaemus youngii* from Nicaragua.

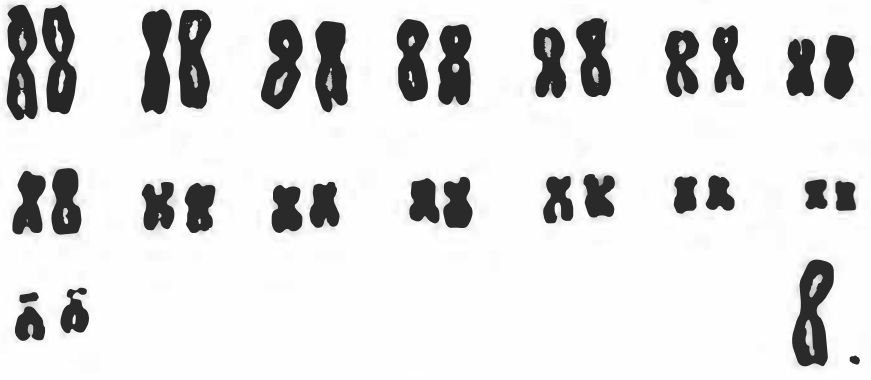

PLATE 60.—Karyotype of a male *Diphylla ecaudata* from Veracruz.

BIOCHEMICAL GENETICS

DONALD O. STRANEY, MICHAEL H. SMITH, IRA F. GREENBAUM,
AND ROBERT J. BAKER

The current view of evolution is very much a genetic one. Theoretical developments since the rediscovery of Mendel's work have produced an intricate mathematical theory, integrating genetic and ecologic characteristics, that provides the basis for our understanding of the evolutionary process. Within this theoretical framework are two genetic factors of critical importance: determination of the genetic basis of fitness and the genetic structure of populations in space and time. Unfortunately, information about these two factors is lacking for most groups of organisms. The first is nearly impossible to establish (Lewontin, 1974), and the second requires intensive breeding studies. Until recently, the spatial and temporal genetic structure of natural populations had been described only for *Drosophila* and a small number of other groups (Dobzhansky, 1970). In order to apply theoretical evolutionary concepts to organisms such as bats, which are difficult to breed in captivity, it has been necessary to assume that these organisms behave genetically in a manner similar to that of *Drosophila.*

Most species of phyllostomatid bats are difficult or impossible to maintain in captivity in the numbers required for genetic breeding studies (see Greenhall, 1976). In addition, lengthy gestation periods and low productivity make chiropterans, in general, an inefficient group with which to work. Bats also exhibit few clear-cut phenotypic variants within populations that could be exploited in genetic studies, as has been done with *Drosophila.* Thus, the genetic properties of chiropterans, in the classical sense, are unknown. It is not surprising that, among mammals, easily tractable, prolific and variable groups, such as the rodent genera *Mus* and *Peromyscus,* have been used to establish genetic baselines (Rasmussen, 1968).

The development of biochemical techniques, such as electrophoresis, has enabled genetic studies to be carried out at the protein level, thereby circumventing many of the traditional problems mentioned above concerning maintaining and breeding animals. Large numbers of individuals now can be assayed quickly, even in species that cannot be bred in the laboratory, to give baseline data documenting the spatial and temporal structure of natural populations. Breeding studies are needed only to establish the inheritance of protein banding patterns, and for most of the species studied so far, the inheritance of these banding patterns appears to be the same (Selander *et al.*, 1971, Straney *et al.*, 1976*a*, 1976*b*). Although electrophoresis and other biochemical techniques do not provide a complete picture of evolutionary genetics, they can furnish information useful in developing models of evolution and do have the potential for providing data that can be used in testing phylogenetic hypotheses. Few families of eutherian mammals are as ecologically diverse as are phyllostomatid bats, but the genetic as-

pects related to this group's adaptive radiation are poorly understood. It is from studies of organisms such as the Phyllostomatidae that information on the relationships of genetic, ecological, and morphological strategies can be obtained. Study of phyllostomatid genetics though, has only begun and is limited to karyotypic (Baker, this volume) and biochemical characters; available information points more toward potential questions than to a unified picture of chiropteran genetics. In this chapter, we review the published works on biochemical genetics of phyllostomatid bats and present new data on several species from Trinidad.

Literature

Several methods have been used to study the biochemical genetics of phyllostomatids. Most involve electrophoresis in some form of supporting medium, such as cellulose acetate, polyacrilimide, or starch gel. Despite differences in medium, the process is the same. Proteins in tissue extracts are placed in the medium and an electric current applied through an electrode bridge. The proteins are ionized by the buffer used in the electrode bridge, migrate in the electrical field in characteristic manners, and are identified by means of appropriate histochemical stains. Differences in mobility between proteins are indicative of variation in net electric charge on the molecules. Charge variation results from changes in the amino acid composition of the proteins, which ultimately reflect codon differences in the genes involved. Hence, differences in mobility of proteins assayed under the same conditions are translatable into genetic differences.

The earliest examinations of chiropteran biochemical genetics focused on vespertilionids and were conducted by Mitchell (1966), working with hemoglobin, and Manwell and Kerst (1966), with hemoglobin, lactate dehydrogenases, esterases, and general tissue proteins. Both papers established the multiple component structure of chiropteran hemoglobin, and Manwell and Kerst (1966) found genetic polymorphisms in several species that involved at least two alleles at the lactate dehydrogenase-1 locus and several alleles at the esterase and tissue protein loci. Differences in protein mobility of several species and genera were interpreted as genetic variation at loci encoding these proteins.

Variation in bat hemoglobins has been studied in some detail by Mitchell (1970), Valdivieso *et al.* (1969), and Tamsitt and Valdivieso (1969). Differences in hemoglobin molecules were found primarily at the familial level, although within the vespertilionids examined there was a high degree of variation and polymorphism; of the phyllostomatids studied, the same hemoglobin moiety was present. Peptide mapping (Mitchell, 1970) confirmed the identity of the phyllostomatid hemoglobins. *Desmodus* hemoglobin (Tamsitt and Valdivieso, 1969) was found to be the same as that for nine other species of phyllostomatids, whereas hemoglobin from *Pteronotus* was unique, results consistent with current taxonomic views (Smith, 1972; Jones and Carter, 1976). Our examination of samples of phyllostomatids from Trinidad (see below) suggests that variation exists in hemoglobins of some species of this family. The inheritance of this variation is

not clear although banding patterns suggest allelic variation in a monomeric protein, possibly in only one of the hemoglobin chains.

Valdivieso and Tamsitt (1974) examined serum proteins of 18 species from four families of Neotropical bats and were able to isolate four to eight protein fractions. Of the 14 species of phyllostomatids they examined, six exhibited polymorphism in α -globulins; only *Artibeus* was polymorphic at both α - and β-globulin loci. All species were monomorphic for α-globulin. Valdivieso and Tamsitt found no polymorphism in phyllostomatid albumins; however, in our samples from Trinidad, albumin is the single most variable protein locus (see below). Although these authors noted differences in albumins between species, genera, and families, their differences are not concordant with our data (Table 1). Their finding that the albumin of *Phyllostomus hastatus* and *P. discolor* differ from all other phyllostomatids appears to be a result of sampling error. Albumin allozymes identical to those of *Phyllostomus* were present in other phyllostomatids in our samples (Table 1). The fact that in their sample *Molossus* albumins were indistinguishable from those of some phyllostomatids is probably due to the use of cellulose acetate as an assay medium. Although cellulose acetate makes a quick and effective medium for assaying serum protein profiles, the accompanying lack of resolution makes it a poor system for surveys of genetic variation. Their (Valdivieso and Tamsitt, 1974) conclusion that serum protein electrophoresis will be of little use in systematic work is a result of the assay medium employed, the number of species examined, and sample size.

Straney *et al.* (1976*a*) and Greenbaum and Baker (1976) used starch gel assay systems to examine genetic variation at 17 and 21 loci, respectively, in populations of *Macrotus.* In 45 individuals sampled from a population of *M. californicus* in Pima County, Arizona, Straney *et al.* described six polymorphic loci, but the level of polymorphism was low, with no locus segregating for more than two alleles. Indeed, the proportion of loci in the heterozygous state in the average individual ($\bar{H}$) in this population was 0.03, a value low for mammals and much less than that found in *Myotis velifer* ($\bar{H} = 0.14$; Straney *et al.*, 1976*a*). The authors suggested that the low level of variation in *Macrotus* was consistent with the niche width-variation hypothesis, as modified by Selander and Kaufman (1973).

Greenbaum and Baker (1976) examined genetic variation and intra and interspecific similarity in *Macrotus californicus* and *M. waterhousii* from Arizona, México, and Jamaica. In addition to the polymorphisms mentioned above, they described others at two gene loci in populations outside of Arizona. Average population heterozygosity ranged from 0.030 to 0.041 in *M. californicus* and from 0.00 (for specimens from an interspecific contact locality) to 0.043 in *M. waterhousii.*

Nei's genetic distance (*D*; Nei and Roychoudhury, 1974) reflects the number of net codon differences per locus between a pair of populations. Genetic distance between populations of the same species of *Macrotus* are less than 0.07. Estimates of *D* among populations of *Macrotus* are within the range reported for other mammals (Greenbaum and Baker, 1976). Jamaican *M. waterhousii* are

TABLE 1.—*Variation in albumin in Neotropical phyllostomatid bats. Listed are those species examined both in this study and by Valdivieso and Tamsitt (1974). Entries are relative mobility of albumin allozymes,* Artibeus jamaicensis *taken as 100. Where more than one allele is present in a population, mobilities are listed in decreasing order of frequency.*

Species	This study	Valdivieso and Tamsitt[1]
Artibeus jamaicensis	100, 101, 103	100, 106
Artibeus lituratus	103, 100	106
Carollia perspicillata	105, 104.5, 100	106
Phyllostomus discolor	104.5	87.5
Glossophaga soricina	111, 127	94
Desmodus rotundus	127	100
Sturnira lilium	127	100

[1]Values from measurements of mobility as indicated in fig. 3 of Valdivieso and Tamsitt (1974). Alb^{100} is taken as the most common allozyme in *A. jamaicensis*.

12 times as distant from mainland populations of this species as the latter are among themselves ($D=0.065$ and 0.005, respectively). Although this difference involves very small D-values and is not statistically significant, it is consistent with the view that Jamaican populations have been isolated from those on the mainland for some time. This isolation might have resulted in genetic differentiation of Jamaican populations sufficient to warrant recognizing them as belonging to a separate subspecies, a conclusion reached by Anderson and Nelson (1965) based on morphological analysis of *M. waterhousii* from Jamaica and México.

The genetic distance between species of *Macrotus* is substantial ($D=0.4$); at least 40 per cent of the loci in the two species having accumulated codon changes since separation from a common ancestor. This value is high for congeneric species of mammals and is near the value reported for intergeneric comparisons of the vespertilionids *Myotis* and *Pipistrellus* (Straney *et al.*, 1976*b*). Indeed, this value is nearly equal to that found separating *Glossophaga* and *Desmodus* ($D=$ 0.35; see below), members of different phyllostomatid subfamilies. It was concluded that the large genetic difference between *M. californicus* and *M. waterhousii* was a product of independent evolution during a long period of separation—current parapatry represents secondary contact. Temporal calibration of Nei's D in phyllostomatids, discussed below, suggests that these species have been separated for approximately 10 million years. Yet, during this time, although protein loci have diverged, morphological change has been slight (Anderson and Nelson, 1965; Davis and Baker, 1974).

The electrophoretic analysis of *Macrotus* (Greenbaum and Baker, 1976) clearly indicated that mainland *Macrotus* represent two species and that Antillean populations are conspecific with Mexican *M. waterhousii.* Their study suggests great potential for electrophoretic application to systematic problems on an intrageneric level. Published information on biochemical genetics of phyllostomatid bats establishes the presence of polymorphic and polytypic genetic variation in members of the family. The results of Greenbaum and Baker (1976) and

TABLE 2.—*Gene loci and assay systems examined in Trinidad phyllostomatids.*

Protein System	Buffer system[1]	pH	Voltage	Time (hr.)
α-Glycerophosphate dehydrogenase (α-GPD)	Tris citrate	8.0	130	3.5
Albumin (ALB)	Lithium hydroxide	8.1	350	5
Alcohol dehydrogenase (ADH)	Phosphate	6.7	130	5
Glutamic oxaloacetic transaminase-1 (GOT-1)	Lithium hydroxide	8.1	350	5
Glutamic oxaloacetic transaminase-2 (GOT-2)	Tris citrate	8.0	130	3.5
Isocitrate dehydrogenase (IDH-1, 2)	Tris citrate	6.7	150	5
Indophenol oxidase (IPO)	Lithium hydroxide	8.1	350	5
Lactate dehydrogenase-1 (LDH-1)	Lithium hydroxide	8.1	350	5
Lactate dehydrogenase-2 (LDH-2)	Lithium hydroxide	8.1	350	5
Malate dehydrogenase-1, -2 (MDH-1, -2)	Tris citrate	6.7	150	5
Phosphoglucomutase-1, -2 (PGM-1, -2)	Tris citrate	6.7	150	5
Phosphoglucose isomerase-1, -2 (PGI-1, -2)	Poulik	8.5	250	3.5
6-Phosphogluconate dehydrogenase (6-PGD)	Tris maleate	7.4	100	5

[1]Details of preparation in Selander *et al.*, 1971.

Straney *et al.* (1976*a*) indicate a low level of genetic variation in the average population of *Macrotus*. The level of divergence observed by Greenbaum and Baker suggests that phyllostomatid taxa may be genetically quite distinct. New data collected on the genetics of phyllostomatids from Trinidad, summarized below, allow these points to be examined in more detail.

IMPLICATIONS OF GENIC VARIATION IN PHYLLOSTOMATIDS FROM TRINIDAD

In August, 1974, we collected samples of 14 species of phyllostomatid bats at six localities in Trinidad. Assay systems were similar to those described by Straney *et al.* (1976*a*) and Greenbaum and Baker (1976). Table 2 lists gene loci examined and conditions of assays. Several proteins were examined but could not be interpreted due to progressive denaturation (malic enzyme-1, -2; hemoglobin). Esterases presented such a complex pattern that it was not possible to establish locus homologies and these proteins have been disregarded.

Table 3 presents a summary of gene frequencies in the populations examined. In many cases sample sizes are quite small and doubtless some polymorphic loci were missed. Albumin was, as mentioned above, the most polymorphic locus, segregating for two or three alleles in the three species of *Artibeus* sampled, as well as in *Chiroderma*, *Carollia*, and *Glossophaga*. Other loci that show relatively high levels of heterozygosity are IDH-1 (*A. jamaicensis* and *Anoura*), α-GPD (*Carollia*), and PGM-1 (*Carollia*). All other variable loci either are present in samples too small to give fair estimates or show a proportion of heterozygotes less than 0.10.

Genetics and Ecology

Table 4 summarizes heterozygosity values for all species of bats thus far examined. Values from this study are restricted to populations with sufficient

TABLE 3.—*Alleles and frequencies (in parentheses) at 16 gene loci in*

Species	Locality[1]	N	αGPD	Alb	GOT-1	GOT-2	IDH-1	IDH-2	IPO
Phyllostomatidae									
Ametrida centurio	5	1	75(1.00)	105.5(1.00)	83(1.00	−100(1.00)	80(1.00)	−67(1.00)	100(1.00)
Artibeus cinereus	1	6	100(0.92)	102(0.92)	56(1.00)	−94(1.00)	87(1.00)	−67(1.00)	200(1.00)
			62(0.08)	101(0.08)					
	4	7	100(0.86)	102(0.72)	56(1.00)	−94(1.00)	87(1.00)	−67(1.00)	200(0.79)
			62(0.14)	101(0.21)					100(0.21)
				103(0.07)					
Artibeus jamaicensis	1	9	100(1.00)	100(0.56)	100(1.00)	−100(1.00)	100(0.50)	−100(1.00)	100(1.00)
				103(0.27)			87(0.50)		
				101(0.17)					
	2	30	100(0.98)	100(0.48)	100(0.98)	−100(1.00)	87(0.57)	−100(1.00)	100(0.93)
			123(0.02)	103(0.32)	56(0.02)		100(0.43)		50(0.07)
				101(0.20)					
	3	10	100(1.00)	100(0.50)	100(0.90)	−100(1.00)	100(0.50)	−100(1.00)	100(0.95)
				103(0.45)	56(0.10)		87(0.50)		50(0.05)
				101(0.05)					
	4	4	100(1.00)	100(0.67)	100(1.00)	−100(1.00)	100(0.62)	−100(1.00)	100(1.00)
				103(0.16)			87(0.38)		
				101(0.16)					
	5	4	100(1.00)	100(0.50)	100(1.00)	−100(1.00)	100(0.62)	−100(1.00)	100(1.00)
				101(0.38)			87(0.38)		
				103(0.12)					
Artibeus lituratus	1, 2, 3, 5	7	100(0.86	103(0.93)	100(0.93)	−94(1.00)	87(1.00)	−67(1.00)	200(1.00)
			62(0.14)	100(0.07)	56(0.07)				
Chiroderma villosum	5	3	100(0.67)	106(1.00)	111(0.67)	−94(1.00)	87(1.00)	−67(1.00)	100(1.00)
			123(0.33)		61(0.33)				
Sturnira (Species "A")	1, 3	2	108(1.00)	98(1.00)	56(1.00)	−100(1.00)	50(1.00)	−100(1.00)	100(1.00)
Uroderma bilobatum	3, 4, 5	5	123(1.00)	106(1.00)	56(1.00)	−50(1.00)	80(0.60)	−67(1.00)	100(1.00)
							100(0.40)		
Vampyrops helleri	1, 3, 4	8	108(1.00)	100.5(1.00)	56(1.00)	−94(1.00)	87(1.00)	−67(1.00)	200(0.94)
									100(0.06)
Carollia perspicillata	1	30	123(0.73)	105(0.98)	136(0.97)	−100(0.90)	67(1.00)	−67(1.00)	−30(1.00)
			146(0.24)	104.5(0.02)	100(0.03)	−50(0.10)			
			108(0.03)						
	3	5	123(0.80)	105(1.00)	136(0.90)	−100(0.60)	67(1.00)	−67(1.00)	−30(1.00)
			146(0.20)		100(0.10)	−50(0.40)			
	4	10	123(0.75)	105(0.95)	136(0.85)	−100(1.00)	67(1.00)	−67(1.00)	−30(1.00)
			108(0.15)	100(0.05)	100(0.15)				
			146(0.10)						
	5	12	123(0.88)	105(0.88)	136(1.00)	−100(0.96)	67(1.00)	−67(1.00)	−30(1.00)
			146(0.08)	104.5(0.08)		−50(0.04)			
			108(0.04)	100(0.04)					
Phyllostomus discolor	3	1	123(1.00)	104.5(1.00)	100(1.00)	−125(1.00)	77(0.50)	−135(1.00)	90(1.00)
							60(0.50)		
Phyllostomus hastatus	1, 3	2	123(1.00)	104(1.00)	17(1.00)	−125(1.00)	70(1.00)	−133(1.00)	90(1.00)
Glossophaga soricina	1, 4, 5	5	108(0.90)	107(1.00)	56(1.00)	−50(1.00)	87(1.00)	−67(1.00)	−25(1.00)
			123(0.10)						
	3	14	108(0.65)	107(1.00)	56(1.00)	−50(1.00)	87(1.00)	−67(1.00)	−25(1.00)
			123(0.35)						
Anoura geoffroyi	6	30	169(1.00)	101(1.00)	66(1.00)	−94(1.00)	87(0.94)	−67(1.00)	150(0.97)
							90(0.03)		250(0.03)
							77(0.03)		
Desmodus rotundus	2, 4	4	123(1.00)	107(1.00)	56(1.00)	−31(1.00)	60(1.00)	−67(1.00)	−25(1.00)
Molossidae									
Molossus molossus	2	30	177(1.00)	104.1(1.00)	63(1.00)	−50(1.00)	73(1.00)	−133(1.00)	75(1.00)
Natalidae									
Natalus	6	30	100(1.00)	99(0.52)	5(1.00)	−97(1.00)	73(1.00)	−133(1.00)	−200(1.00)
				99.5(0.48)					

1. Locality designations are: 1, Las Cuevas, St. George Co.; 2, Maracas Valley, 2 mi. N (by road) St. Joseph, St. George Co.; 3, Guayaguayare, Mayaro Co.; 4, Maracas Valley, 12 mi. N (by road) St. Joseph, St. George Co.; 5, 2 mi. E, 3 mi. S San Raphael, St. George Co.; 6, Tamana Cave, St. Andrew Co.

bats from Trinidad. **N** *is sample size; locus designations are as in Table 2.*

LDH-1	LDH-2	MDH-1	MDH-2	PGM-1	PGM-2	PGI-1	PGI-2	6PGD
100(1.00)	−100(1.00)	100(1.00)	−100(1.00)	100(1.00)	−100(1.00)	175(1.00)	600(1.00)	117(1.00)
100(1.00)	−100(1.00)	100(0.92) 60(0.08)	−100(1.00)	240(0.58) 100(0.42)	−100(1.00)	100(1.00)	100(1.00)	100(0.92) 40(0.08)
100(1.00)	−100(1.00)	100(1.00)	−100(1.00)	100(0.79) 240(0.21)	−100(1.00)	100(1.00)	100(1.00)	100(0.97) 40(0.03)
100(1.00)	−100(1.00)	100(1.00)	−100(1.00)	100(1.00)	−100(1.00)	100(1.00)	100(1.00)	100(0.83) 166(0.17)
100(1.00)	−100(0.98) −50(0.02)	100(1.00)	−100(1.00)	100(0.98) 240(0.02)	−100(1.00)	100(1.00)	100(1.00)	100(0.98) 166(0.02)
100(1.00)	−100(1.00)	100(1.00)	−100(1.00)	100(1.00)	−100(1.00)	100(1.00)	100(1.00)	100(1.00)
100(1.00)	−100(1.00)	100(1.00)	−100(1.00)	100(1.00)	−100(1.00)	100(1.00)	100(1.00)	100(0.88) 166(0.02)
100(1.00)	−100(1.00)	100(1.00)	−100(1.00)	100(1.00)	−100(1.00)	100(1.00)	100(1.00)	100(1.00)
100(1.00)	−100(1.00)	100(1.00)	−100(1.00)	100(1.00)	−100(1.00)	100(1.00)	100(1.00)	100(1.00)
97(1.00)	−100(1.00)	100(1.00)	−100(1.00)	100(1.00)	−100(1.00)	100(1.00)	100(1.00)	100(1.00)
84(1.00)	−100(1.00)	100(1.00)	−100(1.00)	380(0.75) 640(0.25)	−183(1.00)	200(1.00)	800(1.00)	100(1.00)
100(1.00)	−100(1.00)	100(1.00)	−100(1.00)	100(1.00)	−100(1.00)	100(1.00)	100(1.00)	100(1.00)
98(1.00)	−100(1.00)	100(1.00)	−100(1.00)	100(1.00)	−100(1.00)	100(1.00)	100(1.00)	100(1.00)
91(1.00)	−100(1.00)	100(1.00)	−100(1.00)	240(0.97) 380(0.03)	−100(1.00)	62(1.00)	0(1.00)	100(1.00)
91(1.00)	−100(1.00)	100(1.00)	−100(1.00)	240(1.00)	−100(1.00)	62(1.00)	0(1.00)	100(1.00)
91(1.00)	−100(1.00)	100(1.00)	−100(1.00)	240(0.90) 380(0.10)	−100(1.00)	62(1.00)	0(1.00)	100(1.00)
91(1.00)	−100(1.00)	100(1.00)	−100(1.00)	240(0.92) 380(0.08)	−100(1.00)	62(1.00)	0(1.00)	100(1.00)
100(1.00)	−100(1.00)	100(1.00)	−100(1.00)	100(0.50) 240(0.50)	−183(1.00)	160(1.00)	550(1.00)	100(1.00)
100(1.00)	−100(1.00)	100(1.00)	−100(1.00)	240(0.75) 100(0.25)	−183(1.00)	160(1.00)	550(1.00)	100(1.00)
84(1.00)	−100(1.00)	100(1.00)	−100(1.00)	225(1.00)	−100(1.00)	206(1.00)	1000(1.00)	166(1.00)
84(1.00)	−100(1.00)	100(1.00)	−100(1.00)	225(1.00)	−100(1.00)	206(1.00)	1000(1.00)	166(1.00)
96(1.00)	−100(1.00)	80(1.00)	−100(1.00)	380(1.00)	−100(1.00)	175(1.00)	700(1.00)	90(1.00)
84(1.00)	+100(1.00)	100(1.00)	−100(1.00)	380(1.00)	−100(1.00)	206(1.00)	1000(1.00)	166(1.00)
68(1.00)	0(1.00)	40(0.98) 62(0.02)	−133(1.00)	38(1.00)	−183(1.00)		600(1.00)	170(0.98) 190(0.02)
73(1.00)	−200(1.00)	59(1.00)	−133(1.00)	400(1.00)	−200(1.00)	238(1.00)	500(1.00)	200(1.00)

sample size ($N>15$) to permit relatively unbaised calculation of gene frequencies. $\overline{H}$-values listed are those expected under Hardy-Weinberg assumptions, from which none of the phyllostomatid samples deviate significantly. Johnson (1974) has suggested that enzymes in key regulatory positions in metabolic pathways are more variable than those in nonregulatory positions, and that enzymes with variable substrates show highest heterozygostities. There is no consistent agreement of the chiropteran data with this hypothesis (Table 4). Only six of the 11 species have higher heterozygosities in regulatory enzymes than in nonregulatory ones. We agree with Selander (1976) that Johnson's hypothesis will not in itself account for heterozygosity differences seen between loci. Unfortunately, Johnson's hypothesis does not deal with general protein loci, which we found to be the most variable in the phyllostomatids. General proteins usually have exhibited low levels of polymorphism in other mammals (Selander, 1976).

The data presented in Table 4 suggest that phyllostomatids differ from species of *Myotis* in having lower levels of genic heterozygosity. The frequency distributions of per locus heterozygosity (h) differ between these groups (Fig. 1). The average locus in the phyllostomatids examined has a heterozygosity of 0.036, whereas for *Myotis* this value is 0.117. The pattern seen among phyllostomatids is very near to that observed in a variety of rodents (Fig. 1; data for esterases are excluded from this figure). When the h-values for phyllostomatids and *Myotis* are compared in an Analysis of Variance (after arcsine transformation), the difference is highly significant ($P<0.001$). Phyllostomatids possess more monomorphic loci than do species of *Myotis* and do not show a second frequency peak for loci with high heterozygosity. Most of the loci contributing to this second peak in *Myotis* are not in Hardy-Weinberg equilibrium (Straney *et al.*, 1976*a*).

The patterns in Fig. 1 suggest that phyllostomatids might have levels of heterozygosity equivalent to those observed in rodents. This is not apparent when $\overline{H}$-values presented here are compared (average $\overline{H}$ for rodents, 0.059), because esterases account for 43 per cent of rodent $\overline{H}$-values (Selander, 1976). Some *Myotis* populations, however, are more similar in heterozygosity levels to invertebrates (average $\overline{H}=0.12$; Selander, 1976), but this is not true of vespertilionids as a group. *Pipistrellus* populations exhibit low genetic variability, and it has been suggested that this results from demographic factors (Table 4; Straney *et al.*, 1976*b*). Preliminary data on California vespertilionids indicate that other species also have low variability (J. L. Patton, personal communication).

Levels of genic variability in phyllostomatids, and at least some species of *Myotis*, differ greatly, and it is likely that other evolutionary characteristics do as well. A number of factors could produce the differences in heterozygosity observed between phyllostomatids and *Myotis*: stochastic processes, gene flow, adaptation to microgeographic conditions, and the grain of experienced environments (Levins, 1968; Soulé, 1976). Differences, on a much lower level, also are apparent within the phyllostomatids examined (Table 4). *Artibeus, Glossophaga,* and *Carollia*, the most common species in our collections, differ greatly in levels of polymorphism. Population bottlenecks, inbreeding, and drift are not suffi-

TABLE 4.—*Summary of genetic variability in bats.* P *is per cent of loci polymorphic (frequency of major allele >0.95).* $\bar{H}$ *is average heterozygosity or the proportion of loci in a heterozygous state in the average individual of a population (range in parentheses);* $\bar{h}$ *represents average heterozygosity for loci of the designated class.*

	Number of populations	Number of loci	P(%)	$\bar{h}$ Regulatory	$\bar{h}$ Non-regulatory	$\bar{h}$ Variable substrate	$\bar{h}$ General Protein	$\bar{H}$	Source
Myotis velifer	3	16-25	63	0.121	0.195	0.139	0.043	0.144(0.101-0.163)	Straney *et al.*, 1976*a*
Myotis californicus	1	21	38	0.081	0.125	0.133	0.219	0.126	Straney *et al.*, 1976*b*
Pipistrellus hesperus	1	20	10	0	0	0.146	0.021	0.026	Straney *et al.*,1976*b*
Macrotus californicus	5	16-21	14	0.027	0.019	0.062	0	0.033(0.030-0.041)	Greenbaum and Baker, 1976; Straney *et al.*, 1976*a*
Temperate average			31	0.057	0.085	0.120	0.071	0.081	
Macrotus waterhousii	4	21	10	0.055	0.025	0.012	0	0.026(0.000-0.043)	Greenbaum and Baker, 1976
Artibeus jamaicensis	3	17	24	0.003	0.078	0.078	0.641	0.080(0.065-0.091)	this study
Carollia perspicillata	3	17	24	0.055	0.019	0	0.126	0.037(0.035-0.038)	this study
Anoura geoffroyi	1	17	17	0.013	0.015	0.060	0	0.016	this study
Glossophaga soricina	1	17	6	0.380	0	0	0	0.018	this study
Molossus molossus	1	17	6	0.029	0.008	0	0	0.015	this study
Natalus sp.	1	17	12	0.014	0	0	0.480	0.034	this study
Tropical average			14.1	0.068	0.021	0.021	0.178	0.032	

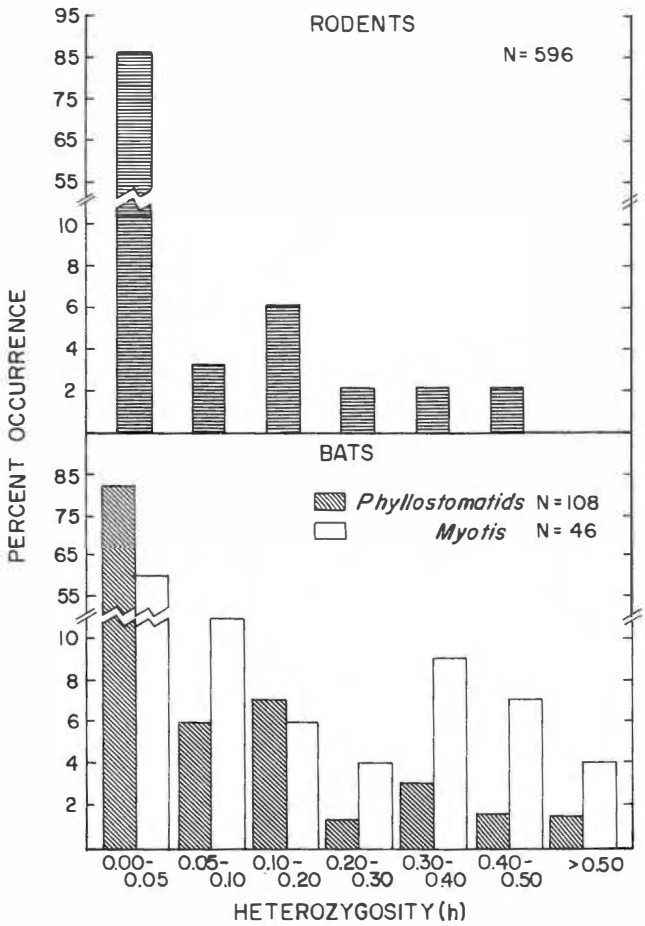

FIG. 1.—Per cent occurrence of loci with different levels of heterozygosity in rodents (summarized in Smith *et al.*, 1978), phyllostomatid bats (this study), and bats of the genus *Myotis* (Table 4). *N* is number of individuals.

cient to explain the low levels of heterozygosity in *Glossophaga, Anoura,* and *Carollia,* compared to the relatively high levels in *Artibeus,* because all four genera are widespread, highly vagile, and abundant. Isolation of the population characteristics that might be responsible for differences in heterozygosity is not possible using genetic data alone. Only genetic studies coupled with extensive ecological investigations will provide the information needed to address this point, and then only if temporal trends also are examined.

Differences in heterozygosity may index more subtle differences in population characteristics. The data presented above suggest that different species of bats have been exposed to different evolutionary forces, which are dictated by differences in population structure. Although we are unable at this point to determine why variation in population structure exists or what evolutionary

forces effect these differences, it is clear that genetic models of chiropteran populations must account for several distinct patterns of variation.

Future studies of ecological genetics in bats should pay particular attention to spatiotemporal structure of populations. With proper experimental design, it is possible to estimate deme size, effective population size, and migration rate using, for example, Kirby's (1976) analysis of Wright's *F*-statistics. More important than estimates of these values, though, is an estimate of their variability through time. Bat populations are conceivably temporally unstable in composition, due in part to their vagility and roosting habits. Turner's (1975) studies of *Desmodus* in Costa Rica indicate that vampire populations can be either ephemeral or relatively stable depending on where the bats roost. It is important to know on what scale this temporal variability acts as well as which ecological factors, such as roost site, can alter its periodicity. Species differences in these parameters are to be expected in a group as diverse as the phyllostomatids, and comparative studies will be necessary to indicate to what degree morphological and ecological diversity is reflected in population structure. The evolutionary process proceeds only within the limits set by the spatiotemporal structure of the populations involved. Hence, a useful approach to understanding patterns of population differentiation, speciation, and phyletic evolution in different lineages is to determine to what extent structural differences in populations determine different evolutionary strategies. Structural parameters of populations are major determinants of the fate of new mutants, the permanence of polymorphisms, and the speed with which adaptive change can be effected.

Genetic Phyletics

An alternative to using traditional characteristics for reconstructing the evolutionary history of a group is to employ measures of genetic comparisons between taxa. Because evolution can be expressed as the change in genomes through time, genetic comparisons can be used to estimate the degree of divergence between taxa. With the advent of biochemical assay systems this has become possible. As genetic comparisons dependent upon breeding studies cannot be used to compare taxa above the species level in most mammals, the early interest in electrophoresis of bat proteins was, in part, systematic.

Manwell and Kerst (1966), Valdivieso *et al.* (1969), Valdivieso and Tamsitt (1974), Tamsitt and Valdivieso (1969), and Mitchell (1970), all working with one or at most a few proteins, concluded that electrophoretic comparisons would be of little use in chiropteran systematics below the family level. These studies did, however, find confirming evidence for placing the mormoopids (*Pteronotus* and *Mormoops*) into a family separate from phyllostomatids and for the inclusion of the vampires as a subfamily in the Phyllostomatidae. However, phylogenetic conclusions based on a few biochemical characters cannot be expected to be any more accurate than those based on a few morphological characters (Avise *et al.*, 1974). Biochemical data used to indicate phylogenetic relationships are based on the assumption that the loci sampled are representative

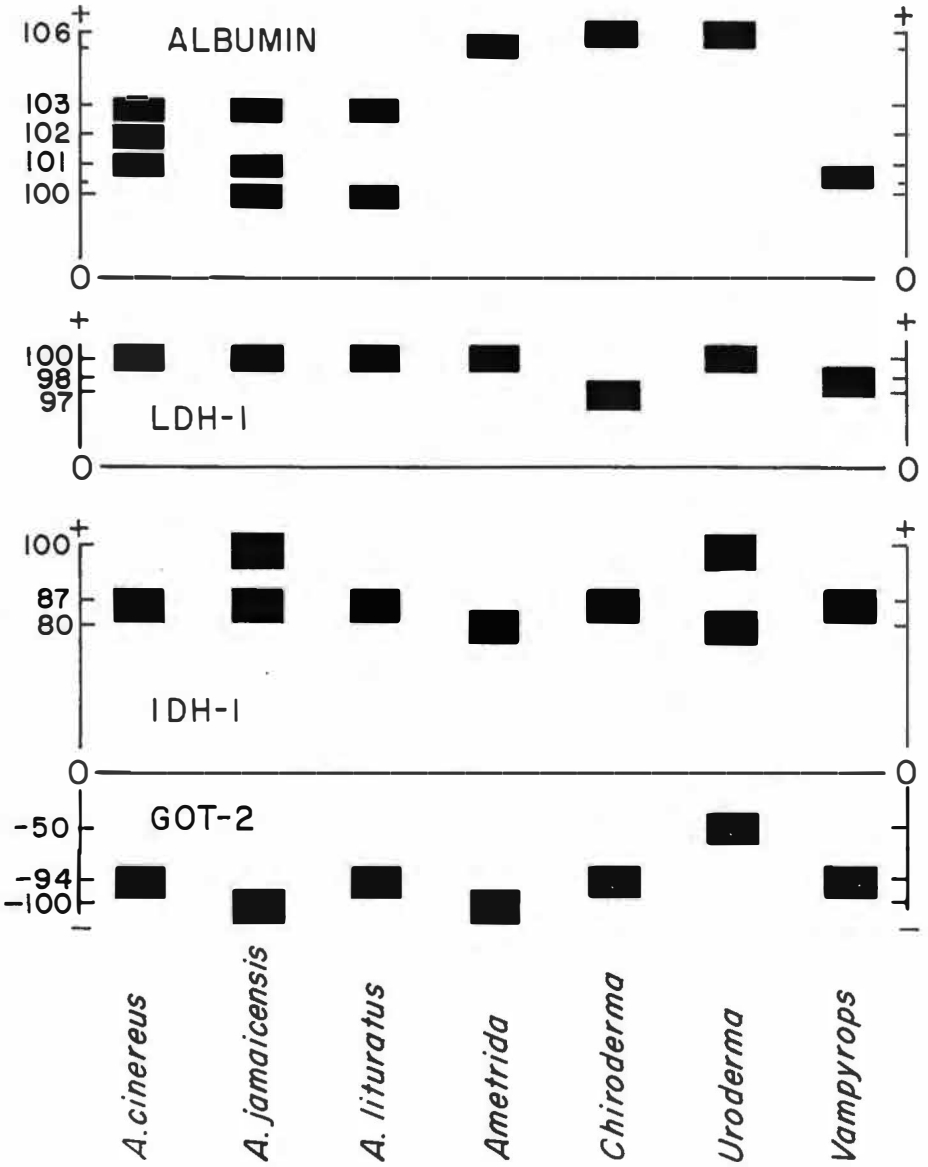

FIG. 2.—Diagramatic representation of banding patterns of four protein gene loci in seven species of stenodermine bats.

of the genome as a whole. The magnitude of sampling error, and the resolving power of genetic divergence estimates, is a direct function of the number of loci examined (Nei, 1976). Thus, electrophoretic comparisons utilizing only a few loci provide data that must be approached with caution.

It is possible that, with a small group of closely related taxa, biochemical data for a few loci will give quite useful information. The utility of this information,

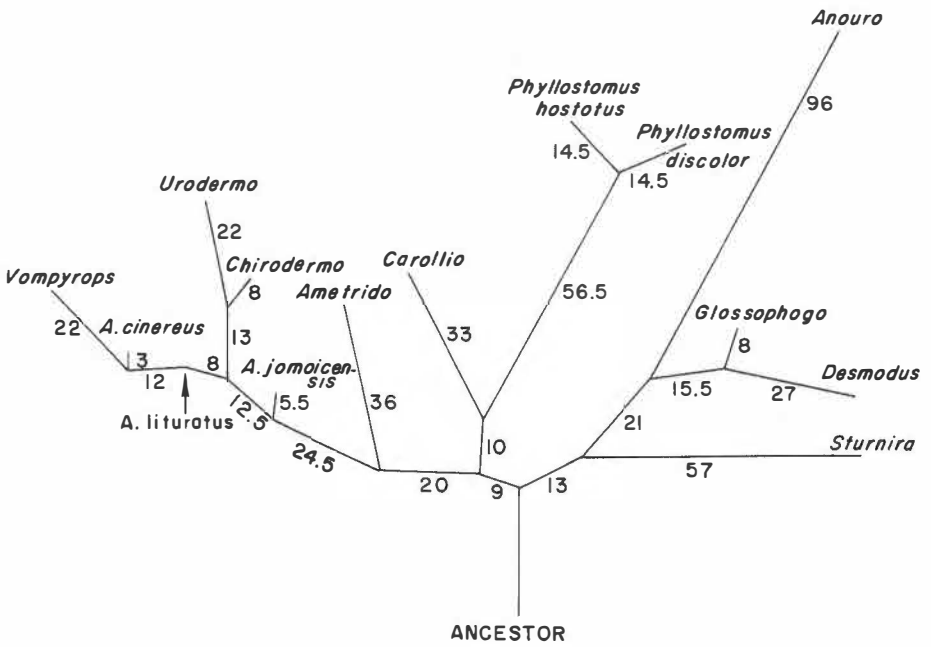

FIG. 3.—Wagner tree calculated from Nei's D ($\times 100$). Numbers are the amount of divergence between branch points and represent the minimum number of net nucleotide changes per 100 loci accumulated along the connecting branch.

however, will depend on the sample of loci examined. Fig. 2 illustrates banding patterns of four gene products for the seven species of stenodermine bats we have examined from Trinidad. Although these four loci are sufficient to identify all seven species electrophoretically, they are insufficient for calculation of genetic distance values, because D-values have large errors when based on only a few loci (Nei and Roychoudhury, 1974).

In Fig. 3 we present a phylogenetic estimate of the relationships among 14 phyllostomatid species, based on the examination of 17 gene loci. The genetic distances between taxa, upon which this tree is based, are summarized in Table 5. Seventeen loci certainly are only a small fraction of the phyllostomatid genome. The sampling error associated with these divergence values is not small (Nei, 1976), and the tree in Fig. 3 must be evaluated in this light. It also should be pointed out that this technique overestimates similarity, and additional refinement and the inclusion of loci such as esterases should reveal further separation of taxa. We present these preliminary data as a starting point for additional work.

Farris' (1972) modified Wagner algorithm for Nei's distance was used to construct the tree in Fig. 3. This method does not assume that evolutionary rates are the same in all lines of descent, as does the use of an unweighted pair-group method for constructing phenograms. The modified Wagner method partitions the genetic distance between taxa into branch lengths of the paths connecting them. This is done in such a way that the resulting estimates of branch lengths are

minimum estimates of the amount of change between cladistic events. Because the tree is based on Nei's *D*, the branch lengths can also be interpreted as the minimum number of net codon changes per locus since a particular cladistic event. Thus, according to Fig. 3, *Artibeus cinereus* and *Vampyrops* share an immediate common ancestor. Since the cladistic splitting of the two, we estimate that *Vampyrops* has accumulated 22 net codon changes per 100 loci, whereas *A. cinereus* has accumulated a minimum of three. Because these taxa share a common ancestor, the difference in divergence is also a difference in evolutionary rate along the two branches. One of the striking characteristics of the tree in Fig. 3 is that the branch lengths are unequal, implying that the rates of evolution have not been the same in all lines of descent. This is consistent with the argument given above that differences in levels of genetic variability within phyllostomatid species mirror underlying differences in population structure, thereby differentially affecting evolutionary potential.

The root in Fig. 3 has been placed using Farris' (1972) minimum variance criterion. This is an iterative procedure whereby the root is placed in the position that minimizes the variance in divergences of terminal taxa from the hypothetical ancestor of the group as a whole. There are three major lineages apparent when the root is placed: 1) stenodermines, 2) *Phyllostomus* and *Carollia*, and 3) glossophagines, *Desmodus*, and *Sturnira*. The average divergence of these three lineages from the ancestor is similar (mean, 86, 76, and 85 codon changes per 100 loci, respectively). An analysis of variance of within and between lineage effects on divergence indicates that 100 per cent of the variance in divergence present in Fig. 3 is within lineages. As we can demonstrate no differences in evolutionary rate between lineages, we can use the average divergence of the lineages (82 codon changes per 100 loci) to estimate the age of the family. Nei's *D* is a linear function of time (Nei, 1976), and studies by Avise and Ayala (1975, 1976) indicate that genetic distance is by and large independent of cladistic history. Sarich (1977) has calibrated Nei's *D* against his albumin clock estimate of divergence time and has provided us with the conversion equation 1.0 $D=28$ million years (for branch length, $1.00=56$ million years). Using this conversion, we estimate that the diversification of the family occurred 40 million years ago during the early Oligocene. Because this is a minimum estimate of age, the age estimated is of diversification not origin, and the estimate is not without sampling error, we feel that these data are comparable with Koopman's (1976) and Smith's (1976) conclusion that the late Oligocene is the latest that the family could have arisen.

Within the error of our estimates, the lineages represented in Fig. 3 appear to have arisen at the same time. These lineages are not well defined, except for the relatively compact stenodermine lineage, and there is no evidence of a "*Macrotus*-like" and "*Phyllostomus*-like" (Smith, 1976) dichotomy within our sample. Genera hypothesized as belonging to one lineage or the other are intermixed in Fig. 3 (compare Smith, 1976, fig. 2). Even though our inability to distinguish this dichotomy may be an artifact of sampling, we think it best to assume that the major adaptive trends within the family are of coeval origin.

Stenodermines

The discreteness of the stenodermine lineage in Fig. 3 probably results from more extensive sampling of members of this subfamily. The radiation of this group appears to be an early one, the line leading to *Ametrida* diverged perhaps 20 million years ago in the late Miocene. *Artibeus* is a basal taxon for the rest of the subfamily represented here and two separate lineages derive from it. The three species of *Artibeus* have undergone little divergence from their respective common ancestors whereas the two lineages involving *Vampyrops* and *Uroderma-Chiroderma* have evolved at a much faster rate. These results suggest that *Artibeus* is a paraphyletic taxon.

With effort, it is possible to identify Smith's (1976) "short-faced, long-faced" dichotomy in our phylogram. The "long-faced" lineage is polyphyletic in our reconstruction although the three members of this group (*Vampyrops*, *Uroderma*, and *Chiroderma*) are derived from a single genus, *Artibeus*. Furthermore, our phylogenetic hypothesis suggests that short-faced is the primitive condition for stenodermines. We have examined too few genera to be certain of this point, but the data at hand indicate that long faces represent parallel derived characters.

Our sample of stenodermine taxa, however, is sufficient to suggest a polarity for Baker's (1973) phylogeny of the subfamily based on gross karyotypic characters. His fig. 5 is quite similar to our Fig. 3 if the root of his phylogram is displaced to the right and if one ignores the absence of *Sturnira*. Karyotypically, *Chiroderma* and *Uroderma* are not related as closely to each other as electrophoretic data indicate; further study could identify additional areas of disagreement. It is, however, reassuring to find the same basic phylogenetic framework emerging from two different and independent data sources.

Phyllostomus and Carollia

There is little that can be said of the association of *Carollia* and *Phyllostomus* presented in Fig. 3. These two genera are not closely related but probably do represent a distinct lineage within the family. Walton and Walton (1968) suggested a similar relationship based on their study of postcranial osteology. There is no indication in our data of close phylogenetic ties between *Carollia* and *Glossophaga* (*sensu* Smith, 1976).

The divergence of the two species of *Phyllostomus* appears to have occurred 8 million years ago during the mid-Pliocene ($D=0.29$). The morphological and ecological differences between *P. hastatus* and *P. discolor* are much greater than those between the two species of *Macrotus* studied by Greenbaum and Baker (1976), even though the latter are separated by a greater genetic distance ($D=$ 0.41-0.50). This represents another of the growing number of cases where genetic and morphological measures of divergence are found to be discordant (King and Wilson, 1975; Avise, 1976).

Glossophagines, Desmodus, and Sturnira

This group forms the most heterogeneous branch of our phylogenetic tree, and the relationships within it are difficult to reconcile with morphological evidence

and current concepts of phyllostomatid systematics. *Anoura* and *Glossophaga* are somewhat closely related, based on electrophoretic data, although this association is overshadowed by the greater amount of protein evolution along the *Anoura* branch. Our placement of *Sturnira* is at variance with current taxonomic opinion. Walton and Walton (1968) postulated a relationship between *Sturnira* and the glossophagines, following a comparison of postcranial morphology. Addition of more genera to this data set would not result in a closer association of *Sturnira* and the stenodermines because additional data would not decrease the large genetic distances between these groups (Table 5). Based on our electrophoretic sample, we are left with the conclusion that *Sturnira* is not genetically a stenodermine bat and is not closely related to any one of the lineages represented in this study.

A close relationship between *Desmodus* and the glossophagines, based on chromosomal, immunological, and sperm morphology data, was proposed by Forman *et al.* (1968). Our data also suggest such a relationship between *Glossophaga* and *Desmodus* (Fig. 3; Table 5). Because of the difference in evolutionary rates along the two branches, it is difficult to estimate the age of this divergence, but we suggest that it is 10 million years. This is consistent with the fossil record to the extent that fossil desmodontines are not known prior to about 1.5 million years BP (Hutchison, 1967).

An overview of the genic and morphological data from this family suggests that there are several examples where there is discordance in the rates of evolution of genic and classical morphological characters. One hypothesis that attempts to reconcile genetic and morphological data assumes that the morphological modifications leading to a specialized taxon have been due to changes in regulatory genes affecting developmental pathways. Such changes, which one would not expect to be reflected in the structural genes assayed in electrophoresis, could result in major and rapid morphological evolution. This form of quantum evolution (*sensu* Simpson, 1953) has recently been invoked by King and Wilson (1975) to explain the small genetic distance between *Homo* and *Pan*. If this hypothesis reflects the true path of evolution followed in these discordant examples, we would predict, following King and Wilson (1975), that DNA hybridization between such taxa would show similarity in the unique DNA fraction consistent with that found electrophoretically and a larger difference in the presumably regulatory medium repeated DNA fraction.

Phylogenetic reconstruction is as much a science as it has been portrayed an art. One proceeds by constructing hypotheses of relationships from different data sources and searching for one that subsumes the others and provides an explanation of their differences. This consistent hypothesis is accepted as "true" either until a more general one is produced or conflicting data are found. The phylogenetic hypotheses of Smith (1976) and those reflected by the checklist of Jones and Carter (1976) are not in accordance with the genetic relationships indicated by our electrophoretic data. We do not view these electrophoretic results as a procrustean bed of truth into which the morphological evidence must be forced in agreement. Rather, they generate a phylogenetic hypothesis

TABLE 5.—*Nei's genetic distance* (D, *upper half matrix) and Rogers' genetic similarity (S, lower half matrix) for bat populations from Trinidad. Where more than one population of a species is listed, numerical designations are as in Table 3. I indicates an infinite value for* D *(Nei's genetic identity I=0.00).*

	AMC	AC1	AC4	AJ1	AJ2	AJ3	AJ4	AJ5	AL	CV	SA	UB	VH	CP1	CP3	CP4	CP5	PD	PH	AG	GS	DR	MM	NS
Ametrida centurio (AMC)		0.89	0.78	0.65	0.66	0.66	0.66	0.66	0.81	0.80	1.15	0.61	0.97	0.97	1.02	0.95	0.96	1.24	1.31	1.16	1.16	1.39	2.77	I
Artibeus cinereus 1 (AC1)	0.40		0.02	0.44	0.42	0.41	0.45	0.44	0.15	0.32	1.15	0.39	0.23	0.86	0.85	0.86	0.86	1.03	1.04	0.94	0.79	1.14	I	2.80
A. cinereus 4 (AC4)	0.45	0.94		0.36	0.34	0.34	0.37	0.36	0.11	0.25	1.08	0.32	0.20	0.89	0.88	0.88	0.89	1.00	1.05	0.90	0.77	1.12	I	2.86
A. jamaicensis 1 (AJ1)	0.52	0.61	0.66		0.00	0.00	0.00	0.00	0.28	0.40	0.80	0.41	0.60	0.95	0.99	0.90	0.95	0.85	1.10	1.43	1.18	1.57	I	2.71
A. jamaicensis 2 (AJ2)	0.51	0.63	0.68	0.97		0.00	0.01	0.00	0.26	0.38	0.78	0.40	0.57	0.92	0.95	0.88	0.92	0.83	1.06	1.41	1.19	1.61	I	2.73
A. jamaicensis 3 (AJ3)	0.52	0.62	0.67	0.97	0.98		0.01	0.01	0.26	0.39	0.76	0.39	0.57	0.93	0.96	0.88	0.92	0.84	1.06	1.47	1.19	1.60	I	2.71
A. jamaicensis 4 (AJ4)	0.52	0.61	0.65	0.98	0.96	0.96		0.00	0.30	0.41	0.79	0.40	0.61	0.95	0.98	0.90	0.94	0.85	1.09	1.47	1.22	1.60	I	2.72
A. jamaicensis 5 (AJ5)	0.52	0.61	0.66	0.97	0.97	0.96	0.98		0.30	0.40	0.78	0.40	0.60	0.93	0.97	0.88	0.93	0.83	1.07	1.44	1.25	1.64	I	2.72
A. lituratus (AL)	0.45	0.83	0.86	0.72	0.74	0.74	0.71	0.72		0.28	1.34	0.43	0.27	0.94	0.92	0.91	0.94	0.86	1.09	0.97	0.94	1.35	I	2.89
Chiroderma villosum (CV)	0.45	0.70	0.74	0.64	0.65	0.65	0.64	0.65	0.74		1.23	0.30	0.34	0.89	0.88	0.88	0.88	1.14	1.21	0.96	0.93	1.28	I	3.13
Sturnira sp. A (SA)	0.32	0.32	0.34	0.45	0.46	0.46	0.45	0.46	0.27	0.33		0.95	0.96	1.14	1.20	1.08	1.12	1.19	1.14	1.74	0.99	1.20	2.76	I
Uroderma bilobatum (UB)	0.54	0.65	0.70	0.65	0.66	0.66	0.66	0.66	0.64	0.72	0.39		0.44	0.81	0.75	0.82	0.80	0.95	0.91	1.37	0.78	0.97	2.76	I
Vampyrops helleri (VH)	0.38	0.77	0.80	0.53	0.55	0.55	0.53	0.54	0.76	0.71	0.38	0.64		0.95	0.95	0.92	0.95	1.23	1.31	0.98	0.70	1.16	I	I
Carollia perspicillata 1 (CP1)	0.38	0.42	0.41	0.39	0.40	0.40	0.39	0.40	0.40	0.41	0.32	0.44	0.39		0.01	0.00	0.00	1.06	1.04	1.35	1.08	1.19	5.05	I
C. perspicillata 3 (CP3)	0.36	0.42	0.42	0.37	0.38	0.38	0.37	0.38	0.40	0.42	0.30	0.46	0.39	0.97		0.01	0.01	1.02	1.02	1.35	1.02	1.17	3.66	I
C. perspicillata 4 (CP4)	0.39	0.42	0.42	0.41	0.42	0.42	0.41	0.42	0.40	0.42	0.34	0.44	0.40	0.97	0.95		0.00	1.03	1.04	1.33	1.07	1.16	I	I
C. perspicillata 5 (CP5)	0.38	0.42	0.41	0.39	0.40	0.40	0.39	0.40	0.39	0.41	0.33	0.45	0.39	0.98	0.95	0.98		1.03	1.02	1.34	1.09	1.15	5.97	I
Phyllostomus discolor (PD)	0.29	0.37	0.38	0.42	0.44	0.43	0.42	0.43	0.42	0.32	0.39	0.42	0.29	0.34	0.35	0.35	0.36		0.29	2.03	1.57	1.39	2.74	I
P. hastatus (PH)	0.27	0.36	0.35	0.34	0.35	0.35	0.34	0.35	0.34	0.29	0.33	0.40	0.27	0.35	0.36	0.35	0.36	0.74		2.06	1.60	1.66	2.06	2.74
Anoura geoffroyi (AG)	0.32	0.39	0.40	0.24	0.25	0.24	0.23	0.24	0.38	0.39	0.18	0.26	0.37	0.27	0.27	0.27	0.27	0.14	0.13		1.16	1.38	I	I
Glossophaga soricina (GS)	0.32	0.45	0.47	0.31	0.31	0.30	0.30	0.29	0.39	0.40	0.37	0.46	0.49	0.34	0.36	0.34	0.34	0.22	0.21	0.32		0.35	2.76	I
Desmodus rotundus (DR)	0.25	0.32	0.34	0.22	0.21	0.21	0.21	0.20	0.26	0.28	0.30	0.38	0.31	0.30	0.31	0.31	0.32	0.23	0.19	0.25	0.70		I	I
Molossus molossus (MM)	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.07	0.07	0.00	0.02	0.03	0.02	0.01	0.08	0.13	0.00	0.07	0.00		1.66
Natalus sp. (NS)	0.06	0.08	0.08	0.10	0.10	0.10	0.09	0.09	0.07	0.06	0.02	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.08	0.01	0.01	0.01	0.12	

sufficiently different from others that have been proposed to indicate that "the great deal of uncertainty and contradictory evidence" (Smith, 1976) surrounding phyllostomatid phylogency will continue in the future. We still lack an hypothesis of the phylogeny of the Phyllostomatidae that is consistent with available data and that also identifies the evolutionary processes producing the differences between morphological and genetic findings.

[*Note added in galley.*—Additional work by us suggests that the distance we report between *Glossophaga* and *Desmodus* is too low. Examination of new material, both at Lubbock and Berkeley, shows that *Desmodus* and *Glossophaga* share very few alleles.]

Conclusions

Biochemical genetics has proven valuable in evolutionary biology through the characterization of population structure in space and time and through generation of phylogenetic hypotheses. By examining the genetic structure of populations, important evolutionary parameters can be identified and quantified to provide a bridge between genetic phylogenies and more traditional evolutionary reconstructions. The study of chiropteran genetics is only 10 years old; yet, in that time it has provided information that both challenges and supports the traditional view of chiropteran evolution. The dynamics of population structure of vespertilionid and phyllostomatid bats does not appear to be the same, although studies of temporal structure will be necessary to confirm this conclusion. The mode of evolution, as reflected by electrophoretic parameters, appears to be different between some lineages of phyllostomatids, particularly the desmodontines. When more genetic data are available on phyllostomatid bats, an integration of genetic, karyotypic, and morphological data should produce a consistent model of evolution in this group, which might be surprising in its complexity.

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SPERM MORPHOLOGY

G. Lawrence Forman and Hugh H. Genoways

Bishop and Austin (1957) in their study of variation in mammalian spermatozoa suggested that the sperm of each mammalian species was probably unique. Although complete volumes have been written on the ultrastructure of spermatozoa (for example Baccetti, 1970), particularly of humans and domestic animals, there is still relatively little information available on the comparative gross morphology of spermatozoa. McFarlane (1963), Forman (1968), and Forman *et al.* (1968) made significant contributions to our understanding of the use of sperm morphology in establishing systematic and phylogenetic relationships of birds and mammals. However, there have been very few similar studies published to this date.

The use of sperm morphology as a systematic character among mammals is relatively new, beginning with the study of British murid rodents by Friend (1936) Other studies dealing with rodent sperm include those of Braden (1959), Hirth (1960), Wooley and Beaty (1967), Genoways (1973), Helm and Bowers (1973), and Linzey and Layne (1974). Hughes (1964, 1965) compared the morphology of sperm of 18 species of marsupials representing five families, and Biggers and Delamater (1965) and Biggers (1966) reported on the spermatozoa of several genera of American marsupials. Griffiths (1968) presented data on the sperm of the echidna and Bedford (1967) reported observations on the fine structure of the spermatozoa of two primates in addition to man. An especially important contribution is that of Martin *et al.* (1975). They used scanning electron microscopy to compare spermatozoa of 16 species of primates representing four families and concluded that sperm morphology might be valuable in gaining better understanding of intrageneric relationships among primates.

Six studies have described the sperm of *Rhinolophus ferrumequinum*, and Hirth (1960), Fawcett and Ito (1965), Wimsatt *et al.* (1966), and Forman (1968) reported on various aspects of the spermatozoa of species of vespertilionid bats. Forman (1968) was the first to present information on the sperm of members of the family Phyllostomatidae. In his study, he presented information on eight species representing four of the six subfamilies. In the same year, Forman *et al.* (1968) reported on two additional phyllostomatid species, *Desmodus rotundus* and *Diphylla ecaudata*, of a fifth subfamily, the Desmodontinae.

Over the past seven years, we have accumulated data on the sperm of phyllostomatid bats in the course of several other studies of this family. This has resulted in material for 35 species, 28 of which have not been studied previously. Through new staining techniques, we also have been able to acquire new information on the seven species for which some data were presented previously. The results of our studies and their systematic implications are discussed below.

Methods and Materials

The spermatozoa of 35 species belonging to six subfamilies of phyllostomatids were examined. To obtain spermatozoa, the epididymides of freshly-killed bats were removed. A small amount of fluid containing mature sperm was taken and suspended in an isotonic solution of sodium citrate. A few drops of the sodium citrate and spermatozoon solution were placed on a microscope slide and allowed to air-dry. Dilution of the spermatozoa with sodium citrate was necessary so that individual spermatozoa would be dispersed for study and photographing. Spermatozoa on slides were fixed with a solution of one part acetic acid and four parts absolute methyl alcohol. Slides were allowed to fix for 10 to 15 seconds and then shaken dry. Fixing for a longer period resulted in destruction of the acrosome.

Slides were stained with Toluidine Blue O and counterstained with PAS. Counterstaining resulted in delineation of the acrosomal material so that the outline of the headcap could be observed. The procedure outlined below was followed in staining slides:

1. fix in solution of acetic acid and methyl alcohol;
2. rinse three times in distilled water;
3. place in 15% Periodic Acid for 10 minutes;
4. rinse in tap water for 10 minutes;
5. rinse briefly in distilled water;
6. place in Schiffs' Reagent for 10 minutes;
7. rinse in metabisulfite with three changes at three minutes each;
8. rinse in tap water for 5 minutes;
9. rinse briefly in distilled water;
10. place in .02% Toluidine Blue O for 30 minutes;
11. place in acetone for 2 minutes;
12. place in solution of acetone plus xylene (1:1) for 2 minutes;
13. place in xylene for two changes at 3 minutes each;
14. mount using cover slip and Permount.

The following characters were measured: total length of head, length of acrosome, nuclear length, head width, midpiece length. The mean, range (in parentheses), and one standard deviation for the aforementioned characters are given beyond in the species descriptions whenever possible. Measurements were taken by means of a Unitron Filar widefield dial micrometer attached to an AO microstar Series 10 research microscope. Measurements are given in microns.

The terms dorsal and ventral refer to the flattened surfaces of the head and midpiece, whereas lateral refers to the narrow sides of the sperm. Length of head included both the acrosome and nuclear area. Width of the head was measured as the distance between extremities when observed in dorsal or lateral view. The tails of sperm were not considered in this study.

Characters considered in this study included: shape of head; shape of apices of acrosome and nucleus; shape of base of head; symmetry of acrosome and head; length of acrosome as compared with nucleus; location of posterior edge of acrosome; placement of the attachment of the neck and midpiece to head; relative amount of acrosome anterior to nucleus; thickness, relative length, and degree

TABLE 1.—*Calculated ratios comparing the dimensions of the spermatozoa of 35 species of phyllostomatid bats.*

Species	Midpiece length/ head length	Head length/ head width	Head length/ acrosome length	Midpiece length/ acrosome length	Nuclear length/ head width	Midpiece length/ nuclear length	Head length/ nuclear length	Nuclear length/ acrosome length
Micronycteris megalotis	1.91	1.53	1.78	3.41	1.19	2.45	1.28	1.40
Micronycteris nicefori	2.01	1.18	1.71	3.44	1.11	2.13	1.06	1.62
Macrotus waterhousii	2.00	1.29	1.50	3.00	0.82	3.12	1.56	0.96
Tonatia bidens	2.44	1.56			1.25	3.05	1.25	
Mimon crenulatum	1.66	1.38	1.62	2.69	1.03	2.23	1.35	1.20
Phyllostomus discolor	1.73	1.46	1.67	2.89	1.12	2.25	1.30	1.28
Glossophaga soricina	2.12	1.19	1.19	2.53	0.90	2.83	1.33	0.90
Anoura geoffroyi	1.44	1.28	1.82	2.62	0.98	1.89	1.31	1.39
Choeronycteris mexicana								
Carollia brevicauda	1.51	1.46	1.48	2.24	0.97	2.27	1.50	0.99
Carollia perspicillata	1.63	1.56	1.59	2.60	1.07	2.39	1.46	1.09
Sturnira lilium	1.92	1.65	1.71	3.27	1.17	2.71	1.41	1.21
Sturnira tildae	1.81	1.59	1.73	3.13	1.27	2.26	1.25	1.38
Uroderma bilobatum	1.86	1.48	2.30	4.29	1.08	2.56	1.37	1.68
Vampyrops helleri	1.72	1.62	1.60	2.76	1.24	2.26	1.31	1.22
Vampyrodes caraccioli	1.69	1.64	1.76	2.98	1.25	2.21	1.31	1.35
Chiroderma improvisum								
Chiroderma trinitatum	1.82	1.39	1.62	2.95	1.18	2.23	1.23	1.32
Mesophylla macconnelli	1.65	1.36	1.63	2.69	1.03	2.19	1.32	1.23
Artibeus cinereus	1.94	1.29	1.42	2.75	1.07	2.35	1.21	1.17
Artibeus toltecus	1.75	1.57	1.66	2.91	1.23	2.23	1.28	1.30
Artibeus jamaicensis	1.94	1.36	1.64	3.17	1.09	2.42	1.25	1.31
Artibeus lituratus	1.73	1.48	1.45	2.51	1.11	2.30	1.33	1.09
Ardops nichollsi	2.09	1.35	1.76	3.67	1.03	2.76	1.32	1.33
Phillops haitiensis	1.79	1.45	1.73	3.11	1.11	2.34	1.30	1.33
Ariteus flavescens	1.97	1.41	1.63	3.21	1.04	2.73	1.36	1.04
Stenoderma rufum	1.86	1.43	1.57	2.91	1.08	2.46	1.32	1.08
Centurio senex	1.72	1.22	1.66	2.85	1.01	2.07	1.21	1.37
Brachyphylla cavernarum								
Erophylla bombifrons	1.44	1.42	1.49	2.15	1.09	1.88	1.30	1.14
Erophylla sezekorni	1.59	1.59	1.70	2.80	1.15	2.19	1.38	1.23
Phyllonycteris poeyi	1.34	1.40	1.55	2.09	1.03	1.82	1.35	1.15
Desmodus rotundus	2.47	1.74	1.58	3.91	1.42	3.03	1.23	1.29
Diaemus youngii	2.23	1.80	1.75	3.91	1.45	2.78	1.23	1.41
Diphylla ecaudata	2.10	1.32	1.58	3.32	2.09	1.00	1.58	

of tapering of midpiece. Table 1 gives statistical ratios based on measurements taken. Figs. 1-5 compare the total head length, nuclear length, and midpiece length of the species studied. Voucher specimens are deposited in The Museum of Texas Tech University (TTU) and Carnegie Museum of Natural History (CM). Most specimens were collected under a grant from the National Science Foundation (GB-41105) to Robert J. Baker and Hugh H. Genoways.

ACCOUNTS OF SPECIES

SUBFAMILY PHYLLOSTOMATINAE

Micronycteris megalotis (Gray, 1842)

Description (Fig. 1A).—Head oval, rear portion tapered slightly but considerably more than that of *Macrotus*; bilaterally symmetrical; apex narrowly rounded; acrosome no wider than nucleus; base slightly convex; nuclear portion

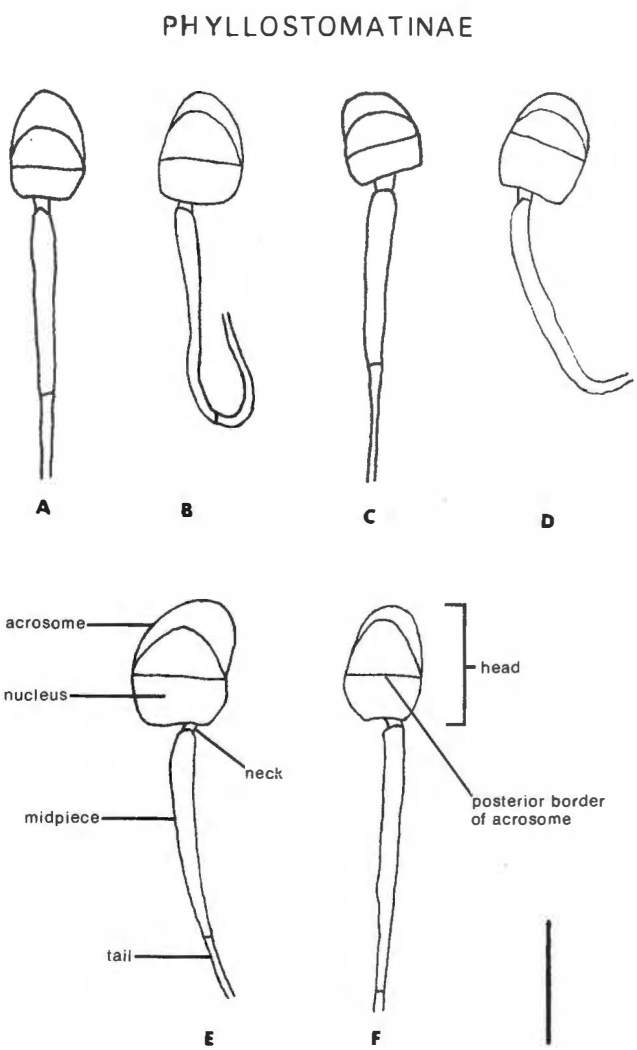


FIG. 1.—Sperm of six phyllostomatine bats. A) *Micronycteris megalotis*; B) *Micronycteris nicefori*; C) *Macrotus waterhousii*; D) *Tonatia bidens*; E) *Mimon crenulatum*; F) *Phyllostomus discolor*. Scale equals 5 microns.

has blunt apex, more rounded than that of acrosome; acrosome longer than nucleus and constituting a substantial portion of the head length; head length 4.46(4.19-4.65) ±0.138, 4.87(4.56-5.12) ±0.237, acrosome length 3.00(2.79-3.07) ±0.102, 2.73(2.42-2.98) ±0.188, nuclear length 3.65(3.44-3.91) ±0.160, 3.81(3.17-3.19) ±0.072, head width 2.92(2.79-3.07) ±0.088, 3.19(3.07-3.35) ±0.091. Neck short, joins head midway at base of head. Midpiece extremely thin, relatively long, length 9.45(9.11-9.95) ±0.286, 9.32(8.84-9.58) ±0.251.

Remarks.—Morphology of the sperm head of *Micronycteris megalotis* is substantially different from that of *Macrotus waterhousii*, with the sperm head of *M. megalotis* considerably narrower than that of *M. waterhousii*.

Specimens examined.—TRINIDAD: Blanchisseuse, St. George, 1 (TTU 23754); Maracas, St. George, 1 (TTU 23759).

Micronycteris nicefori Sanborn, 1949

Description (Fig. 1B).—Head wider than that of *M. megalotis*, more rounded; bilaterally symmetrical; base flattened, not convex; acrosome substantially shorter than nucleus, in sharp contrast to condition found in *M. megalotis*; nuclear portion extremely rounded; apex of acrosome and nucleus similar in shape; head length, 4.00(3.72-4.37) ±0.299, acrosome length 2.34(2.23-2.60) ±0.145, nuclear length 3.78(3.62-3.91) ±0.092, head width 3.40(2.98-3.72) ±0.177. Neck short, not joining head midway along base. Midpiece extremely narrow, difficult to distinguish from tail; length 8.04(7.91-8.18) ±0.115.

Remarks.—Morphology of the spermatozoa of *M. nicefori* is similar to that of *M. megalotis* but does differ in several ways. Most noticeably, the acrosome is shorter than the nucleus in *M. nicefori* but longer than the nucleus in *M. megalotis*. *M. nicefori* also has a wider sperm head than *megalotis* and a flattened rather than convex base of head.

Specimen examined.—TRINIDAD: 2 mi. N, 2 mi. E Valencia, St. Andrew, 1 (TTU 23768).

Macrotus waterhousii Gray, 1843

Description (Fig. 1C).—Head not rounded, triangular; bilaterally symmetrical; base strongly convex; apex of acrosome broadly rounded, bullet-shaped; posterior border of acrosome sharply defined; acrosome no wider than nucleus and similar in length; nuclear portion small, with extremely blunt apex, and more rounded than apex of acrosome; head length 3.73(3.53-4.00) ±0.150, 3.67(3.44-3.81) ±0.100, nuclear length 2.39(2.32-2.70) ±0.132, 2.49(2.32-2.79) ±0.156, acrosome length 2.49(2.32-2.70) ±0.178, 2.23(2.14-2.32) ±0.068, head width 2.90(2.70-3.16) ±0.156, 2.95(2.79-3.07) ±0.112. Neck short, joining head midway at base of head. Midpiece extremely short; demarcation with tail distinctive; length 7.46(7.34-7.63) ±0.112, 7.66(7.16-7.91) ±0.183.

Remarks.—The form of the sperm head in this species is unique with no comparable conformation found in any other genus. Also of interest is the extremely short midpiece.

Specimens examined.—JAMAICA: Green Grotto, 2 mi. E Discovery Bay, St. Ann Parish, 3 (TTU 21501-02, 21504).

Tonatia bidens (Spix, 1823)

Description (Fig. 1D).—Head rounded to broadly oval; acrosome can contribute markedly to total length of head; acrosome bilaterally symmetrical, rear terminus only slightly beyond apex of nucleus; apex of acrosome broadly rounded but less so than nucleus; acrosome considerably shorter than nucleus and never wider than nucleus; nucleus rounded, with extremely blunt apex; base of head concave; head length approximately 4.64(4.46-4.84), nuclear length 3.72(3.58-4.00), head width 2.98(2.88-3.07). Neck relatively long and slightly off center of

point of attachment to head. Midpiece relatively long, anterior portion broad, tapering sharply posteriorly; length 11.36(9.49-11.25).

Remarks.—Among the phyllostomatines, the head of the spermatozoon of *T. bidens* is most similar in general shape (acrosome and nucleus) to *Micronycteris nicefori* and *Phyllostomus discolor.*

Specimen examined.—TRINIDAD: 2 mi. N, 2 mi. E Valencia, St. Andrew, 1 (TTU 23794).

Mimon crenulatum (É. Geoffroy St.-Hilaire, 1810)

Description (Fig. 1E).—Head bluntly rounded; acrosome keel-shaped, extremely asymmetrical; acrosome slightly broader, at widest point, than nucleus; acrosome terminates posteriorly about midway along length of nucleus, adding about 25 per cent to length of head; nucleus slightly longer than acrosome; nuclear portion extremely rounded, apex narrowly rounded terminating in broad point; base of nucleus rounded but slightly concave; head length 5.42(5.12-5.86) ±0.194, acrosome length 3.34(3.16-3.53) ±0.134; nuclear length 4.02(3.91-4.09) ±0.068, head width 3.92(3.72-4.09) ±0.119. Neck short with attachment to head slightly off center. Midpiece of moderate breadth anteriorly; moderate length; length 8.98(8.56-9.39) ±0.213.

Remarks.—The sperm head of *Mimon* differs in general morphology from both *Macrotus* and *Micronycteris* and is exceptionally large. The asymmetry of the acrosome is in striking contrast to the generally symmetrical acrosome of other phyllostomatines.

Specimen examined.—TRINIDAD: 2 mi. E San Rafael, St. George, 1 (TTU 23770).

Phyllostomus discolor (Wagner, 1843)

Description (Fig. 1F).—Head narrowly rounded; acrosome only slightly asymmetrical, shorter than nucleus, and terminating posteriorly about half-way along length of nucleus; acrosome slightly wider, at widest point, than is nucleus; nucleus triangular in shape with broad base, apex narrowly rounded, pointed; base of nucleus slightly concave; head length 5.19(4.93-5.58) ±0.239, acrosome length 3.11(2.79-3.44) ±0.240, nuclear length 3.99(3.53-4.37) ±0.230, head width 3.55(3.26-3.72) ±0.159. Neck extremely short, junction with head considerably off center; joins head on same side as most distinct portions of the apex of the acrosome. Midpiece of moderate length, thin, tapering gradually to distinctive junction with tail; length 8.98(8.56-9.58) ±0.316.

Remarks.—The head of the spermatozoon of *Phyllostomus discolor* has morphological similarities with both *Mimon* and *Micronycteris* but is identical to neither; the head is most similar to that of *M. nicefori* except that the acrosome is slightly asymmetrical. The nucleus is narrower than in *Mimon* with broad, triangular base as in *M. nicefori.*

Previous study.—Two specimens from Nicaragua (Forman, 1968:905).

Specimen examined.—TRINIDAD: Las Cuevas, St. George, 1 (TTU 23777).

Subfamily Glossophaginae

Glossophaga soricina (Pallas, 1766)

Description (Fig. 2A).—Head extremely small, short, and quite rounded; base of head broad giving a shovellike shape; base has well-developed concavity; apex of acrosome nearly symmetrical, being somewhat more narrowly rounded than the broadly rounded apex of nucleus; acrosome nearly as long as nucleus; posterior limit of acrosome considerably behind midpoint of nucleus; only a small portion of acrosome occurs anterior to nucleus; acrosome never wider than nucleus; head length 3.80(3.53-4.00) ±0.162, acrosome length 3.19(3.09-3.26) ±0.202, nuclear length 2.86(2.70-3.26) ±0.268, head width 3.19(3.07-3.26) ±0.091. Neck moderate in length, junction with head only slightly off center. Midpiece extremely broad, tapering gradually posteriorly; junction with tail quite distinctive; length 8.08(7.63-8.46) ±0.316.

Remarks.—Sperm morphology in this species is notably similar to that of *Anoura*; heads are extremely small compared to those of most other species.

Previous study.—Four specimens from Chiapas (Forman, 1968).

Specimens examined.—Veracruz: 4 km. W, 5 km. S Sontecomapa, 1 (TTU 28900); Yucatan: Merida, 1.

Anoura cultrata Handley, 1960

Description (after Forman, 1968).—Head rounded, its breadth approximately seven-eighths of length, broadest in basal region, bluntly rounded at apex; base slightly concave (the acrosome was not examined in the previous study). Neck not observed. Midpiece short when compared to length of tail; width uniform throughout.

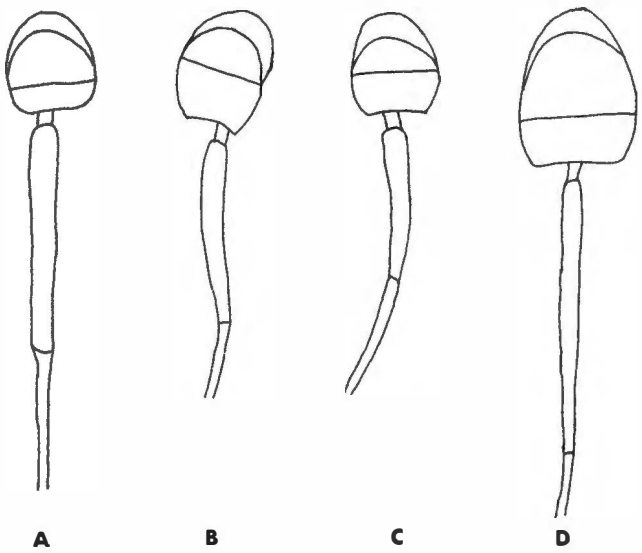
Remarks.—The spermatozoa of *Anoura cultrata* are distinct from those of *Glossophaga soricina.* The head is broader in *A. cultrata* than in *G. soricina,* the ratio of length to breadth being 1.15 as opposed to 1.28 in *G. soricina* (Forman, 1968).

Previous study.—Two specimens from Panamá (Forman, 1968).

Anoura geoffroyi Gray, 1838

Description (Fig. 2B, 2C).—Head quite rounded; base slightly convex; acrosome slightly asymmetrical, with apex occasionally somewhat pointed; acrosome shorter than nucleus and contributing markedly to total head length; acrosome only slightly broader than nucleus at widest point; apices of acrosome and nucleus usually broadly rounded, that of the nucleus particularly so; head length 3.92(3.53-4.09) ±0.184, 4.05(3.91-4.37) ±0.151, acrosome length 2.23 (2.05-2.32) ±0.09, 2.23(2.05-2.42) ±0.116, nuclear length 3.08(2.79-3.44) ± 0.216, 3.09(2.88-3.35) ±0.165, head width 3.14(2.88-3.26) ±0.128, 3.16(2.98-3.35) ±0.104. Neck of moderate length, junction with head slightly off center; attachment to head on same side as longest portion of acrosome. Midpiece ex-

GLOSSOPHAGINAE



CAROLLIINAE

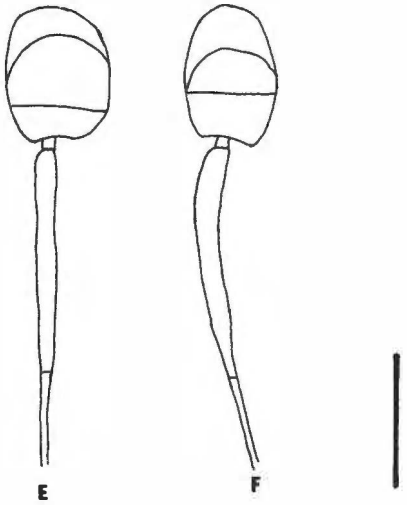


FIG. 2.—Sperm of some glossophagine and carolliine bats. A) *Glossophaga soricina*; B-C) *Anoura geoffroyi*; D) *Choeronycteris mexicana*; E) *Carollia brevicauda*; F) *Carollia perspicillata*. Scale equals 5 microns.

tremely wide at anterior end, tapering abruptly towards posterior end; junction with tail distinctive; length 5.57(4.93-6.14) ±0.358, 5.84(5.58-6.05) ±0.149.

Remarks.—The spermatazoon of this species is quite similar to that of *Glossophaga soricina*, the only species of the genus examined.

Specimens examined.—HIDALGO: 13 km. WSW Tehuetlan, 2 (TTU 15477-78). TRINIDAD: 2 mi. N, 2 mi. E Valencia, St. Andrew, 1 (TTU 23802); Las Cuevas, St. George, 1 (TTU 23798).

Choeronycteris mexicana Tschudi, 1844

Description (Fig. 2D).—Head oval, somewhat triangular or shovel shaped; extremely large (in length and breadth); acrosome symmetrical, relatively long, posterior terminus well posterior to midpoint of head, and apex broadly rounded; acrosome difficult to distinguish from nucleus, blending in at the sides of the head; acrosome adds only slightly to total length of head; nucleus extremely rounded, apex rounded; base concave, corners rounded; head length 5.09(4.74-5.58) ± 0.259, acrosome length 3.37(3.26-3.44) ±0.089, nuclear length 4.26(4.00-4.46) ±0.158, head width 3.99(3.62-4.19) ±0.145. Neck short, attached to base of head nearly at its midpoint. Midpiece narrow, moderate length, tapering only slightly posteriorly; length 8.59(8.37-9.02) ±0.182.

Remarks.—Spermatozoa from *Choeronycteris mexicana* are easily distinguishable by their larger size from those of other glossophagines. Glossophagines examined to date appear relatively consistent and uniform in sperm morphology.

Specimen examined.—TLAXCALA: 5 km. E, 3 km. N Tlaxcala, 1 (TTU 25347).

SUBFAMILY CAROLLIINAE

Carollia castanea H. Allen, 1890

Description (after Forman, 1968:909).—Head rounded, somewhat heart-shaped; apex broadly rounded; base concave and symmetrical, narrowing laterally at point of junction with neck (acrosome not observed in this study). Neck short but distinct; junction with head near center of base. Midpiece short, anterior end at distinct angle to base of head, tapering only slightly posteriorly.

Remarks.—A spiraled midpiece was observed in this species, confirming the existence of such a structure in at least one member of the Phyllostomatidae (Forman, 1968).

Previous study.—Three specimens from Panamá (Forman, 1968).

Carollia brevicauda (Schinz, 1821)

Description (Fig. 2E).—Head rounded; acrosome long, posterior border located from midway to two-thirds back along the length of the nucleus; acrosome slightly asymmetrical and terminating in broadly rounded apex; acrosome extremely large and longer than nucleus, possibly somewhat wider than nucleus at its widest point; nucleus rounded with broadly rounded apex; base of head slightly concave;

head length 5.22(4.84-5.49) ±0.180, acrosome length 3.53(3.26-3.81) ±0.167, nuclear length 3.48(3.26-3.72) ±0.118, head width 3.58(3.44-3.81) ±0.135. Neck of moderate length; attachment to head off center, with attachment on same side as longest portion of acrosome. Midpiece narrow, moderate length, tapering gradually to posterior; junction with tail distinctive; length 7.90(7.53-8.28) ± 0.208.

Remarks.—Overall shape of the sperm head in *C. brevicauda* is more rounded, wider, and generally greater in size than that of *C. perspicillata. C. brevicauda* shares several characteristics with *C. perspicillata*, including an acrosome that is often longer than the nucleus and a nucleus that is rounded with a broadly rounded apex.

Specimen examined.—VERACRUZ: 4 km. W, 5 km. S Sontecomapa, 1 (TTU 28901).

Carollia perspicillata (Linnaeus, 1758)

Description (Fig. 2F).—Head relatively narrow (because significant amount of acrosome is anterior to apex of nucleus; portion of acrosome anterior to apex of nucleus may exceed 30 per cent of total length of head); acrosome slightly asymmetrical, as long as or slightly longer than the nucleus in many cases; acrosome terminates posteriorly about 40 to 50 per cent of way back along the length of the nucleus; acrosome only slightly wider than nucleus at its widest point; nucleus rounded, base concave, and apex broadly rounded; head length 5.23 (5.02-5.39) ±0.103, acrosome length, 3.29(3.07-3.53) ±0.148, nuclear length 3.58(3.26-3.81) ±0.201, head width 3.35(3.16-3.53) ±0.131. Neck short, attached to base of head slightly off center. Midpiece of moderate length, gradually tapering; junction with tail distinctive; length 8.55(8.18-9.11) ±0.281.

Remarks.—Morphology of the spermatozoon of *Carollia perspicillata* resembles that of *Micronycteris megalotis*, but the head differs in several respects from that of *C. brevicauda.* Large sperm heads might be characteristic of the genus *Carollia.*

Specimens examined.—QUINTANA ROO: 14 km. NE Playa del Carmen, 1 (TTU 18421); TRINIDAD: Blanchisseuse, St. George, 1 (TTU 23859).

SUBFAMILY STENODERMINAE

Sturnira lilium (É. Geoffroy St.-Hilaire, 1810)

Description (Fig. 3A).—Head large, relatively narrow oval; acrosome symmetrical, shorter than nucleus; acrosome large, terminating anteriorly in moderately rounded apex and posteriorly about halfway along length of nucleus; distinctive portion of acrosome lies anterior to nucleus; acrosome may be narrower at base than nucleus at its widest point or they may be of equal breadth; nucleus oval, apex more broadly rounded than that of the acrosome; base extremely narrow (relative to greatest breadth of nucleus) and concave; head length 5.15(4.93-5.49) ±0.179, acrosome length 3.02(2.70-3.16) ±0.150, nuclear length 3.64 (3.44-4.00) ±0.158; head width 3.12(2.98-3.26) ±0.085. Neck moderate in

length, attached to head slightly off center. Midpiece long, stains dark; broad at anterior end, sharply tapering posteriorly; junction with tail distinctive; length 9.87(9.39-10.14) ±0.224.

Remarks.—The overall similarity of sperm from *Sturnira lilium* to that found in other stenodermines supports the inclusion of this genus within the subfamily.

Previous study.—Two specimens from Chiapas (Forman, 1968).

Specimens examined.—TRINIDAD: 2 mi. N, 2 mi. E Valencia, St. Andrew, 1 (TTU 23901); Blanchisseuse, St. George, 1 (TTU 23899).

Sturnira tildae de la Torre, 1959

Description (Fig. 3B).—Head similar in structure to *S. lilium* but differs from it in several ways; base of head less concave than that of *S. lilium* and sometimes lacking concavity; apex of acrosome symmetrical, as much as half of the acrosome occurring anterior to nucleus; acrosome covers only a very small portion of the nucleus; nucleus ovoid; head length 4.81(4.56-5.02) ±0.121, 4.82(4.65-4.93) ±0.151, acrosome length 2.78(2.51-3.07) ±0.149, 2.43(2.23-2.70) ±0.177, nuclear length 3.85(3.62-4.37) ±0.186, 3.78(3.44-4.09) ±0.237, head width 3.02(2.88-3.26) ±0.136, 3.00(2.79-3.35) ±0.162. Neck relatively long, attached to middle of base. Midpiece slightly shorter than that of *S. lilium*, extremely narrow, and tapering slightly posteriorly; length 8.71(8.28-9.11) ±0.250, 8.81(8.37-9.02) ±0.293.

Remarks.—Spermatazoa of *Sturnira tildae* differ from those of species in this genus mainly in that base of head is less concave and midpiece shorter. The small acrosome may be unique to *S. tildae*, but that possibility awaits examination of the acrosome of *Sturnira ludovici*. The nucleus is similar in configuration to that of *Artibeus cinereus*.

Specimens examined.—TRINIDAD: 2 mi. N, 2 mi. E Valencia, St. Andrew, 1 (TTU 23907); Blanchisseuse, St. George, 1 (TTU 23904).

Sturnira ludovici Anthony, 1924

Description (after Forman, 1968).—Head much as in *S. lilium*, differing only in proportions; apex blunt; no concavity in base (acrosome not examined). Neck not discernible. Midpiece broad, nonhelical, and long.

Remarks.—The gross morphology of spermatozoa of *Sturnira ludovici* is similar to that of *S. lilium*. However, according to measurements given by Forman (1968), length of sperm head and length of midpiece are greater in *S. ludovici*.

Previous study.—Eight specimens from Panamá (Forman, 1968).

Uroderma bilobatum Peters, 1866

Description (Fig. 3C).—Head similar in overall morphology to that of *Artibeus jamaicensis*; relatively narrow; acrosome symmetrical or slightly asymmetrical, narrowly rounded at apex; acrosome notable in being extremely short terminating posteriorly one-third or less the way along the length of the

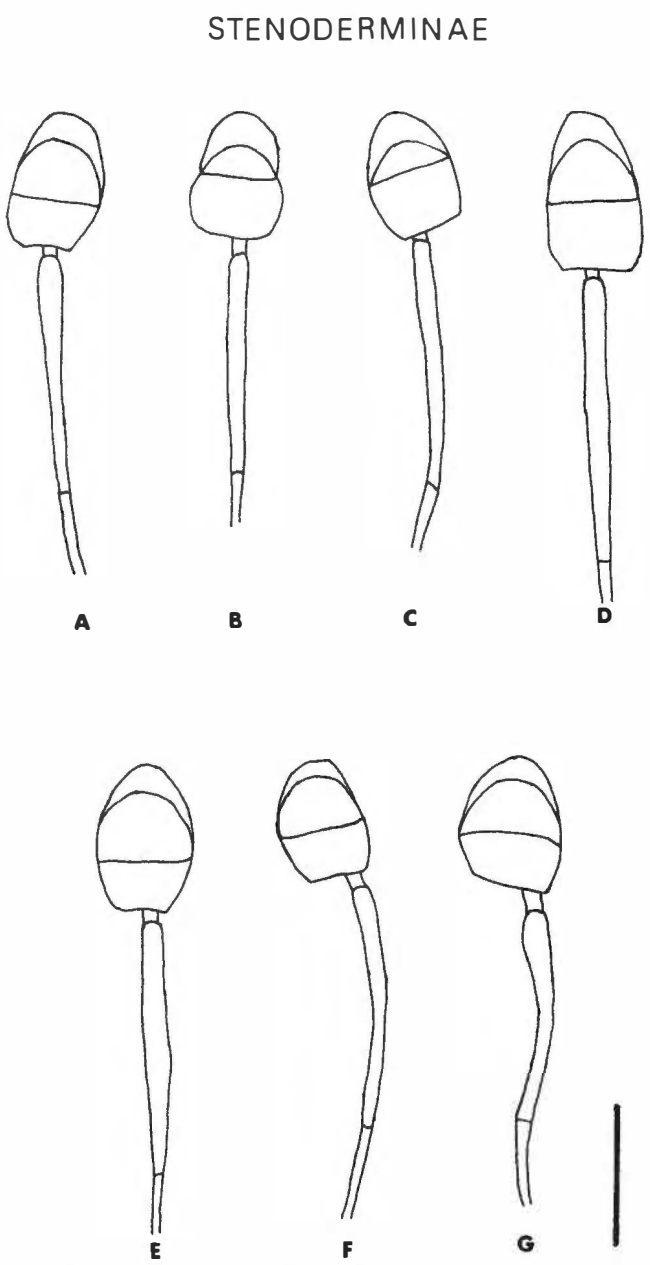


FIG. 3.—Sperm of some stenodermine bats. A) *Sturnira lilium*; B) *Sturnira tildae*; C) *Uroderma bilobatum*; D) *Vampyrops helleri*; E) *Vampyrodes caraccioli*; F) *Chiroderma improvisum*; G) *Chiroderma trinitatum*; H) *Mesophylla macconnelli*. Scale equals 5 microns.

nucleus; approximately half of acrosome visible anterior to nuclear apex; acrosome also appearing to be narrower in width than the nucleus; nucleus ovoid; base of nucleus flattened or slightly concave with pointed corners; head length 4.56 (4.09-4.84) ±0.23, acrosome length 1.98(1.67-2.32) ±0.27, nuclear length 3.32(3.16-3.53) ±0.12, head length 3.08(2.98-3.16) ±0.08. Neck extremely short, junction with head well off center. Midpiece of moderate length; thin but tapering slightly posteriorly; length 8.49(7.91-8.84) ±0.29.

Remarks.—Morphology of the sperm head of *Uroderma* resembles most closely that of *Artibeus*, particularly *A. jamaicensis*. The acrosome of this species is unusually short and covers an extremely small portion of the nucleus. The flattened base of the head is an unusual feature.

Specimen examined.—TRINIDAD: Guayaguayare, Mayaro, 1 (TTU 24046).

Vampyrops helleri Peters, 1867

Description (Fig. 3D).—Head long and narrow, nucleus relatively long compared with other species; acrosome narrow and asymmetrical (terminus of apex on same side of head as the attachment of the midpiece to the head), appears to be slightly narrower than nucleus; apex of acrosome narrowly rounded and may be somewhat pointed; posterior limit of acrosome terminates midway along the length of the nucleus; a substantial portion of acrosome occurs anterior to the apex of the nucleus; nucleus strongly ovoid with rounded base that is strongly concave; apex of nucleus rounded; head length 5.54(5.39-5.77) ±0.14, acrosome length 3.46(3.16-3.72) ±0.26, nuclear length 4.22(4.09-4.37) ±0.11, head width 3.41(3.26-3.53) ±0.14. Neck short, junction with head only slightly off center. Midpiece long, extremely thin; junction with tail distinctive; length 9.54(8.74-10.14) ±0.41.

Remarks.—Structure and size of the sperm head within this species is unique among those studied because it is unusually long; it closely resembles that of *Artibeus jamaicensis*.

Specimen examined.—TRINIDAD: Guayaguayare, Mayaro, 1 (TTU 24063).

Vampyrodes caraccioli (Thomas, 1889)

Description (Fig. 3E).—Head most complete oval of any phyllostomatid studied with base of head extremely narrow; head egg-shaped, long, relatively narrow, similar in size but slightly smaller than that of *Vampyrops*; nucleus and acrosome usually with a symmetrical apex at anterior end, apices narrowly rounded or pointed, acrosomal apex especially pointed; acrosome usually symmetrical and equal in width to nucleus, in some cases nucleus appears to be only slightly longer than accompanying acrosome; posterior limit of acrosome sometimes behind midpoint of nucleus; substantial portion of acrosome occurs anterior to apex of nucleus; base of head extremely narrow and flattened to concave, with pointed corners; head length 5.25(4.84-5.49) ±0.202, acrosome length 2.98(2.79-3.16) ±0.13, nuclear length 4.02(3.72-4.28) ±0.16, head width

3.21(3.07-3.44) ±0.13. Neck extremely short, attachment to base of head only slightly off center or is centered. Midpiece of moderate length and breadth; length 8.89(8.28-9.21) ±0.39.

Remarks.—Head morphology is unique in being long and having an unusually narrow apex and base. Sperm resembles somewhat that of *Vampyrops*, but unlike *Vampyrops*, *Vampyrodes* has a symmetrical acrosome and an extremely narrow and flattened head base.

Specimen examined.—TRINIDAD: Blanchisseuse, St. George, 1 (TTU 24060).

Chiroderma improvisum Baker and Genoways, 1976

Description (Fig. 3F).—Head similar to that of *C. trinitatum*, but slightly less rounded; acrosome sometimes appears to be asymmetrical, short, and with a small portion extending anterior to nucleus; posterior limit of acrosome lies in front of midpoint of nucleus and appears less arched than in *C. trinitatum*; nucleus ovoid, apex considerably more rounded than the more pointed apex of the acrosome; base of head asymmetrical, but less so than in *C. trinitatum*; base slightly concave; head length 4.74(4.37-5.30) ±0.28, acrosome length 2.65(2.60-2.79) ±0.08, nuclear length 3.96(3.81-4.19) ±0.14, head width 3.17(2.88-3.26) ±0.18. Neck relatively long, junction with head well off center as in *C. trinitatum*. Midpiece of moderate breadth, tapering posteriorly; length 8.64(7.53-9.95) ±0.71.

Remarks.—Although similar to that of *Chiroderma trinitatum*, the sperm head in *C. improvisum* is slightly less rounded, its base less asymmetrical, and it possesses a shorter acrosome. The spermatozoa of species of *Chiroderma* can be distinguised easily from other stenodermines.

Specimen examined.—GUADELOUPE: 2 km. S, 2 km. E Baie-Mahault, Basse-Terre, 1 (TTU 19900).

Chiroderma trinitatum Goodwin, 1958

Description (Fig. 3G)—Head morphology generally variable; shape ovoid to rounded; nucleus ovoid with pointed apex; acrosome nearly symmetrical, short, with apex only slightly more rounded than that of nucleus; terminal border of acrosome appears to be slightly arched with apex directed anteriorly; acrosome terminates posteriorly at midpoint of nucleus and extends anteriorly only very slightly beyond apex of nucleus; base of head flattened or very slightly concave and is unusual in being asymmetrical with the greatest posterior extension occurring on the side of the head that is in contact with the neck; base of head narrower than girth of head, with corners pointed; head length 4.87(4.56-5.39) ±0.26, acrosome length 3.00(2.70-3.35) ±0.23, nuclear length 3.97(3.62-4.28) ±0.25, head width 3.37(3.07-3.62) ±0.175. Neck relatively long, junction with head well off center and nearly to the edge of base of head. Midpiece thin, tapering gradually posteriorly and short relative to length of head; length 8.84 (8.56-9.11) ±0.21.

Remarks.—The morphology of the spermatozoa head in this species, although variable, is distinctly different from that of other stenodermines. Only a very small

portion of the acrosome extends anterior to nucleus, the base of the head is asymmetrical, and the point of midpiece attachment is substantially off center.

Specimen examined.—TRINIDAD: 2 mi. N, 2 mi. E Valencia, St. Andrew, 1 (TTU 24026).

Mesophylla macconnelli Thomas, 1901

Description (Fig. 3H).—Head relatively long and narrow, not large; acrosome with pointed asymmetrical apex, tip of apex on same side of head as attachment of midpiece; acrosome short and an extremely small portion of it occurs anterior to the apex of the nucleus; posterior limit of acrosome slightly anterior to midpoint of nucleus; acrosome considerably shorter than the nucleus (often only slightly more than half its length) and the same breadth as the nucleus at its posterior limit; nucleus ovoid, apex symmetrical; base of head flattened with slight concavity; base of head narrower than its girth, asymmetrical with corner nearest the midpiece being more pointed than the other; head length 4.71(4.56-5.02) ±0.14, 4.68(4.28-4.93) ±0.19, acrosome length 2.73(2.51-2.88) ±0.12, 2.64(2.51-2.88) ±0.13, nuclear length 4.01(3.62-4.19) ±0.15, 3.99(3.81-4.37) ±0.22, head width 3.13(2.98-3.34) ±0.12, 3.25(3.07-3.44) ±0.10. Neck relatively long, junction with head well off center and near the pointed corner of the head base. Midpiece short, broad anteriorly, tapering abruptly posteriorly; junction with tail indistinct; length 7.61(7.25-7.92) ±0.23, 7.66(7.25-8.18) ±0.27.

Remarks.—Most notable among the characteristics of sperm from *Mesophylla* is the minute amount of acrosome anterior to the nuclear apex and the unusual asymmetry of the base of the head. The head is somewhat similar to that of *Phyllostomus discolor*, but the base and apex of the nucleus are dissimilar. An extremely short midpiece distinguishes *M. macconnelli* from other stenodermines, with the exception of *Centurio*.

Specimen examined.—TRINIDAD: Guayaguayare, Mayaro, 2 (TTU 24039, 24044).

Artibeus cinereus (Gervais, 1855)

Description (Fig. 4A).—Head broad in midsection, tapering distinctively both anteriorly and posteriorly; acrosome extremely pointed, nearly cone-shaped, slightly shorter than nucleus, and terminating posteriorly about midway along nucleus; nucleus rounded; base of head slightly convex or often lacking concavity, base of head notably rounded at the corners; head length 4.59(4.28-4.84) ±0.495, acrosome length 2.93(2.51-3.26) ±0.339, nuclear length 3.62(3.35-3.91) ±0.104, head width 3.15(2.98-3.26) ±0.084. Neck short, junction with head very slightly off center. Midpiece broad anteriorly, tapering gradually posteriorly; length 8.74 (8.37-9.02) ±0.342.

Remarks.—Sperm morphology in this species is very similar to that of *Artibeus jamaicensis, Ardops nichollsi*, and *Ariteus flavescens*. The most unusual feature is the extremely pointed, exceptionally tapered apex to the symmetrical acrosome.

Specimens examined.—TRINIDAD: Guayaguayare, Mayaro, 1 (TTU 23924); 2 mi. E San Rafael, St. George, 1 (TTU 23936).

STENODERMINAE

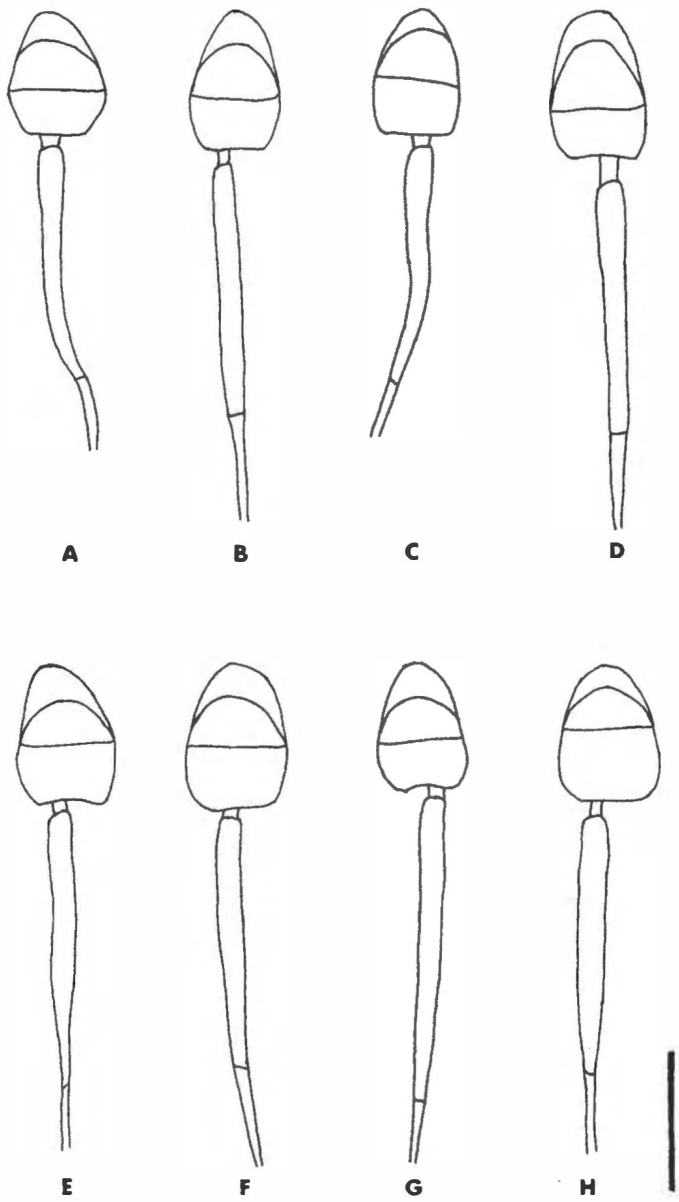


FIG. 4.—Sperm of some stenodermine bats. A) *Artibeus cinereus*; B) *Artibeus toltecus*; C) *Artibeus jamaicensis*; D) *Artibeus lituratus*; E) *Ardops nichollsi*; F) *Phyllops haitiensis*; G) *Ariteus flavescens*; H) *Stenoderma rufum*; I) *Centurio senex*. Scale equals 5 microns.

Artibeus toltecus (Saussure, 1860)

Description (Fig. 4B).—Head quite long, appearing relatively narrow, similar to other species of *Artibeus*; nucleus ovoid with relatively narrow apex and base; acrosome symmetrical and pointed at apex; posterior limit of acrosome extending to midway along length of nucleus; head length 4.96(4.84-5.12) ±0.10, acrosome length 2.99(2.79-3.07) ±0.09, nuclear length 3.88(3.62-4.19) ±0.20, head width 3.16(2.98-3.35) ±0.12. Neck short, junction with head well off center. Midpiece short, compared to length of head, and narrow; tapering posteriorly; length 8.69(8.37-9.02) ±0.21.

Remarks.—General shape of head similar to *Ardops, Ariteus*, and other species of *Artibeus*, particularly *A. lituratus*; however, the head in general is less rounded than in other species. Heads of spermatozoa from *A. toltecus* are longer than in other stenodermines.

Specimen examined.—VERACRUZ: 4 km. W, 5 km. S Sontecomapa, 1 (TTU 28902).

Artibeus jamaicensis Leach, 1821

Description (Fig. 4C).—Head similar in morphology to that of *Ardops* and *Ariteus*; acrosome usually symmetrical, but, if asymmetrical, only slightly so; apex of acrosome narrowly rounded to nearly pointed; portion of acrosome anterior to nucleus always less than in *Ariteus* and *Ardops*; nucleus narrowly rounded at apex; base of nucleus broad and slightly concave; head length 4.48 (4.28-4.65) ±0.119, acrosome length 2.74(2.51-2.98) ±0.148, nuclear length 3.59(3.35-4.00) ±0.159, head width 3.30(3.16-3.44) ±0.089. Neck short, junction with head off center. Midpiece nearly twice head length, thick anteriorly, and tapering posteriorly; length 8.69(8.09-9.21) ±0.316.

Remarks.—Morphology of the heads of spermatozoa from *A. jamaicensis* is quite similar to that of both *Ariteus* and *Ardops*, but the portion of the acrosome anterior to the nucleus was always less in *A. jamaicensis*. The acrosome has less symmetry than other species of *Artibeus* that have been examined.

Previous study.—One specimen from Dominica and one specimen from Nayarit (Forman, 1968).

Specimen examined.—HAITI: 1 km. E Lebrun, Dept. du Sud, 1 (TTU 22649).

Artibeus lituratus (Olfers, 1818)

Description (Fig. 4D).—Head similar to other *Artibeus*; acrosome relatively larger (as compared with nucleus) than that of other species within the genus; acrosome only slightly shorter than the nucleus, with somewhat narrowly rounded, symmetrical apex; acrosome distinctly triangular, its posterior limit consistently well behind the midpoint of the nucleus; acrosome sometimes slightly narrower than nucleus, otherwise equivalent in width at its posterior limit; distinctive portion of acrosome found anterior to nuclear apex; apex of nucleus rounded but rarely as narrowly as acrosome; base of head asymmetrical with corner nearest neck slightly more posterior than the rounded corner on the other side of the base;

base slightly concave; head length 4.77(4.46-5.21) ±0.229, acrosome length 3.30(3.16-3.53) ±0.132, nuclear length 3.59(3.35-3.72) ±0.103, head width 3.23(3.07-3.35) ±0.140. Neck relatively long, junction with head off center. Midpiece length similar to other species of *Artibeus*; tapering gradually posteriorly; junction with tail quite distinctive; length 8.27(7.91-8.46) ±0.158.

Remarks.—Head morphology of sperm of *A. lituratus* is similar to that of other species of *Artibeus* but is most like *A. toltecus, A. jamaicensis,* and *Vampyrops helleri.*

Previous study.—Two specimens from Chiapas (Forman, 1968).

Specimen examined.—TRINIDAD: Guayaguayare, Mayaro, 1 (TTU 24010).

Ardops nichollsi (Thomas, 1891)

Description (Fig. 4E).—Head bullet shaped with pointed apex; acrosome asymmetrical (but sometimes nearly symmetrical); apex pointed or very narrowly rounded; a moderate portion of acrosome extends forward beyond nucleus; some acrosomes narrower than nucleus; acrosome shorter than nucleus, terminating posteriorly at a point slightly anterior to midpoint of nucleus; nucleus extremely rounded at apex; base broad and deeply concave; head length 4.25(4.00-4.65) ±0.150, 4.31(3.81-4.56) ±0.262, acrosome length 2.42(2.32-2.60) ±0.132, 2.58(2.42-2.70) ±0.117, nuclear length 3.22(3.07-3.44) ±0.125, 3.37(3.16-3.53) ±0.115, head width 3.14(2.88-3.44) ±0.260, 3.03(2.88-3.16) ±0.096. Neck short, junction with head off center. Midpiece of moderate length, thin, gradually tapering posteriorly; junction with tail not distinctive; length 8.88(8.74-9.30) ±0.192, 8.54(8.09-9.02) ±0.277.

Remarks.—The symmetry of the acrosome appears to be variable in this species. In some spermatozoa, acrosomes are asymmetrical, but in others, nearly symmetrical. Spermatozoa are similar to those of *Ariteus* and *Artibeus.*

Specimens examined.—GUADELOUPE: 1 km. S Basse-Terre, Basse-Terre, 1 (TTU 20816); 1 km. N, 1 km. W St. François, Grande-Terre, 1 (TTU 20847).

Phyllops haitiensis (J. A. Allen, 1908)

Description (Fig. 4F).—Head usually somewhat triangular in shape; acrosome only slightly asymmetrical; posterior terminus of acrosome at midpoint of nucleus; substantial portion of acrosome occurring anterior to the apex of the nucleus; acrosome shorter than nucleus with similar morphology and placement (orientation) on the nucleus as *Artibeus, Ardops,* and *Ariteus*; nucleus rounded with broadly rounded apex; base of nucleus with rounded corners and a slight concavity or no concavity in center of basal border; head length 4.90(4.28-5.12) ±0.23, 4.82(4.65-5.12) ±0.13, acrosome length 2.80(2.51-3.07) ±0.16, 2.78(2.60-2.98) ±0.14, nuclear length 3.76(3.62-3.91) ±0.20, 3.70(3.53-3.91) ±0.11, head width 3.57(3.35-3.72) ±0.13, 3.32(3.26-3.44) ±0.06. Neck extremely short, junction with head only slightly off center. Midpiece of moderate length and breadth, tapering only slightly posteriorly; junction with tail distinctive; midpiece length 8.74(8.37-9.30) ±0.31, 8.64(8.37-9.11) ±0.23.

Remarks.—The morphology of the sperm head of *Phyllops* is similar to that of *Artibeus, Ariteus,* and *Ardops.* Nuclear morphology is most like that of *Artibeus cinereus,* but the base of the nucleus is less concave than in most species of *Artibeus.*

Specimens examined.—HAITI: 2 km. N, 2 km. E Lebrun, Dept. du Sud, 1 (TTU 22672); 1 km. S, 1 km. E Legrun, Dept. du Sud, 1 (TTU 22697); 4 km. S Lebrun, Dept. du Sud, 1 (TTU 22733).

Ariteus flavescens (Gray, 1831)

Description (Fig. 4G).—Head nearly identical in morphology to that of *Ardops nichollsi*; triangular; acrosome extremely pointed at apex and acrosome can be asymmetrical or symmetrical; acrosome shorter than nucleus; base of head broad and concave; head length 4.60(4.37-4.84) ±0.156, acrosome length 2.83 (2.60-3.16) ±0.233, nuclear length 3.27(2.88-3.53) ±0.208, head width 3.49 (3.26-3.62) ±0.136. Neck short, junction with head off center. Midpiece of moderate breadth anteriorly, tapering posteriorly; junction with tail distinctive; length 9.08(8.56-9.30) ±0.304.

Remarks.—The head of spermatozoa from this species bears a striking resemblance to that of *Ardops nichollsi.* The two also are extremely similar in dimensions of the nucleus, acrosome, and length of midpiece.

Specimens examined.—JAMAICA: Queenhythe, St. Ann Parish, 1 (TTU 21774); Duanvale, Trelawny Parish, 1 (TTU 21781).

Stenoderma rufum Desmarest, 1820

Description (Fig. 4H).—Head most similar in shape to those of *Ariteus, Ardops,* and *Artibeus*; more or less triangular, both nucleus and acrosome generally symmetrical; acrosome short and usually quite pointed at apex; acrosome usually narrower at base than is nucleus at its widest point; acrosome can be slightly asymmetrical at apex in that sometimes it is offset to side of head with attachment to neck; one-third to half of acrosome occurring anterior to the apex of nucleus; posterior border of acrosome lies anterior to midpoint of nucleus; nucleus nearly triangular with broadly rounded apex and quite rounded corners at the base; base slightly concave to nearly flattened; head length 4.58(4.19-4.84) ±0.18, 4.48(4.37-4.65) ±0.13, acrosome length 2.92(2.60-3.26) ±0.16, 2.81(2.42-2.98) ±0.17, nuclear length 3.46(3.26-3.81) ±0.13, 3.56(3.44-3.81) ±0.11, head width 3.20(2.88-3.35) ±0.15, 3.21(3.07-3.35) ±0.10. Neck relatively long, junction with base of head moderately off center. Midpiece relatively broad, tapering gradually posteriorly; junction of midpiece and tail distinctive; length 8.50(8.18-8.84) ±0.20, 8.33(8.09-8.65) ±0.16.

Remarks.—Head of sperm in this species is most similar to that of *Ariteus flavescenes, Ardops nichollsi,* and members of the genus *Artibeus* but is distinguishable from all of them. The most unusual feature of the spermatozoa of this species is the narrowness of the acrosome relative to the breadth of the nucleus. Also, the nucleus and acrosome are extremely similar in outline, a situation rarely observed.

Specimens examined.—PUERTO RICO: El Verde, 2 (TTU 22361, 22362).

Centurio senex Gray, 1842

Description (Fig. 4I).—Head short, nuclear portion extremely rounded; acrosome symmetrical with extremely pointed apex, forming an isosceles triangle, as wide as nucleus; posterior limit of acrosome lies in front of center of nucleus; acrosome shorter than nucleus; moderate portion of acrosome occurs anterior to the nuclear apex, which is narrowly rounded; nucleus usually as wide as it is long with its anterior border often appearing flattened on either or both sides; base of head flattened or even slightly convex, giving base a rounded appearance; head length 4.44(4.19-4.74) ±0.20, acrosome length 2.68(2.42-3.07) ±0.28, nuclear length 3.68(3.44-4.00) ±0.18, head width 3.65(3.35-3.91) ±0.17. Neck long, junction with head well off center. Midpiece extremely thin, short; length 7.36 (7.34-7.91) ±0.20.

Remarks.—The morphology of the sperm head in *Centurio senex* is distinctive and unique. The acrosome is extremely pointed, the nucleus nearly circular. Perhaps the greatest contrast in degree of pointedness of nuclear and acrosomal apices is observed in this species.

Specimen examined.—TRINIDAD: Blanchisseuse, St. George, 1 (TTU 24019).

SUBFAMILY PHYLLONYCTERINAE

Brachyphylla cavernarum Gray, 1834

Description (Fig. 5A).—Head of moderate length, narrow; acrosome symmetrical, considerably shorter than nucleus, and with its posterior limit well anterior to midpoint of nucleus; nucleus more ovoid than that of *Ardops*, *Ariteus*, and *Artibeus*; base slightly concave; head length 4.60, 5.12, acrosome length 2.79, 2.79, nuclear length 3.26, 3.53, head width 2.79, 1.98. Neck short, junction with head near center. Midpiece of moderate width, long, tapering posteriorly; junction with tail distinctive.

Remarks.—The sperm of *Brachyphylla* is different from other phyllonycterines and does not possess features generally found among other members of the subfamily (for example, *Brachyphylla* differs in shape and size of the acrosome, relative length of the midpiece, symmetry of the head).

Specimens examined.—GUADELOUPE: 1 km. S Basse-Terre, Basse-Terre, 1 (TTU 20966); 1 km. N, 1 km. W St. François, Grande-Terre, 1 (TTU 20976).

Erophylla bombifrons (Miller, 1899)

Description (Fig. 5B).—Head extremely long, ovoid and generally robust; acrosome large and encompassing a distinctive portion of the head; acrosome with slight asymmetry, anteriormost limit of apex on the same side of head as attachment of tail, and with an apex quite similar in shape to that of the nucleus; acrosome only slightly wider than the nucleus, terminating posteriorly just beyond midpoint of nucleus; acrosome only slightly shorter than nucleus; nucleus broad

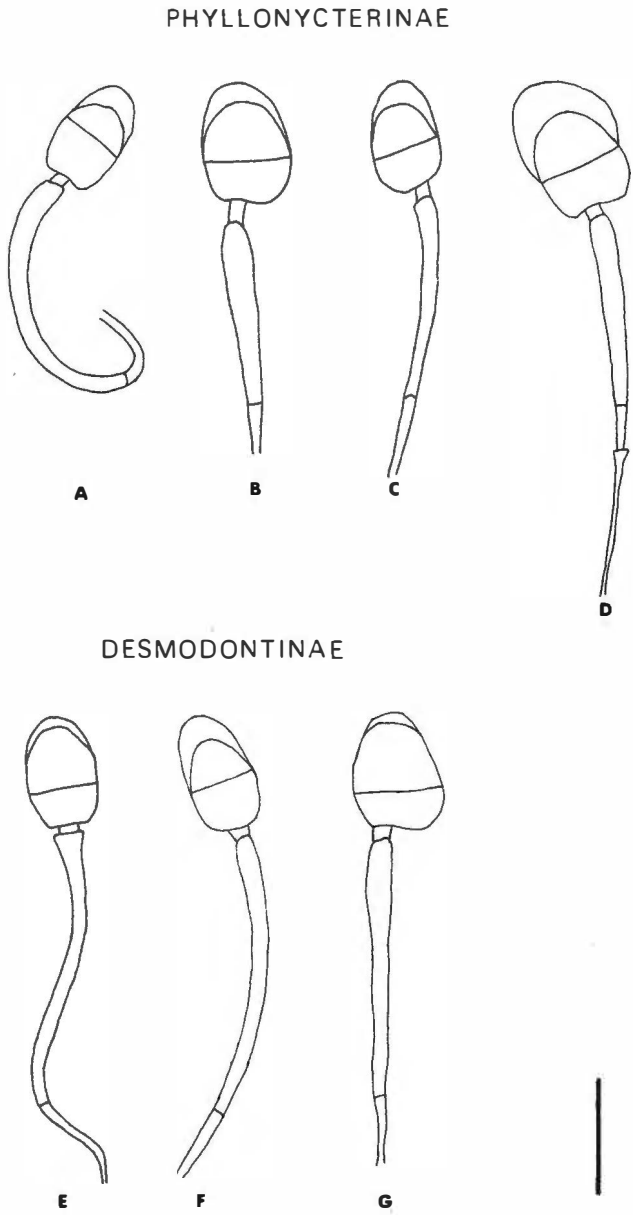


FIG. 5.—Sperm of some phyllonycterine and desmodontine bats. A) *Brachyphylla cavernarum*; B) *Erophylla bombifrons*; C) *Erophylla sezekorni*; D) *Phyllonycteris poeyi*; E) *Desmodus rotundus*; F) *Diaemus youngii*; G) *Diphylla ecaudata*. Scale equals 5 microns.

and usually rounded, apex symmetrical; base of nucleus strongly asymmetrical and concave, with corner nearest attachment of midpiece often less rounded than other corner; head length 5.14(4.84-5.30) ±0.148, acrosome length 3.45(3.26-3.62) ±0.142, nuclear length 3.95(3.62-4.09) ±0.146, head width 3.62(3.53-

3.81) ±0.09. Neck appears extremely long; junction with base of head off center. Midpiece broad anteriorly, tapering abruptly; length 7.42(7.07-8.37) ±0.379.

Remarks.—The head of the sperm of *Erophylla bombifrons* is similar to that of *Phyllonycteris poeyi*; however, the acrosome of *E. bombifrons* is smaller and not so asymmetrical. The midpiece of this species is exceptionally thick at its anterior end.

Specimens examined.—PUERTO RICO: 1 mi. W Corozal, 2 (TTU 22426, 22429).

Erophylla sezekorni (Gundlach, 1861)

Description (Fig. 5C).—Head narrow and long, oval in general shape; acrosome exceedingly asymmetrical with apex on same side of head as midpiece attachment; acrosome slightly wider than nucleus at its widest point; posterior terminus of acrosome at or slightly posterior to midpoint of head; acrosome shorter than nucleus by small amount and with apex more narrowly rounded than that of nucleus; nucleus an egg-shaped, rounded oval with broadly rounded apex; base of head rounded or slightly concave; amount of acrosome anterior to nucleus variable but generally amount is moderate; head length 4.74, 4.84, acrosome length 2.79, 2.98, nuclear length 3.44, 3.53, head width 2.98, 3.07. Neck moderate in length, junction with head slightly off center. Midpiece short, broad anteriorly (but considerably less so than in *E. bombifrons*), and tapering gradually posteriorly; junction with tail indistinct; length, 7.53.

Remarks.—The head of the sperm of *Erophylla sezekorni* is like that of *E. bombifrons* but is more similar to that of *Phyllonycteris poeyi* in general characteristics. The acrosome in *Erophylla* is much smaller than in *Phyllonycteris* and with considerably less exposed acrosome than in sperm of *Phyllonycteris*. The thickened area of the tail just distal to the midpiece in *P. poeyi* was not observed in either species of *Erophylla*.

Specimen examined.—JAMAICA: Orange Valley, St. Ann Parish, 1 (TTU 21894).

Phyllonycteris poeyi

Description (Fig. 5D).—Head extremely long and broad because of enormous asymmetrical acrosome; acrosome slightly wider than long with apex extremely broad and on same side of head as midpiece attachment; apex of acrosome even more removed from the midline of nucleus than midpiece, with result that the apex is often so far off center as to be outside the axis of the nucleus; acrosome broadest of any phyllostomatid studied and broader than nucleus; acrosome terminates posteriorly slightly beyond the midpoint of nucleus; nucleus bilaterally symmetrical except for base; nucleus a broad oval, being slightly longer than acrosome; base of nucleus concave, and of moderate breadth, apex rounded; head length 6.42(6.14-6.98) ±0.214, 6.67(6.32-6.88) ±0.204, acrosome length 4.13(3.81-4.50) ±0.215, 4.56(4.28-5.02) ±0.234, nuclear length 4.74(4.56-5.02) ±0.156, 4.73(4.46-5.02) ±0.201, head width 4.60(4.19-4.74) ±0.169, 4.57(4.19-4.74) ±0.157. Neck short, junction with head off center. Midpiece of moderate length; broad anteriorly and tapering posteriorly; unusual tapered

thickening of tail just distal to junction of tail and midpiece; length 8.63 (8.18-8.84) ±0.204, 8.63(8.28-8.93) ±0.237.

Remarks.—The sperm of *P. poeyi* exhibits several unique characteristics. The acrosome has an unusual morphology including having the apex far offset and being the broadest of any species studied. This is the only species examined in which over half of the area of the acrosome occurs anterior to the apex of the nucleus. There is an unusual thickening in the tail of all specimens that occurs just distal to the junction of the tail and midpiece; the thickened area tapers posteriorly into a narrow tail.

Specimens examined.—HAITI: 1 km. E Lebrun, Dept. du Sud, 1 (TTU 22773); 1 km. S Lebrun, Dept. du Sud, 1 (TTU 22782); 4 km. S Lebrun, Dept. du Sud, 1 (TTU 22798).

SUBFAMILY DESMODONTINAE

Desmodus rotundus (É. Geoffroy St.-Hilaire, 1810)

Description (Fig. 5E).—Head long, narrow, and extremely ovoid with narrowly rounded apex and narrow base; acrosome long, terminating posteriorly well behind midpoint of nucleus, apex symmetrical; most of acrosome in contact with nucleus, only an extremely minute portion anterior to nuclear apex; viewed dorsally, nucleus comprises most of head; acrosome no wider than nucleus, apex of acrosome slightly more rounded than that of nucleus; base of head quite narrow, with distinctive concavity at junction with neck; head length 4.71(4.46-4.93) ± 0.183, acrosome length 2.98(2.88-3.07) ±0.067, nuclear length 3.84(3.62-4.09) ±0.162, head width 2.71(2.51-2.88) ±0.103. Neck extremely short; attaches at center of head. Midpiece extremely long, thickened or even flared at neck; tapers gradually posteriorly; junction with tail moderately distinctive; length 11.64 (11.16-12.18) ±0.277.

Remarks.—The heads of the spermatozoa of *Desmodus rotundus* show much greater symmetry than other phyllostomatid subfamilies. The other unique features of the sperm of this species include the relatively long and narrow head, long midpiece that is flared at the anterior end, and an acrosome closely attached to the nucleus.

Previous study.—Two specimens from Nicaragua (Forman *et al.*, 1968).

Specimens examined.—TRINIDAD: 2 mi. N, 2 mi. E Valencia, St. Andrew, 1 (TTU 24086); Blanchisseuse, St. George, 1 (TTU 24080).

Diaemus youngii (Jentink, 1893)

Description (Fig. 5F).—Head very similar in structure to that of *Desmodus rotundus*, however, acrosome protrudes well anterior of apex of nucleus; acrosome symmetrical, relatively narrow compared to *D. rotundus*, and with posterior limit often well in front of the midpoint of the nucleus; apex of acrosome somewhat more rounded than that of the nucleus; nucleus longer than acrosome; nucleus nearly identical to that of *Desmodus* except base is concave or flattened; head length 5.61(5.21-5.95) ±0.249, acrosome length 3.20(2.98-3.53) ±0.170, nuclear length 4.50(4.28-4.74) ±0.135, head width 3.11(2.98-3.35) ±0.104.

Neck extremely short, junction with head at center or very slightly off center. Midpiece extremely long and extremely broad anteriorly; tapering abruptly then gradually posteriorly; length 12.51(11.81-12.83) ±0.255.

Remarks.—Sperm of *Diaemus youngii* is very similar to that of *Desmodus rotundus* but quite different from the sperm of the third member in the subfamily, *Diphylla ecaudata.* The difference in head length between *Desmodus* and *Diaemus* is due, in part, to the position of the acrosome on the nucleus. The midpiece of *Diaemus* is longer than any other species of phyllostomatid studied and appears to lack the flared anterior end found in the sperm of *Desmodus.*

Specimen examined.—TRINIDAD: La Brea, St. Patrick, 1 (CM 45371).

Diphylla ecaudata Spix, 1823

Description (Fig. 5G).—Head clearly a shovel-shaped, extremely broad, rounded triangle; acrosome closely applied to front of nucleus as in *Desmodus*; acrosome barely anterior to the nuclear apex (in some cases it cannot be seen); acrosome large, generally assumes shape of the nucleus at its apex but can be more pointed; acrosome terminates posteriorly well beyond the midpoint of the nucleus as in *Desmodus*; acrosome the same width as the nucleus throughout most of its length; nucleus considerably longer than acrosome, its base asymmetrical, broad, with corners somewhat pointed; a distinctive depression in base of head at junction with neck; head length 4.57(4.37-4.84) ±0.160, acrosome length 2.89 (2.70-3.16) ±0.154, nuclear length 4.22(4.02-4.63) ±0.154, head width 3.46 (3.26-3.62) ±0.126. Neck slightly longer and somewhat broader than other vampires; attachment to base of head at one corner of base. Midpiece long, broad anteriorly and tapering gradually posteriorly; junction with tail not distinctive; length 9.60(9.21-10.14) ±0.294.

Remarks.—Morphology of the sperm head of *Diphylla ecaudata* is quite different from the other two species of vampires—most distinctive is the great breadth of the nucleus and the attachment of the head farther off center than noted for any other species examined.

Previous study.—Two specimens from Nicaragua (Forman *et al.*, 1968).

Specimen examined.—YUCATAN: 3 km. S, 1 km. W Calcehtoc, 1 (TTU 18447).

DISCUSSION

The spermatozoa of 35 species representing all six of the subfamilies of the Phyllostomatidae were examined in this study. Descriptions of three additional phyllostomatid species are available in the literature (Forman, 1968). The morphology of all species studied is basically similar, and this serves to distinguish members of the Phyllostomatidae from those of other families of bats. The acrosome proved to be the most variable structure, more variable than even the nuclear region.

Below we will discuss the relationships by subfamily that were observed in this work.

Phyllostomatinae.—Acrosomes within this subfamily were almost universally asymmetrical and always extended well anterior to the nuclear apex. Sperm from *Mimon crenulatum* and *Macrotus waterhousii* were most dissimilar from other members of the subfamily and from each other. *Mimon* possesses a strikingly enlarged and asymmetrical acrosome, whereas *Macrotus* is characterized by the unusual configuration of the nucleus, particularly by its unique broad base. Sperm of *Phyllostomus*, *Micronycteris*, and *Tonatia* were quite similar, and *Phyllostomus* and *Micronycteris* were characterized further among the phyllostomatines by a relatively long midpiece.

Glossophaginae.—Heads of the spermatozoa from this subfamily were rather rounded. Sperm from *Choeronycteris* showed a larger head and a substantially longer midpiece than either *Anoura* or *Glossophaga*. *Anoura* was distinguished from other glossophagines by a more strongly concave base to the head and from other phyllostomatids by an unusually short midpiece.

Spermatozoa were found to be no more variable within this subfamily than they were among the phyllostomatines or desmodontines. Therefore, sperm morphology does not support the contentions based on karyology (Baker, 1967), dental anatomy (Phillips, 1971), and immunologic comparisons (Gerber and Leone, 1971) that the glossophagines are a polyphyletic grouping.

Carolliinae.—The sperm of three species of the genus *Carollia* that have been studied were similar, with the nuclei being quite rounded. However, the species can be distinguished from each other based on overall head morphology.

Stenoderminae.—Morphology of the sperm heads of stenodermines was highly variable. Acrosomes varied from pointed and nearly symmetrical (*Centurio*) to broadly rounded at the apex and strongly asymmetrical (*Chiroderma*). There was considerable variability in the point of attachment of the neck and midpiece to the base of the head and ranged from nearly central attachment to attachment near the edge of the base of the head. However, the length and breadth of the midpiece of stenodermines was similar, except for *Mesophylla*, in which the midpiece was shorter than in other species.

Sperm from *Ardops*, *Ariteus*, *Stenoderma*, *Phyllops*, and *Artibeus* were alike in size and morphology of the nucleus and acrosome. Members of the first four genera are Antillean endemics characterized by shortened rostra and white spots on their shoulders. These genera are believed to have resulted from a single invasion of the Antilles (Baker and Genoways, 1978) with subsequent radiation. Morphology of the sperm supports this hypothesis and also suggests that members of this group may share a close ancestor with members of the genus *Artibeus*. *Uroderma bilobatum* is similar in morphology to members of this group, except that in *Uroderma* the base of the head is flattened and has pointed corners.

Sperm heads of *Centurio senex* were unusually triangular in form with the base of the head unusually broad. In members of the genus *Vampyrops*, the nucleus was extremely long, but in *Vampyrodes*, the distinguishing feature was the narrow base of the head. In addition to the shortened midpiece, *Mesophylla* is characterized by the strongly asymmetrical base of the head.

The sperm of *Chiroderma improvisum* and *C. trinitatum* were the most unique in head morphology among the stenodermines examined. In both species, only a very small portion of the acrosome extends beyond the apex of the nucleus. Furthermore, the base of the nucleus is asymmetrical with the greatest posterior extension occurring on the side of the head that is in contact with the neck. The sperm of these two species are similar but *C. improvisum* can be distinguished from *C. trinitatum* by the head of the former being slightly less rounded, acrosome shorter, and base of head less asymmetrical.

Until recently, members of the genus *Sturnira* were placed in a separate subfamily, Sturnirinae. However, recent authors (Baker, 1967; Slaughter, 1970; Jones and Carter, 1976) have placed them in the subfamily Stenoderminae. The morphology of the sperm of the three species described herein were similar, all being characterized by nearly symmetrical acrosomes. Sperm head morphology of species of *Sturnira* was most similar to that of stenodermines, among the subfamilies we examined, and we believe our data support placement of members of the genus *Sturnira* in the subfamily Stenoderminae. Although the sperm of the three species of *Sturnira* were similar, they could be distinguished on the basis of size and details of morphology.

Phyllonycterinae.—The sperm of *Brachyphylla cavernarum* was completely unlike that of any other phyllonycterines examined. Similarity in sperm morphology does not support placement of *Brachyphylla* in the Phyllonycterinae, as suggested by Silva Taboada and Pine (1969) from morphological and behavioral investigations and Baker and Lopez (1970) based on karyology. Our data indicate that it would be best to follow Miller (1907) and place *Brachyphylla* in the subfamily Stenoderminae. Among the stenodermines, the sperm of *Brachyphylla* could be distinguished by its long midpiece.

The sperm head of other phyllonycterine species studied was more uniform than that of species within other subfamilies; heads were all relatively narrow and acrosomes were large and asymmetrical. Spermatazoa from *Erophylla bombifrons, E. sezekorni*, and *Phyllonycteris poeyi* were especially similar to those of *Anoura* and *Carollia.*

The sperm of *Phyllonycteris poeyi* possesses a unique enlargement in the tail just distal to its junction with the midpiece. This structure was not seen in any other phyllostomatids examined.

Desmodontinae.—Sperm from the three species of vampire bats were markedly different; the only common feature among the three was a midpiece that proved to be the longest among the Phyllostomatidae. *Diphylla* possessed sperm heads that were substantially broader and more rounded than those of *Desmodus* and *Diaemus.* The nuclear portion of the head was similar in *Desmodus* and *Diaemus*; however, in *Diphylla* the nucleus was broader. Sperm from *Diphylla* was also characterized by the neck and midpiece juncture with the head being placed farther off center than any other phyllostomatid studied.

Spermatazoa of *Desmodus* and *Diphylla* show great similarity in the close application of the acrosome to the nucleus, with little space between the apices of the acrosome and the nucleus. The acrosome also extends posteriorly beyond

the midpoint of the nucleus. Neither of these two characteristics appear in *Diaemus*.

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ALIMENTARY TRACT

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Bats of the family Phyllostomatidae have extremely diversified dietary habits. Although accurate and detailed dietary data often are unavailable, there nevertheless are generalizations that can be made and certain trends seem obvious (Gardner, 1977; Phillips *et al.*, 1977). In addition to differences in diet, there also are differences in feeding behavior and in feeding strategies. Nonalimentary structural specializations such as reduced dentitions, elongate tongues (Phillips *et al.*, 1977), elaborate lip ridges, and complex palatal topography also are common in leaf-nosed bats.

In view of the great variability in alimentary function, it is reasonable to hypothesize that the gut tube itself might be unusually variable within the Phyllostomatidae. This is especially true in comparison to other families of bats, in which the dietary habits are not nearly so diversified. Current data suggest that at least certain portions of the alimentary tract are in fact highly variable.

This account reviews what already is known about gastrointestinal structure in phyllostomatids and reports new information, particularly with regard to histology and histochemistry of the stomach. However, certain alimentary regions, such as the intestine and esophagus, still require investigation for almost nothing is known about them. A survey of esophageal structure could prove particularly interesting because of the wide array of food items ingested by leaf-nosed bats. In all likelihood, the esophagus will reflect diet-specific morphological adaptations. Continuing comparative analysis of digestive tract morphology undoubtedly will prove important to our understanding of systematic relationships as well as to our understanding of the evolutionary process.

Materials and Methods

Some information presented in this chapter was extracted from a Ph.D. dissertation by Rouk (1973). In that study, the following histological and histochemical procedures were employed: fixation—10 per cent neutral, buffered formalin; straining of sections—a, Harris hematoxylin and eosin; b, aldehyde-fuchsin for elastin and acid mucopolysaccharides; c, Hale's colloidal iron followed by acid fuchsin, Ponceau 2R, and phosphotungstic acid sequence for acid mucopolysaccharides and chief cells; and d, Masson's triple connective tissue stain.

Esophagus

The histological organization of the esophagus in phyllostomatids is similar to that of other bats and other kinds of mammals as well. As is typical for the Chiroptera, the phyllostomatid esophagus in preserved specimens appears to be unusually narrow. The luminal surface is characterized by protruding

longitudinal folds of stratified squamous epithelium. The esophagus of large-sized phyllostomatids can be relatively narrower than that of smaller species; for example, Robin (1881) found that the esophagus of one species of *Artibeus* was only slightly broader than that of a species of *Glossophaga*, even though the body of the former was three times that of the latter.

Kolb (1954), who reviewed esophageal structure in bats, found some specific variation in the amount of cornification (keratinization) of the esophageal epithelium. He (Kolb, 1954) thought that such variation could reflect adaptations for the ingestion of particular foods. A similar finding was reported for the oral cavity (Phillips *et al.*, 1977), and it also was suggested that the degree of cornification could be a local response to a given amount of surface stress rather than a specific, inherited feature. The most complete histological study of the esophagus of a phyllostomatid is that by Moller (1932), who investigated *Glossophaga soricina*. As might be predicted, he found that the esophagus of *G. soricina* lacked significant corneum, particularly in the lower abdominal portion. Cells lining the esophageal lumen had ovoid nuclei, unlike those characteristic of dead, cornified cells. This feature probably is reflective of the general absence of abrasive food in the diet of *Glossophaga* and certainly is in contrast to the histology of insectivorus species in which the esophogeal surface is cornified.

Stomach

Comparative gastrointestinal structure and function is of particular interest because of the variability in diet among phyllostomatid species. It is because of this diversity in diet that the phyllostomatids have been subjects of more detailed studies of alimentary structure (especially the stomach) than have other families of bats. The following account, therefore, deals predominantly with morphology of the stomach because knowledge of variability in this structure in leaf-nosed bats even exceeds that for most other groups of small mammals. Comments on the small intestine, insofar as data are available, also are included.

In most cases, stomachs of phyllostomatids can be described in terminology that has been applied to other mammals. In those instances in this account where unusual or less familiar terms apply, a brief explanation parenthetically follows the term.

In all species thus far studied, the stomach has the form of a local dilation of the enteron. Torsion produces a saclike structure with a lesser curvature (anterior) and a greater curvature (posterior). Specific variability in topography, therefore, has been accomplished by evolutionary modification of this general plan. Gastric glands occur throughout the mucosa of all species studied. Squamous epithelium, on the other hand, has been lacking. The summary given in the following paragraphs is based predominantly on the works of Forman (1971*a*, 1971*b*, 1972, 1973), Rouk and Glass (1970), and Rouk (1968, 1973).

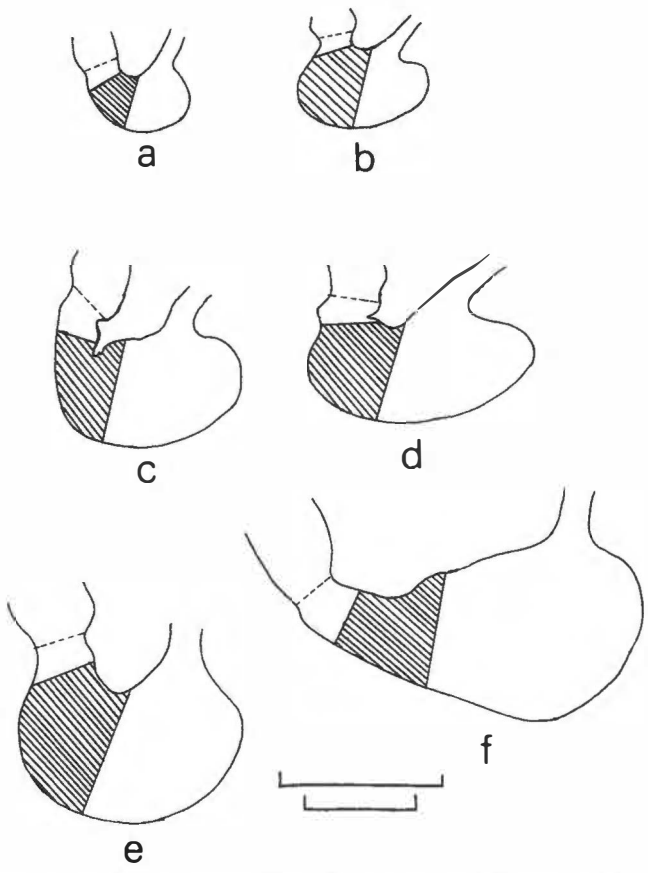

FIG. 1.—Semidiagramatic representations of the stomachs of selected phyllostomatines. The hatched area indicates the region of pylofundic transition glands: a, *Micronycteris megalotis*; b, *Macrophylum macrophylum*; c, *Tonatia bidens*; d, *Phyllostomus discolor*; e, *Phylloderma septentrionalis*; f, *Vampyrum spectrum*. Scale is 10 mm.; upper scale is for figs. a to e; lower scale, f.

Gross Morphology

Phyllostomatinae

The phyllostomatines have the simplest and least specialized stomachs. This probably relates to their somewhat unspecialized or primitive feeding habits that include insectivorous, carnivorous, and omnivorous diets. The stomach in *Micronycteris* is extremely simple in configuration; a cardiac vestibule usually is lacking. The pyloric tube (portion between the esophagus and duodenum) usually is short, with that of *M. nicefori* being relatively longer than that of *M. hirsuta* or *M. megalotis* (Fig. la). The fundic caecum (=cardiac caecum) is modestly developed in all three of these species. The stomachs of *Macrotus waterhousii* and *Macrophyllum macrophyllum* (Fig. 1b) also are simple and generally resemble those of *Micronycteris*.

The stomach in *Tonatia* varies somewhat from those previously mentioned, and that of *Tonatia minuta* varies intraspecifically. For example, the stomach of *T. minuta* may have a poorly developed fundic caecum. Additionally, the pyloric tube is bent at a right angle to the general orientation of the stomach, as observed in *T. bidens* (Fig. 1c), or it may more closely approximate the simple, symmetrical configuration found in species of *Micronycteris*. The esophageal entrance is located about midway along the lesser curvature. The pyloric tube in *Chrotopterus auritus* differs from that in species of *Micronycteris* only in being relatively longer.

The stomach of *Phylloderma stenops* (Fig. 1e) is more globular than those of other phyllostomatines, but otherwise it does not differ substantially from those found in species of *Micronycteris*. The stomach of *Trachops* is *Micronycteris*-like but still is more tubular, and the lesser and greater curvatures are nearly parallel.

The stomachs of several other phyllostomatines differ more distinctively from the *Micronycteris*-like configuration. For example, in *Phyllostomus discolor* (Fig. 1d) and *P. hastatus* the fundic caecum is well developed and often is dilated at its terminus. The pyloric portion is distinctively elongated and sometimes there is a prominent constriction in front of the gastroduodenal junction. A small, but perceptable cardiac vestibule occurs between the lesser curvature and the gastroesophageal junction. Although this vestibule is not nearly so expansive as that in some frugivores, it nevertheless is more distinctive than that of phyllostomatines described above. The stomach of *P. hastatus* generally resembles that of *P. discolor*, except for its considerably larger size. The greater and lesser curvatures are nearly parallel in both species.

The stomach of *Vampyrum spectrum* (Fig. 1f), a carnivore that often feeds on other bats (see Rouk, 1973), is noticeably pearshaped with a moderately developed fundic caecum and a long, well differentiated pyloric tube. A cardiac vestibule is lacking and the lesser curvature is longer than in other phyllostomatines. This is because the pyloric tube exits to the side (right side of the body) with only very slight anterior recurvature of the terminal portion of the stomach. The stomach of this species, with its straight pyloric tube, has a strong resemblance to those of many species of the Insectivora (see Allison, 1948; Myrcha, 1967).

Simplicity of stomach form is evident in the Phyllostomatinae. Some elongation of the pyloric portion, along with some dilation of the caecum also, is evident in comparison with stomachs of insectivorous bats of other families. These slight modifications likely are associated with increased volume of food ingested.

Glossophaginae

The stomach of *Glossophaga soricina* (Fig. 2a) is large and saccular. Although its diet includes insects along with nectar, pollen, and fruit, the stomach is decidedly more specialized than that of any of the Phyllostomatinae, including the omnivorous *Phyllostomus discolor*.

The fundic caecum in *G. soricina* is dilated and bulbar. The caecum can be distinguished from the remainder of the stomach by a distinctive furrow or sulcus on the dorsal surface. The stomach is curved in both frontal and transverse

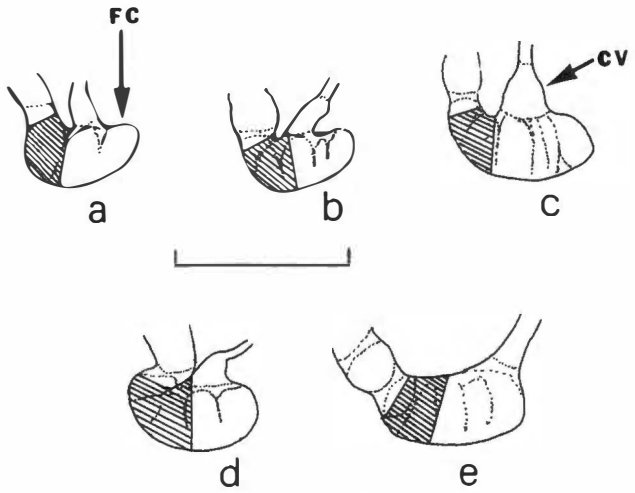

FIG. 2.—Semidiagramatic representations of the stomachs of selected glossophagines and a carolliine. The hatched area indicates the region of pylofundic transition glands: a, *Glossophaga soricina*; b, *Hylonycteris underwoodi*; c, *Lonchophylla robusta*; d, *Lichonycteris obscura*; e, *Carollia perspicillata*. Scale is 10 mm. for e; for all others, 8 mm. Symbols are FC, fundic caecum; CV, cardiac vestibule.

planes. A small cardiac vestibule has been observed in some specimens, but seems to be absent in others. This variable feature possibly is an individual response to opportunistic feeding by this species. *Glossophaga commissarisi* has a stomach that is similar to that of *G. soricina* except for its even more distinctive cardiac vestibule. The fundic caecum is relatively longer and narrower than that of *G. soricina*. The pyloric tube is enlongated and more distinctive than in *G. soricina*.

Even though stomachs of *Hylonycteris underwoodi* (Fig. 2b), *Lonchophylla robusta, Anoura geoffroyi, Choeronycteris mexicana*, and *Leptonycteris* all bear a general resemblance to those in *Glossophaga*, distinguishing characteristics can be observed in most. For example, *Hylonycteris* has a relatively long, narrow fundic caecum (Fig. 2b) that is nearly tubular and is marked by numerous deep sulci. The extemely broad pyloric tube is short, but decidedly arched from left to right. The stomachs of *Anoura geoffroyi* and *Choeronycteris mexicana* bear striking resemblance to those of *Glossophaga*. In comparison to the other glossophagines, *Lonchophylla robusta* has an unusual stomach (Fig. 2c) in that both the cardiac vestibule and fundic caecum are developed distinctively. The gross morphology of this stomach approaches that of some fruit-eating stenodermines.

The stomachs of *Leptonycteris nivalis* and *L. sanborni* are nearly identical. They also are somewhat distinctive because of an unusually elongated, extremely pointed fundic caecum. Also, the terminal portion of the stomach (pylorus) is tubular and elongated to the point of being recurved to lie juxtaposed to the cardiac vestibule. Therefore, the stomach assumes a C-shaped configuration

when viewed from the front. This striking elongation and recurvature of the pyloric stomach in *Leptonycteris* and in *Lichonycteris* as well (and to a lesser extent in *Choeroniscus* and *Glossophaga*) might represent an adaptation to permit intake of an increased percentage of plant material in the diet. Increased length of the pyloric tube is one way to increase gastric volume.

The stomachs of *Choeroniscus godmani* and *Lichonycteris obscura* (Fig. 2d) possess well-developed cardiac vestibules and broad terminal portions that can be recurved sharply toward the gastroesophageal junction. The fundic caeca of these two species are shallow; unlike the other species of glossophagines, the caeca are not delineated by a sulcus (= incisura cardiaca) from the cardiac vestibule. Therefore, the vestibule merges gradually into the caecum on the greater curvature of these two.

Carolliinae

The stomachs of two species from this subfamily have been examined. *Carollia perspicillata* (Fig. 2e) and *C. castanea* generally are quite similar but apparently are individually variable in gross morphology. The terminal (= pyloric) portion is elongate and strongly recurved anteriorly. This recurvature possibly functions to retard gastric emptying. A cardiac vestibule is present; in some specimens it is moderately developed, whereas in others it is quite small. The caecum is baglike and dilated and is more prominent in *C. castanea* than it is in C. *perspicillata*. Overall, the stomachs of these two species are in many ways intermediate between those of glossophagines and those of stenodermines. The Carolliinae exhibit the overall simplicity of most glossophagine stomachs in combination with some specialization of the caecum (especially the pyloric tube), which is characteristic of fruit-eating stenodermines.

Stenoderminae

An extensive array of stenodermine species, most of which are considered to be frugivores, have been studied. The stomachs of stenodermines are substantially more complex and more specialized than those of the previously described species. Virtually all gross features of the stomach are enlarged or lengthened, especially in comparison with the simpler stomachs of the phyllostomatines and glossophagines.

The stomachs of *Sturnira lilium* and *S. ludovici* (Fig. 3a) are similar to one another. In *S. lilium*, which is typical, the cardiac vestibule is elongate and tapers so that the gastroesophageal junction lies well superior to the gastroduodenal junction. The fundic caecum is saccular and thinwalled, forming a spacious chamber with an apex that varies from being rounded to being tapered. A fold of the stomach wall distinguishes the cardiac vestibule from the fundic caecum. The tubular (= pyloric) portion of the stomach is long and narrow (*S. ludovici* has a shorter pylorus and a somewhat larger cardiac vestibule giving the stomach a more robust appearance than that of *S. lilium*). The stomach from a single

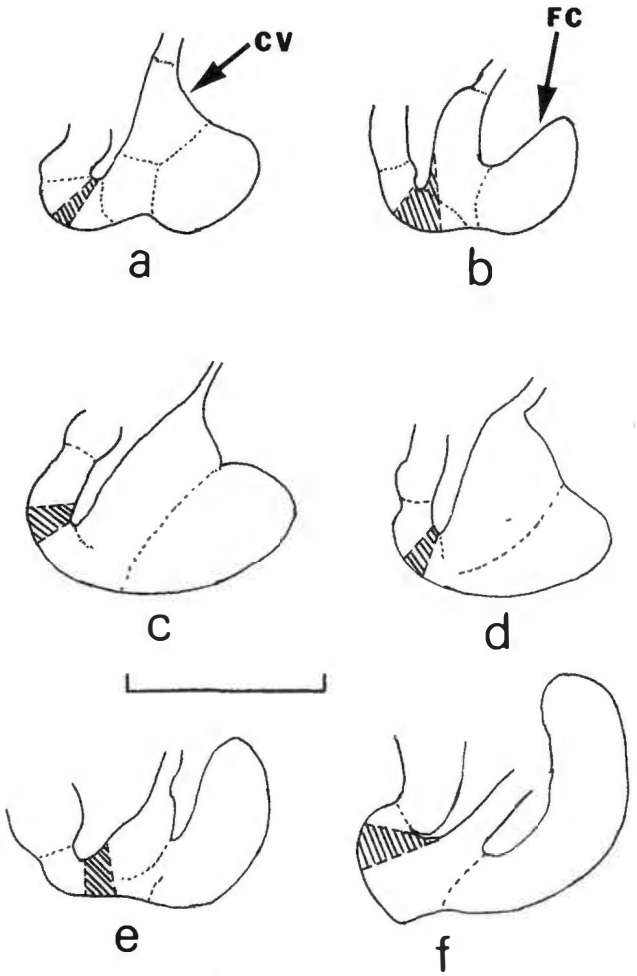

FIG. 3.—Semidiagramatic representations of the stomachs of selected stenodermines. The hatched area indicates the region of pylofundic transition glands: a, *Sturnira ludovici*; b, *Uroderma magnirostrum*; c, *Artibeus lituratus*; d, *Centurio senex*; e, *Vampyrodes caraccioli*; f, *Chiroderma villosum*. Scale is 10 mm. Symbols are identified in Fig. 2.

specimen of *S. mordax* was examined by Rouk (1973) who found it to have a a considerably simpler gross morphology than those of other species of *Sturnira*. Rouk (1973) reported that the terminal portion was relatively unspecialized and that the caecum was poorly developed. However, the stomach in *S. mordax* does possess a moderately large cardiac vestibule.

The remaining stenodermines for which stomachs have been examined show increased specialization by way of elongation or enlargement of one or more portions of the stomach. The stomachs of seven species of *Artibeus* (*aztecus, inopinatus, jamaicensis, lituratus, phaeotis, toltecus*, and *watsoni*) have been studied (see Fig. 3c). These seven, along with that of *Centurio senex* (Fig. 3d),

have tremendously enlarged cardiac vestibules that permit temporary storage of large amounts of plant material. In *Vampyressa, Vampyrops, Uroderma, Vampyrodes,* and *Chiroderma,* the cardiac vestibule varies from small to moderately large, with the fundic caecum being variously drawn out into a baglike or nearly tubelike structure.

Stomachs of *Uroderma bilobatum* and *U. magnirostrum* (Fig. 3b) share gross characteristics with *Sturnira,* as well as with *Artibeus,* and could be said to be intermediate between the two. The caecum is elongate and narrowed nearly to a point at its apex. The stomachs of *Vampyrops helleri* and *V. vittatus* differ from that of *Uroderma* only slightly in that the caecum of *V. helleri* and *V. vittatus* is somewhat broader.

The stomachs of *Vampyressa pusilla* and *V. nymphaea* are nearly identical to one another. The cardiac vestibule is small in comparison with most of the other stenodermines. The elongate fundic caecum is recurved anteriorly, as it is in *Uroderma, Vampyrops, Vampyrodes, Chiroderma,* and some *Artibeus,* and it is dilated at its terminus.

The remaining two species to be discussed in this account, *Vampyrodes caraccioli* (Fig. 3e) and *Chiroderma villosum* (Fig. 3f), possess greatly enlarged fundic caeca. The stomach of *Vampyrodes* somewhat resembles that of *Uroderma* except that the cardiac vestibule is much reduced. A distinctive narrowing occurs between the cardiac vestibule and fundic caecum of both species so that there is only a small region where the two are contiguous. The fundic caecum of *Vampyrodes* is about 1.5 times the length of the remainder of the stomach, and that of *Chiroderma* is in excess of twice the length.

The stomach of *C. villosum,* which has a tubular caecum, represents perhaps the most extreme specialization for plant feeding in the Phyllostomatidae. This condition closely parallels that observed in some Old World megachiropterans. The caecum is marked externally by a series of parallel constrictions that surround it for nearly its entire length. The duodenum at the gastrointestinal junction is unusual in being grossly dilated on the lesser curvature to produce what amounts to a small ampulla or caecum. The function of this dilation is unknown.

It would appear that there are two adaptive trends within the Stenoderminae. Each apparently represents a different response to increased need for stomach volume in these frugivores. One trend, which is best illustrated in *Artibeus* and in *Centurio,* was to increase size of the cardiac vestibule while minimizing the importance of the fundic caecum. The other approach, seen so vividly in such genera as *Vampyressa, Vampyrodes,* and *Chiroderma,* was to minimize, or even to nearly eliminate, the cardiac vestibule while correspondingly enlarging the caecum into an obviously useful storage chamber. Both trends would permit increased consumption or storage, or both, of plant materials that presumably are difficult to digest.

Phyllonycterinae

Rouk (1973) examined the stomach of only one member of this subfamily, *Brachyphylla cavernarum* (Fig. 4a). The esophagus enters the stomach quite near

the gastroduodenal junction. Therefore, the lesser curvature between esophagus and duodenum is extremely short. The fundic caecum is extremely well developed into a "bag" that appears to be nearly compartmentalized into a two-chambered structure. The caecum bends abruptly anteriorly about midway along its length. At this location, there is a suggestion of a sphincter, although this constriction in the muscularis externa has not been demonstrated to have a sphincteric function. The duodenum is quite enlarged at its junction with the stomach, which is separated from the intestine by a distinctive constriction. The stomach of *Brachyphylla* clearly is distinctive among phyllostomatids. Other phyllonycterines should be examined to determine if this distinctive form is consistent within the group.

Desmodontinae

The gastric morphology of *Desmodus rotundus* (Fig. 4b) has been variously described and illustrated by a number of workers (Huxley, 1865; Rouk and Glass, 1970; Hart, 1971; Forman, 1972). Its simple, tubular form is predominately an elongate caecum of generally uniform breadth that lacks a cardiac vestibule or demonstrable pyloric portion (although pyloric glands are present). The terminal-most part of the caecum frequently is dilated into a thin-walled sac; the distal one-half is folded back upon the proximal one-half. There is no conclusive evidence of any sphincters within the stomach, except for that adjacent to the duodenum.

In *Diaemus youngii* (Fig. 4c), the stomach bears strong resemblance to that of *Desmodus* except that the caecum may be less tubular and more conical in this species. The terminal part of the caecum is slightly dilated. In the stomach of *Diphylla ecaudata* (Fig. 4d), numerous semilunar folds within the distal one-half of the caecum divide it into smaller compartments. The caecum, with its haustra coli, therefore, bears strong resemblance to the colon of man. The "pouches" thus formed in the caecum of *Diphylla* would tend to retard gastric emptying, important in vampires because the stomach is specialized for absorption. Additionally, the folds in the caecum would tend to increase the surface area to volume ratio, thereby increasing the efficiency of absorption from the stomach.

Gastric Mucosa

The stomachs of all species of phyllostomatids are completely lined with a glandular mucosa. There is no uncornified or cornified squamous epithelium in the stomach. A zone, usually narrow, of mucuous-producing cardiac glands is found at the gastroesophageal junction. A broader zone of pyloric glands, which also are mucuous producing and which are similar in structure to cardiac glands, are located at the gastroduodenal junction in all species. The remainder of the mucosa is occupied by a broad region of fundic glands composed of mucous cells, parietal cells, and chief (= zymogenic) cells. A zone of transitional glands that is extremely variable in length occurs between fundic and pyloric mucosa. This transitional area is rather broad in species of the Glossophaginae but is relatively narrow in the Stenoderminae. Species of

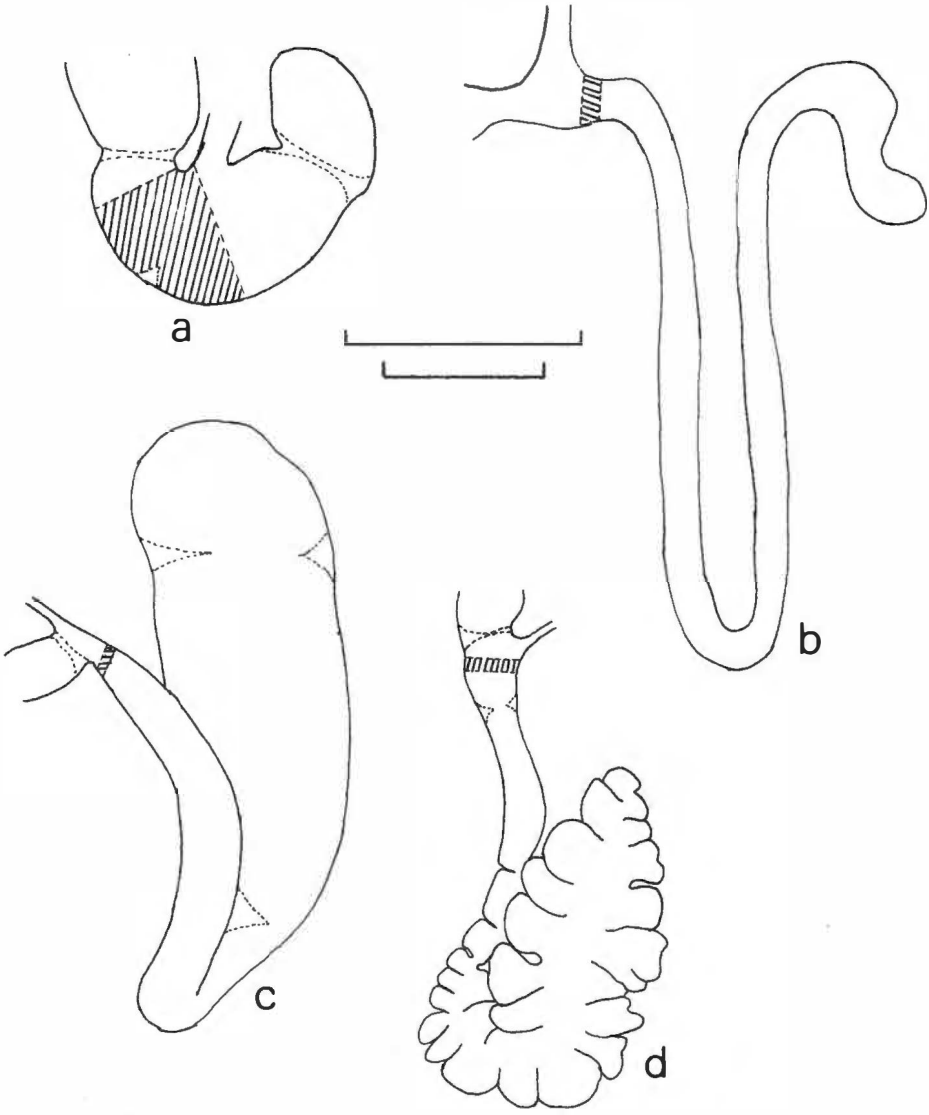

FIG. 4.—Semidiagrammatic representations of the stomachs of one phyllonycterine and three desmodontines. The hatched area indicates the region of pylofundic transition glands: a, *Brachyphylla cavernarum*; b, *Desmodus rotundus*; c, *Diaemus youngi*; d, *Diphylla ecaudata*. Scale is 10 mm.; upper scale is for a; lower scale, all others.

Artibeus, along with *Centurio* and *Vampyrodes*, consistently have extremely narrow "transition" zones. This narrowness of the transition zone seems to be due to a relatively extensive proximal advancement of pyloric glands within the pyloric tube.

Depth of the gastric mucosa varies slightly within stomachs and among species. The mucosa is shallowest in the vampires, with fundic glands being

only 50 to 75 micrometers in *Desmodus*. The gastric glands of vampires are reduced to shallow acini in comparison to the tubular form of other species. This is accompanied by a general reduction in all cellular constituents, although zymogenic, parietal, argentiffin, and mucous neck cells all are present. Mucous neck cells comprise the most abundant cellular component of the mucosa, whereas parietal (= HCl-producing) cells are extremely sparse.

The gastric mucosa of other species varies from 100 to 600 micrometers, in depth, although 200 to 250 micrometers is most commonplace. Pyloric glands frequently are longer than are the fundic glands within a species; for example, in *Artibeus* they are 50 to 80 per cent longer. In many species, the fundic glands are somewhat longer at the apices of rugae than on the stomach wall proper. In striking contrast is the fundic portion of the mucosa of stenodermines, such as *Artibeus* and *Centurio*, in which the glands are of extremely uniform depth. Relative constancy of cell frequency accounts for the uniformity of mucosal depth. In some phyllostomatines, especially *Micronycteris* and *Chrotopterus*, the fundic mucosa is quite shallow at the apex of the caecum.

The stomach wall of all species is thrown into rugae, which occur everywhere within the stomach. These folds generally are oriented along the longitudinal axis and are arranged in parallel rows in the terminal, tubular stomach. They occur in wavy, parallel rows throughout the remainder of the stomach in many other species. In stenodermines, all species that have been examined with respect to rugal organization reveal some degree of "complication" or interdigitation of folds. In *Vampyressa*, *Vampyrops*, *Chiroderma*, and *Sturnira*, they are distributed diagonally (toward the pyloric sphincter), but only within the caecum. Rugae are slanted only within the midregion of *Uroderma*. In most stenodermines that have been studied, folds interdigitate only to a moderate degree, but in *Artibeus* and *Centurio* an extremely complex interlocking of folds produces an elaborate maze because folds are highly branched. This arrangement likely would be effective in retarding gastric emptying, a particularly important digestive adaptation in obligate plant feeders.

Histochemistry of the Gastric Mucosa

Few systematic groupings of mammals have been examined comparatively with respect to the histochemistry or cytochemistry of the stomach lining. Phyllostomatids are an exception to this in that the mucous cells and their secretory products have been studied with a variety of techniques. Procedures have been employed that elucidate acid as well as neutral mucopolysaccharides.

A positive periodic acid-Schiff (PAS) reaction is thought to indicate an abundance of mucosubstance and, thus, it provides an overall estimate of the quantity of mucus within or on the surface of cells in the stomach or intestine (see Lillie, 1965). In all examined species phyllostomatids, there is a moderate to intense coloration of mucous material in the apical portion of the cytoplasm of surface columnar cells. In *Desmodus rotundus* (the only desmodontine examined to date), the intensity of this reaction in surface mucus is somewhat reduced

in comparison with that of other phyllostomatids. In many species having well-developed fundic caeca, the staining is stronger in the foveolae of the fundic glands of the caecum than elsewhere in the fundus. Mucus possibly accumulates to a greater extent in the caecum than elsewhere in phyllostomatids.

Mucous cells beneath the surface (the so-called mucous neck cells), which are scattered among the parietal cells, react much more variably to the PAS reaction than do the surface columnar cells. Mucous neck cells of frugivorous species generally are less reactive than are those of carnivorous and omnivorous kinds. Those of *Desmodus* (and perhaps the other desmodontines) react only weakly.

The upper portions of the tubules of cardiac and pyloric glands stain intensely with PAS. There is only slight variability among species. As in the case of fundic glands, reactivity in these upper portions is somewhat reduced in frugivorous species. Among studied species, the most intense reaction has been found in an omnivore, *Phyllostomus discolor.* The quantity of gastric mucus in this species exceeds that of frugivorous phyllostomatids. On the other hand, in *Desmodus* the reactivity is weak in comparison with nondesmodontine phyllostomatids.

Two procedures, or their variants, have been employed in an effort to elaborate the relatively acidic components of gastric mucus in phyllostomatids. Forman (1972) employed Alcian blue 8GX, and Rouk (1973) and Forman (1971*b*) used Hale's colloidal iron procedure in efforts to categorize acid mucopolysaccharides in stomachs of selected species of phyllostomatids. A summary of their results is presented here.

Acid mucopolysaccharides are found most consistently in the cardiac glands (those at the gastroesophageal junction) and within the few transitional and fundic glands adjacent to the cardiac glands. Nearly all species of phyllostomatids studied to date showed some positive staining of cardiac glands. The only exceptions are species of *Sturnira* (including *S. lilium, S. ludovici,* and *S. mordax*). In these species, the cardiac glands are either weakly reactive or non reactive to procedures intended to demonstrate the presence of acid mucopolysaccharides. Present evidence also suggests that *Centurio* and *Desmodus* have reduced amounts of acid mucopolysaccharides in their cardiac glands. The reaction of the pyloric glands to Hale's colloidal iron and Alcian blue is similar to that of the cardiac glands. There is, however, less consistency among species, less uniformity within the zone of pyloric glands, and often less intensity in comparison to the histologically similar cardiac glands.

In most species of phyllostomatines, the pyloric glands are nonreactive; the exception is *Vampyrum spectrum,* in which these glands are weakly reactive with Hale's colloidal iron.

In the glossophagines, there are two general conditions of stainability of the pyloric glands with Alcian blue and Hale's colloidal iron. With Hale's iron (as employed by Rouk, 1973) pyloric glands stain intensely within the basal one-third of the tubules in *Glossophaga soricina* and *Lonchophylla robusta.* Forman (1971*b*) studied glossophagine cardiac glands with Alcian blue. In his study of five species of glossophagines, the lower portion of each pyloric gland tubule was Alcian blue positive in three (*Glossophaga soricina, G. commissarisi,*

and *Anoura geoffroyi*) but negative in two others (*Choeroniscus godmani* and *Lichonycteris obscura*).

Among the phyllostomatids, the most widespread and distinctive reactivity to procedures for acid mucopolysacchardies in the stomach are found in certain of the carolliines and stenodermines. For example, pyloric glands in *Vampyrodes, Vampyressa, Chiroderma, Centurio*, and in seven species of *Artibeus* that have been studied, react intensively with Hale's colloidal iron either throughout or nearly throughout the length of the tubule. Rouk (1973) determined that nearly all glands in the stomach of *Vampyressa pusilla* contain noteworthy amounts of Hale positive mucin. In these same stenodermines, as well as in *Uroderma, Vampyrops*, and *Sturnira mordax*, the mucous neck cells within the upper portions of fundic gland tubules also react moderately or strongly with Hale's iron. Reactivity in these cells rarely has been observed in nonstenodermines.

These results suggest that a relationship might exist between gastric acid mucopolysaccharides and plant feeding in phyllostomatids. Whether their function is protective, digestive, or both remains to be determined.

Pyloric Sphincter

The muscular portion of the sphincter at the gastroduodenal junction is unusually variable in form in phyllosotmatids. Numerous variations in the form of this circular muscle mass have been observed in leaf-nosed bats, and at least part of this variability appears to be related to diet. The sphincter is in some way asymmetrical in the majority of species that have been examined. In kinds where asymmetry is present, the valve on the greater curvature is larger than that portion on the lesser curvature. This condition always prevails in insectivorous and carnivorous species. The valves of *Macrotus, Micronycteris, Tonatia minuta*, and *Glossophaga* are short to moderate in length and generally are robust with broadly rounded apices. In *Centurio*, the valve of the greater curvature is fully three times the mass of the "lesser" valve. This form of valvular asymmetry is maximized in *Tonatia minuta* in which the greater valve is long and extremely thick, whereas the lesser valve is absent, or nearly so. Two noteworthy instances in which the valve is greatest in mass on the lesser curvature are found in *Uroderma bilobatum* and in *Chiroderma villosum*. This asymmetry might result in some sort of "milking" action that permits slow release of stomach contents into the duodenum.

Two trends in pyloric sphincter morphology are evident in frugivorous species as well as in some pollenivorous and nectarivorous kinds. One trend involves increased symmetry, whereas the other involves the amount of muscular contribution to the valve.

First, the pyloric valve of some fruit-eating stenodermines and carolliines, including *Artibeus, Sturnira, Vampyressa, Carollia perspicillata* and perhaps others, is of nearly uniform length throughout its circumference. It would appear that increased symmetry of the valve in these species is related to consumption of plant material. None of the insectivorous or carnivorous kinds has a symmetrical valve; indeed, the most pronounced asymmetry always is

observed in these species. The pyloric valve of *Desmodus rotundus* is reduced in bulk, as compared with other phyllostomatids, but it also is nearly symmetrical. It is possible that symmetry may be related to passage of liquid food into the duodenum, both in vampires and in plant feeders.

Second, bats that consume plant material including fruit, nectar, and pollen have a valve flap that nearly always is longer and thinner than valves of bats that eat animal material. This feature is particularly well developed in stenodermines and in *Brachyphylla cavernarum*. In species of *Artibeus, Centurio, Chiroderma, Uroderma, Vampyressa, Vampyrops*, and *Vampyrodes*, the flap achieves such length that its apex is directed up into the duodenum. This results in valve flaps that are parallel with the intestinal wall. In addition, the apex of the muscular flap is quite pointed in species of *Artibeus*. Most glossophagines that have been examined, including species of *Lonchophylla, Lichonycteris, Choeronycteris*, and *Hylonycteris*, but excluding *Glossophaga*, have thin valves that are similar to those of stenodermines. *Anoura* and *Leptonycteris* are intermediate between the *Glossophaga*-type and stenodermine-type valve, but most similar to the latter. It is reasonable to hypothesize that these longer, thinner, often symmetrical valve flaps might improve the efficiency of gastric closure, thus delaying gastric emptying and improving digestion (by increasing time) in these plant feeders.

The pyloric sphincters of *Sturnira lilium* and *S. ludovici*, although symmetrical, are unique in that identifiable muscular flaps either are absent or nearly so as barely to be perceptable. The functional significance of this apparent degeneracy is unknown.

Tunica Muscularis

All stomachs of phyllostomatids possess two layers in the tunica muscularis, an outer longitudinal and an inner circular one. An extremely thin muscularis mucosae occurs just inside the external tunic. It is separated from the outer musculature by an extremely sparse complement of loose submucosa. Both external muscle layers often are variably thicker on the greater curvature than on the lesser curvature. The musculature generally is thicker in phyllostomatines and phyllonycterines than in the other subfamilies.

Considerable variability in the relative thickness of the two outer layers has been observed within the stomachs of phyllostomatids. In most species, the layers are subequal, with the circular layer being the more robust of the two. The circular layer is not infrequently organized into bundles, cross-sections of which are easily viewed in longitudinal stomach sections. This "bundling" is most pronounced in the caecum (when present) where it is prominent in the greater curvature in the majority of stenodermines that have been examined. In a variety of leaf-nosed bats, particularly glossophagines and stenodermines, these bundles are particularly thick just beneath the folds (= rugae) in the stomach lining. In *Chiroderma villosum*, circumferential, parallel, external constrictions occur in the elongate caecum as a result of the distinctively thickened circular bands beneath the rugae.

The circular layer clearly is the dominant portion within the aboral pyloric tube of nearly all species. *Macrophyllum macrophyllum* is a noteworthy exception because in this species the aboral circular layer is thinner than elsewhere in the stomach. In stenodermines, the pyloric circular layer thickens progressively from cardiac vestibule to pyloric sphincter.

Species that feed predominantly or exclusively on plant material have enlarged cardiac vestibules and fundic caeca. This development of "sub-compartments" is accompanied by a progressive reduction in the thickness of the muscularis externis in the enlarged areas. In species that apparently are omnivorous (for example, *Glossophaga soricina, Phyllostomus discolor,* and species of *Micronycteris*), the muscularis externis is reduced in thickness in the apex of the caecum. Such a reduction could be regarded as an intermediate condition or as reflective of a trend toward a frugivorous diet.

Intestine

Bats most often have short, small intestines in comparison to other kinds of small mammals. Most comparative measurements of intestinal lengths in bats (see Eisentraut, 1950; Robin, 1881) have revealed that frugivores usually have relatively long intestines (in relation to body length) when compared to insectivorous, carnivorous, or nectarivorous species. This finding applies to Phyllostomatidae as well as to the Microchiroptera in general.

Eisentraut (1950) noted that of numerous species of bats with a variety of feeding habits, those with an intestinal length greater than four times the body length always were fruit-eating phyllostomatids, and that others had intestines of relatively lesser length. Among species with the longest intestines (relative to body length) are *Chiroderma villosum, Vampyrops vittatus,* and several species of *Artibeus* and *Brachyphylla* (Forman, unpublished data). Vampires have intestines of moderate length. Based on only scattered and incomplete data, those few glossophagines for which measurements are available generally have relatively short intestinal tubes.

In general morphological features, the intestine differs little from that of most other groups of small mammals. Both "small" and "large" intestinal segments are present and a short duodenum is distinguished by noteworthy breadth. One noteable feature, shared with other groups of bats, is the lack of an ascending or transverse colon so that the large intestine is restricted to a relatively short descending colon.

A caecum always is lacking. However, at the junction of small and large intestines there frequently is a small ampulla formed as a result of a hypertrophic dilation of the muscularis externa. Abundant lymphoid tissue (nodules of Peyer's patches) always are present within the ampulla, which is displaced well away from mesenteric attachment to the gut (Forman, 1974*a*, 1974*b*). This ampulla first was observed in *Carollia perspicillata* (Schultz, 1965). Schultz likened this "protrusion," in size and location, to the abbreviated ileocolonic caecum in species of the Old World microchiropterans *Rhinopoma* and *Megaderma.*

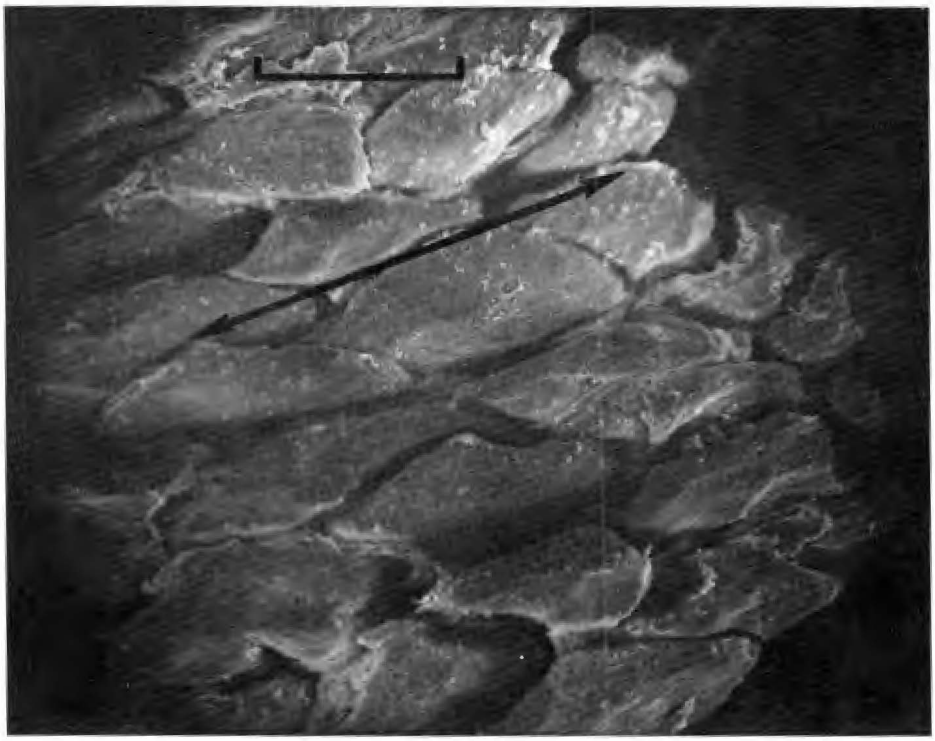

FIG. 5.—Scanning electron micrograph of intestinal villi in the middle portion of the small intestine of *Phyllonycteris aphylla*. The arrow indicates a plane of orientation of rows of villi that is diagonal with respect to the intestinal wall. Note the generally pyramidal shape of each villous and that villi in one row lie between villi in an adjacent row when they are viewed directly from left to right. Scale is 0.25 mm.

Although an ileocaecal valve is lacking in all species that have been examined, Schultz (1965) noted the presence of a valvelike flap within the middle portion of the intestine in *Diphylla ecaudata*. Whether this structure functions as a valve is not known.

The complete gastrointestinal tracts of six species of phyllostomatids were figured by Schultz (1965) in his monograph on blood vessel supply to the digestive tract of bats. Several of his figures of the gut of *Glossophaga soricina* reveal an extremely complex "looping" of the intestine in this species. The first loop of the intestine is joined to the terminal portion of the ileum by a mesenteric ligament. The intestine then proceeds into considerable looping, the extent of which is a function of intestinal length. The attachment of the first intestinal loop to the terminal ileum by a ligament also was illustrated by Schultz in a figure of the gut of *Carollia perspicillata*.

Torsion is extensive in the intestine of most phyllostomatids. In *Carollia* and *Glossophaga*, it is as much as 270° (Schultz, 1965). In most phyllostomatids, the intestine is considerably displaced to the right within the abdominal cavity. One exception is *Macrotus californicus*, in which the intestine is not displaced.

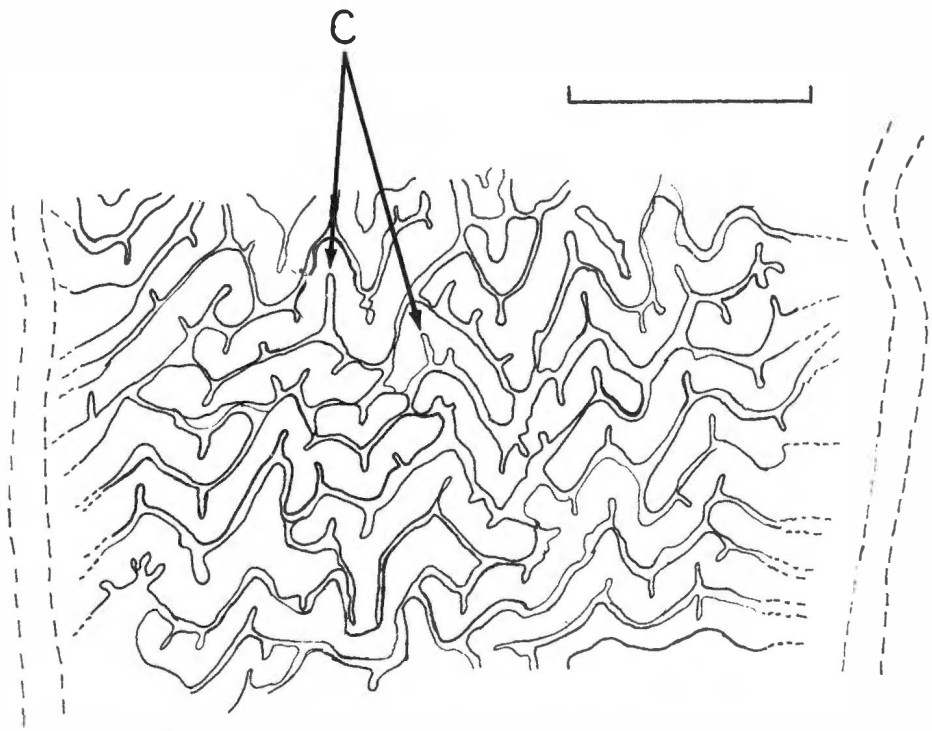

FIG. 6.—Surface view of intestinal folds (= villi) in one specimen of *Artibeus jamaicensis*. Note the complex interdigitation and maze-like organization of ridges. Also, note the narrow channels (C) within the intestinal epithelium. These are most distinctive, in breadth and depth, at the angles or bends of the intestinal folds. Scale is 0.5 mm.

The small intestines of vampires (*Desmodus* and *Diphylla*) are not grossly different from those of other phyllostomatids. However, twisting is only slight, and most of the intestine is folded back upon itself in a series of numerous compact winding folds.

The topography of the mucous membrane of the large intestine generally is uniform among the few species that have been examined. Folds are longitudinal and usually have smooth surfaces with an abundance of goblet cells.

Considerable variation in the topography of the mucous membrane of the small intestine occurs within and among species of phyllostomatids. Projections of the membrane into the lumen can be in the form of fingerlike villi, nearly continuous transverse folds, or projections of a form to some degree intermediate between the other two extremes. Although variation is extensive, a review of the literature, along with some observations of gut morphology in phyllostomatids by the senior author, reveals one apparent pattern of villous distribution within the family. This pattern occurs most consistently within fruit-eating species. Fingerlike villi, if present, usually are located within the distal-most portion or ileum. As one progresses upward toward the gastroduodenal junction, "pyramid-shaped" projections, which are oriented in transverse rows, become

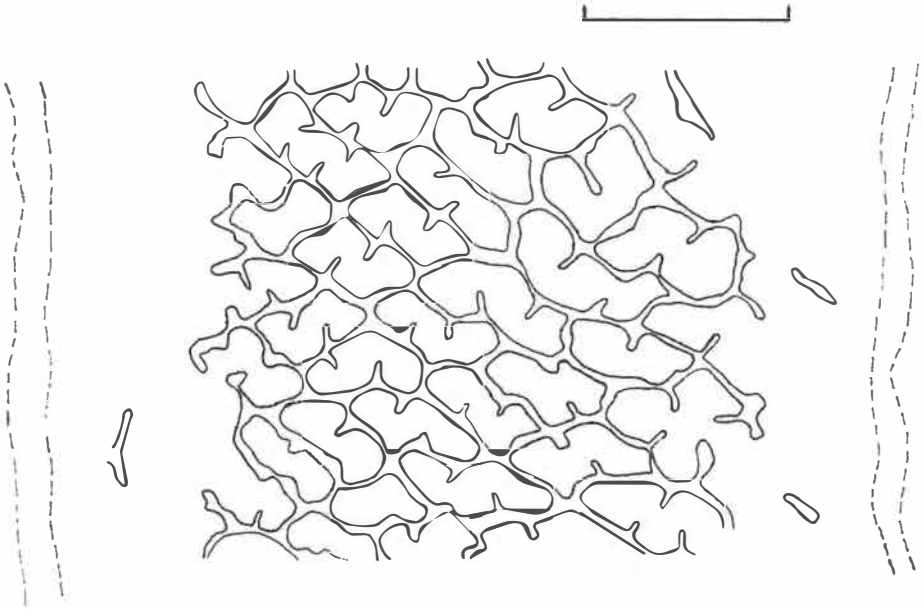

FIG. 7.—Surface view of intestinal folds (=villi) in one specimen of *Carollia perspicillata*. Scale is 0.5 mm.

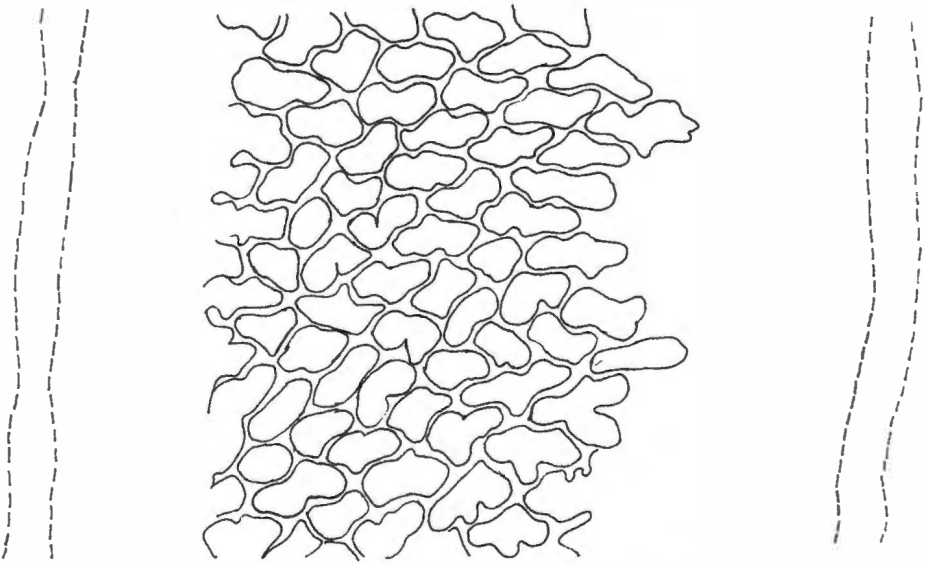

FIG. 8.—Surface view of intestinal folds (=villi) in one specimen of *Chrotopterus auritus*. Note the simplicity of folds as compared with those of *Artibeus jamaicensis* and *Carollia perspicillata*. Scale is 0.5 mm.

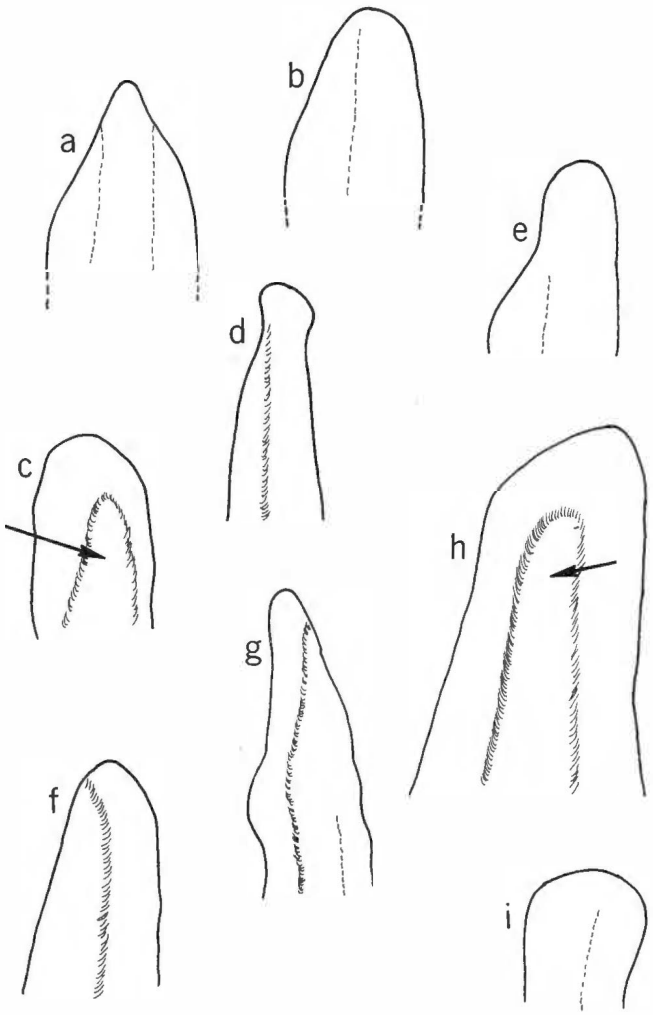

FIG. 9.—Several forms of villi observed within the small intestine (middle portion) of *Macrotus waterhousii*. Arrows indicate the presence of a groove on the surface of some villi. All villi are drawn to scale.

abundant and increase in lateral dimension. These projections are distributed in rows that assume a zig-zag configuration when viewed from the top. The zig-zags in most kinds become progressively more flattened from the middle portion of the intestine through the duodenum. Also, the transverse folds or "pennant-shaped villi" (after Schultz, 1965), which interdigitate with and are interrupted by one another within the lower portions of their distribution, often loose much of this complexity in the upper portions of the small intestine.

The most detailed descriptions of intestinal mucous membrane topography of phyllostomatids are those of Mathis (1928) and Schultz (1965). Mathis

described the villous pattern in *Phyllostomus hastatus* and *Glossophaga soricina* and reported that in his view villi, as such, were lacking in portions of the intestine in *Phyllostomus.* Also, the broad villi in the uppermost intestine were set in oblique rows. This latter pattern also occurs in other species within the family (see Fig. 5). Mathis reported that the villi of *G. soricina* in some areas can be tightly compact without any arrangement into rows. Digitate or club-shaped villi may be interspersed among "transverse folds" and be of somewhat greater height than the folds. Schultz's (1965) description of villous morphology in *G. soricina* generally agrees with that of Mathis (1928); Schultz further stated that the configuration in *Anoura geoffroyi* is "just as with *G. soricina.*" The extent to which the pattern as observed in these two species can be applied to other glossophagines is unknown.

Intestinal villi of the fruit-eating stenodermines frequently are arranged in extremely elaborate interdigitating networks (see Fig. 6). This complicated arrangement likely helps to impede transport of food. Other fruit-eating species have less elaborate villous arrangements (Fig. 7). One carnivorous kind (Fig. 8) has villi uncomplicated in cross-sectional configuration and nearly fingerlike in their appearance.

Villi often are arched from side to side. This feature in combination with staggered arrangement of villi in oblique rows produces a mechanism for entrapment of food material between villi at their bases. This likely results in improved food assimilation or absorption inasmuch as food would tend to be retained in the small intestine for longer periods of time.

Some variability in the structure of villi occurs within localized portions of the small intestine in phyllostomatids. Villi within the middle portion of the intestine of *Macrotus waterhousii* can have narrowly rounded (Fig. 9a) or relatively broadly rounded apices (Fig. 9c). The "arching" of villi, with subsequent entrapment of food material, might be augmented by an apparent groove on the superior surface of some villi (see Figs. 9c, h). Food could become trapped at the base of these folds.

The intestinal topography of *Desmodus* is not known to be particularly specialized. Villi are known to be present in the intestines of both *Desmodus* and *Diphylla* (Schultz, 1965) but generally are not fingerlike, and they are arranged in a pattern of interdigitation. Rouk and Lane (1970) reported that the crypts of Lieberkuhn appear to be reduced in comparison to other species.

The types of cells present within the small intestine of phyllostomatids essentially are the same as those of other groups of bats and other eutherians. The Paneth cells of bats have been examined by Schaaf (1970) in relation to food habits. Schaaf's study group included three insectivorous species as well as *Artibeus jamaicensis, Bachyphylla nana, Phyllonycteris poeyi,* and *Monophyllus redmani.* The results of selected histochemical tests were uniform for prosecretion granules and mucopolysaccharides in all species. Strong acidophilia was present in the cells indicating the probable presence of lysosomes. Secretion granules contained a mixture of protein and carbohydrates. The results agree well with those for other species of mammals. Therefore,

Paneth cells presently are not known to be specialized to permit the assimilation of large quantities of any particular food material by phyllostomatids, for which food habits are highly varied but generally obligate.

The glands of Brunner are mucus producing and generally restricted in distribution to an extremely narrow submucosal ring at the gastroduodenal junction. Several unusual conditions with respect to Brunner's glands occur within the Phyllostomatidae. These conditions might relate to the varied food habits that occur within the family.

The stomachs of *Sturnira lilium* and *S. ludovici* have cells within the bases of the pyloric glands that are histologically identical to the submucosal glands of Brunner within the uppermost duodenum. Several species of *Artibeus* (Forman, 1972; Rouk, 1973) have similar cells within their pyloric stomachs. Cells of Brunner's glands in the duodenum and those cells at the base of pyloric glands stain identically with the periodic acid Schiff reaction for neutral mucopolysaccharides. This staining is considerably different from that within remaining cells of the pyloric glands. Cells such as those of Brunner's glands may provide for better protection of the pyloric mucosa from large amounts of hydochloric acid that likely are produced by the considerable number of parietal cells in some fruit-eating phyllostomatids.

Of those studied, the Brunner's glands of *Phyllostomus hastatus* and *P. discolor* are best developed. Other species of phyllostomatines (those of *Tonatia*, *Micronycteris*, and *Chrotopterus*) have relatively numerous Brunner's glands but they nevertheless are less distinctive than are those of *Phyllostomus*.

The numerous species of stenodermines, carolliines, and some species of glossophagines are in marked contrast to the phyllostomatines. Although only a few species of *Artibeus* have been examined, it is known that the Brunner's glands of *A. lituratus* and *A. jamaicensis* are extremely sparse in the most proximal portion of the duodenum and that they are absent in at least some specimens of *Artibeus phaeotis* and in *A. inopinatus*. It is reasonable to hypothesize that other species of *Artibeus* harbor few of these glands. In addition to species of *Artibeus*, the following bats have been reported to lack Brunner's glands at the gastroduodenal junction: *Centurio senex*, *Chiroderma villosum*, *Uroderma bilobatum*, *Vampyrodes caraccioli*, *Vampyressa pusilla*, *V. nymphaea*, and *Vampyrops helleri*. *Artibeus toltecus* and *Vampyrops vittatus* are reported to have numerous Brunner's glands at the gastrointestinal junction. The basal cells of the pyloric glands in *Centurio senex* are histologically similar to the Brunner's glands of *Artibeus lituratus*. Also, it is noteworthy that all species of stenodermines that lack Brunner's glands in the upper duodenum, except for *Chiroderma*, have relatively extensive zones of pyloric mucosa in the stomach. It is reasonable at this point to suggest that the pyloric mucosa in these animals may be performing the "neutralization" action on the food bolus that ordinarily is believed to be performed by the glands of Brunner in other species of mammals.

Additionally, several species of nectar-feeding glossophagines (*Lichonycteris obscura* and *Choeroniscus godmani*) have been observed to have few Brunner's glands (Forman, 1971*a*). The only phyllonycterine that has been examined,

Brachyphylla cavernarum, has no glands of Brunner. These observations, along with those on stenodermines, clearly indicate that the conditions in certain phyllostomatids do not support the widely held view that mammals consuming plant material have more abundant glands of Brunner than do animals eating animal material.

The connective tissue of the intestine of bats generally is extremely sparse. The intestine of *Desmodus rotundus* (and perhaps the other two sanguivorous species) is a noteworthy exception. Both the submucosa and the lamina propria of the villi are unusually thick and dense. They are highly vascularized and harbor a considerable lymphatic network.

Studies of organized gut-associated lymphoid tissue (Peyer's patches) in New World bats (Forman, 1974*a*, 1974*b*) have revealed differences in abundance, distribution, and morphology of this tissue within the Phyllostomatidae. These differences possibly relate to diet. For example, fruit-eating species usually have the most patches when compared with nectarivorous or with carnivorous and insectivorous kinds. Also, the patches can occur almost anywhere along the length of the small intestine in fruit eaters, frequently including the duodenum. These patches have relatively large nodules with extremely large geminal centers. The patches and nodules of insect eaters and carnivores, in contrast, are relatively small with small germinal centers typically indicating a low state of activity. Patches in these species usually are restricted to the submucosa of the ileum.

These observations suggest that at least within the family Phyllostomatidae organized lymphoid tissue within the gut might be differentially responsive to intestinal contents including food material and associated microbial populations as well.

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MORPHOMETRIC ANALYSIS OF CHIROPTERAN WINGS

JAMES DALE SMITH AND ANDREW STARRETT

Bats are unique among mammals in their possession of wings. The evolution and adaptation of these anatomically complex structures along with the development of an acute ability to orient acoustically has contributed markedly to one of the most interesting examples of adaptive radiation in vertebrate history. Yet the morphometric properties of bat wings have remained poorly understood. Biologists have described chiropteran diversity and faunal complexity throughout the world, but the flight behavior of only a few species has been reported (see Eisentraut, 1936; Dwyer, 1965; Kulzer, 1968; Norberg, 1970, 1976*a*, 1976*b*; Pennycuick, 1971; Schnitzler, 1971).

Revilliod (1916) was the first to attempt to describe the morphometrics of chiropteran wings. In this much overlooked paper, he utilized several indices to demonstrate the degree of adaptation to flight by several families of bats. Poole (1936) was among the earliest investigators to report wing loading values for bats, and Struhsaker (1961) was the first to calculate aspect ratios of bat wings. Bader and Hall (1960) were the first investigators to use computer techniques to analyze the osteometric variation of bat wings. In this study, they employed correlation coefficients to assess the interrelationships among the skeletal elements of the wing and foot of *Myotis lucifugus* and *M. sodalis.*

Other studies, although important contributions, have been limited in their scope and coverage. Among these are Vaughan's (1959) detailed anatomical analysis of three bat species from North America; a more recent survey of the skeletal and muscular system and aerodynamics appears in Vaughan (1970*a*, 1970*b*, 1970*c*). Hartman (1963), Gaisler (1964), Farney and Fleharty (1969), and Jones and Suttkus (1971) have reported wing loading and aspect ratios for numerous species of bats. Pearson *et al.* (1952), Orr (1954), Short (1961), and Jones (1967) have contributed important information relative to the growth and development of chiropteran wings. Seasonal changes in wing loading of several North American species were examined by Davis (1969) and O'Farrell and Studier (1976), and Norbert (1969, 1972) reported on functional osteology and myology of the wings of several bats.

By far, the most extensive analysis of the morphometric properties of bat wings is that by Findley *et al.* (1972). In this study, they relied on regression and correlation procedures as well as factor analysis to examine the wings of approximately 135 species. Our initial goal was to expand on this study with our primary focus on the bats of the family Phyllostomatidae. However, it soon became apparent to us that a meaningful interpretation of the morphometrics of phyllostomatid wings required a broader understanding of the overall variation in size and shape of wings in the Chiroptera.

Methods

Methods of deriving the form and extent of chiropteran wings for the purpose of studying size and shape have been variable. For example, some workers have traced the outline of the extended wing of freshly killed bats or individuals preserved in alcohol. From such tracings, they have derived the area of the wing and other aerodynamic parameters by using a planimeter or by some other time-consuming procedure. While these efforts are to be commended, such techniques do not readily permit an overall consideration of the diversity of the chiropteran fauna of the world.

In addition, most past studies of wing morphology have neglected to consider the influence of the fourth digit in determining the size and shape of the wing. Typically, the lengths of the forearm and digit III are taken to describe the span of the wing, and the length of digit V, its width. These measurements have been used to derive the aspect ratio and wing loading of chiropteran wings, which, characterized in this manner, are assumed to be rectangular in shape. For determination of wing loading, such calculations tend to result in over-estimates of area due to the inclusion of an intrinsic portion of the rectangular shape that, in fact, does not exist in the real wing (Fig. 1). These calculations also may lead to mistaken estimates of similarity between markedly different wings and may mask subtle differences between similarly shaped wings. Furthermore, most past studies have considered only the total lengths of digits rather than examining the variability of digital composition and its influence on wing size and shape.

In this study, 11 wing measurements, length of the head and body, and weight, were obtained from 1456 museum specimens, which comprised 433 species and 147 genera from 17 families of bats. Most of these specimens were conventional study skins, although in some cases only specimens preserved in alcohol were available. The wing measurements included the length of the forearm (as described by Smith, 1972) and the individual lengths of the metacarpal and phalangeal elements of digits III, IV, and V. The length of the often curved and cartilaginous portion of the terminal phalange of the third digit was recorded as the greatest radius of the arc. When available, the length of the head and body and the weight of the specimens were recorded from the specimen label. Head and body length was measured directly on specimens preserved in alcohol. The weights of many specimens, especially those in alcohol, were not recorded at the time of capture. In these cases, weights were estimated (see below). All measurements were recorded in millimeters (by means of dial calipers, calibrated in twentieths of a millimeter) or grams.

Derived Variables

At the outset of our analysis, we, like many others before us, converted our raw variables, *a priori*, into a number of derived variables such as aspect ratio, wing loading, tip index, and so forth. The subsequent analysis of these derived variables was beset with a number of problems. Foremost among these were inflated correlations, which resulted from linear dependence of the derived variables. This resulted in obscuring the sources of dependency. Atchley (1978),

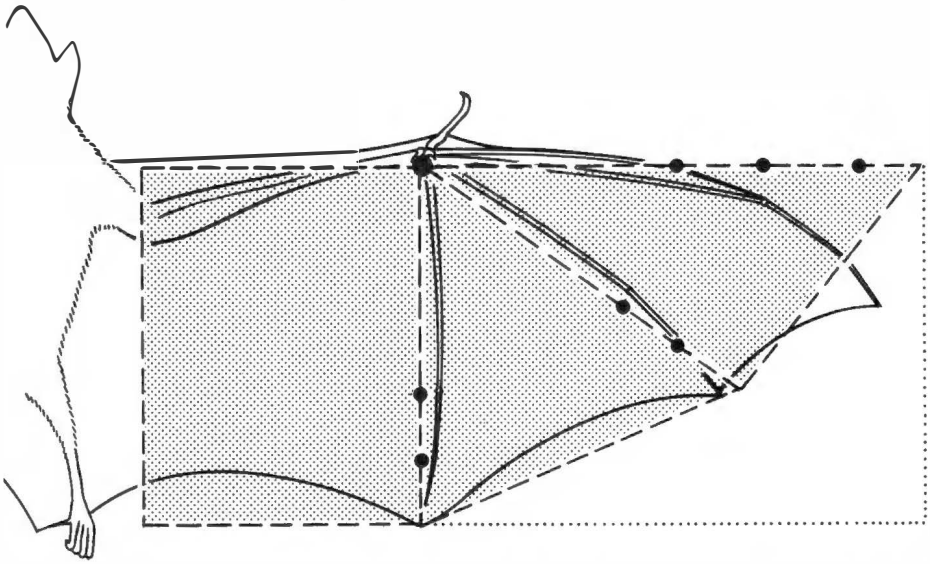

FIG. 1.—Diagrammatic comparison of an actual wing and the construct of the wing (stippled area) used in this study. The dotted line indicates the assumed shape of the wing if only the length (forearm plus digit III) and width (digit V) are considered.

Atchley and Anderson (1978), Atchley *et al.* (1976), and Pimentel (1978) recently presented discussions regarding the statistical properties of derived variables such as ratios and indices. Although derived variables can be useful in some cases, they should be scrutinized closely and avoided when possible. Because the goal of our investigation was to examine, insofar as possible, the interactions among wing components and because these interactions were largely masked by the difficulties noted above, we chose to analyze only our original raw variables. However, after these analyses were completed (*a posteriori*), we found that some of our derived variables could be used in a generalized descriptive sense. Those which were found to be most useful are presented in the Appendix (Tables A1-A21) and are described below.

Weight.—This variable was essential to the computation of wing loading. To circumvent the problem of missing data, Findley *et al.*(1972, table 3) utilized the predicting qualities of a simple linear regression to derive estimated weight from head and body length. We also examined this relationship for 1082 specimens using a similar regression model on known head and body length (X) and weight (Y) and found that the residuals (Y-Y') were lowest at the small-sized end of the variation. However, the residuals increased markedly at the large-sized end of the spectrum. In an attempt to reduce these overestimates, we computed a second degree polynomial regression. This reduced the magnitude of the residuals in the upper range of variation, but the analysis did not provide, in our opinion, totally satisfactory results. As did Findley *et al.* (1972), we partitioned our data into recognized taxonomic groups corresponding to familial and subfamilial categories and obtained different functions for nearly every grouping (Table 1).

TABLE 1.—*Results of the second degree polynomial regression analysis of head and body length (X-axis) and weight (Y-axis). Symbols are: correlation coefficient, r; Y-intercept, A; linear regression coefficient, B1; and quadratic regression coefficient, B2. Significant correlation coefficients and* F*-values are indicated with an asterisk.*

Taxon	*N*	r	A	B1	B2	*F*
Pteropodidae	119	0.967*	26.53	−0.892+0.256	0.011+0.001	928.24*
Emballonuridae	36	0.877*	26.89	−1.104+0.720	0.014+0.005	60.35*
Rhinolophidae	153	0.978*	2.37	−0.375+0.162	0.010+0.001	1680.94*
Nycteridae	34	0.651*	−45.59	1.789+1.508	−0.013+0.014	12.66
Megadermatidae	18	0.573*	−239.29	6.235+2.784	−0.035+0.017	7.46
Noctilionidae	26	0.925*	−218.56	5.229+1.340	−0.023+0.008	121.54*
Phyllostomatinae	168	0.943*	−12.33	0.024+0.184	0.007+0.001	659.23*
Glossophaginae	85	0.865*	24.61	−0.813+0.297	0.010+0.002	136.63*
Carolliinae	12	0.967*	20.76	−0.830+0.658	0.012+0.006	76.95*
Stenoderminae	128	0.955*	26.59	−1.196+0.476	0.017+0.003	678.55*
Desmodontinae	42	0.833*	−10.85	−0.123+1.898	0.008+0.012	44.91*
Phyllostomatidae[1]	391	0.912*	−12.78	0.017+0.130	0.007+0.008	1212.65*
Vespertilionidae	157	0.933*	0.45	−0.116+0.120	0.005+0.001	524.80*
Molossidae	120	0.979*	1.54	−0.227+0.092	0.006+0.001	1442.02*
All bats	1108	0.961*	6.52	−0.422+0.045	0.009+0.001	1990.05*

[1]Combined sample of the family Phyllostomatidae.

The results of our linear regression model (not shown) agreed, for the most part, with those presented by Findley *et al.* (1972). We found in our regression analyses that the regression coefficients (B1 or B2) had relatively little effect on the slope of the line. More importantly, the *Y*-intercept values (*A*) varied greatly, in both our analysis and theirs, and in the majority of cases these intercept values departed, negatively, from zero (the theoretical intercept in these analyses). Therefore, these models predicted extremely low or even negative weights for bats of extremely small body size. In those cases where the departure of the *Y*-intercept was positive, weight would be given to a bat that had zero head and body length. An *a priori* manipulation of the regression model certainly might improve the "fit" of the line, but we suspect biologic reality is quickly obscured by such practice; biological meaning is not automatically ascribed by statistical significance. Furthermore, we suspect that the complexity of the relationships of weight to head and body length and other meristic parameters is more complicated than can be measured precisely with regression/correlation statistics, and we strongly caution other investigators against placing much faith in such predictions. With an awareness of these difficulties in mind, we utilized the predictions of weights generated by our polynomial regression model. However, the weight values obtained in this manner were used only to compute wing loading for comparative purposes and these were not used in any further rigorous analyses. In those groups where there were insufficient numbers to compute a regression function, we utilized the function of the most closely related group for which there was a function. All weights (actual or estimated) were converted to Newtons (Nt).

Wing areas.—The computation of the area of the wings was necessary for the calculations of both aspect ratio and wing loading. The *area of the plagiopatagium* was calculated as the area of a rectangle (length of forearm × length of digit V).

In deriving the area of the wing tip, we attempted to consider an attenuated (polygonal) tip rather than a simplistic, rectangular tip as has been the practice. To accomplish this, using measurements from museum material, we considered a construct of the wing (Fig. 1) in which the fourth digit was an integral component. We noted from empirical observations that the posture of this digit varied among species and that estimates of the tip area varied with this posture. In addition, we found that in most instances, when the wing was fully extended, the fifth digit projected at approximately a right angle from the leading edge (forearm and digit III). Although our testing of empirical data was limited, we found that we could geometrically estimate the angle of projection of digit IV (alpha angle), with 90 per cent confidence, when the panel areas A^1 and A^2 (Fig. 2) were considered to be equal or nearly equal. More precisely, the *alpha angle* equals the arc tangent of (length of digit V/length of digit III). Alpha angles are given in degrees of rotation from digit III. Bats with relatively long fifth digits tended to possess large alpha angles, whereas those with relatively long third digits had lower alpha angles (Table A1).

Once the alpha angle was determined, calculating the area of the two triangles A_1 and A_2 (Fig. 2) was simply: *area of the wing panel between digits III and IV* equals (cosine alpha angle $\times$ (length of digit III $\times$ digit IV) and *area of the wing panel between digit IV and V* equals sine alpha angle $\times$ (length of digit IV $\times$ digit V). The *total area of the wing*, or any portion thereof, was derived by summing the respective areas and multiplying by 2. All areas were converted into square meters (m^2).

Wing loading.—This variable was obtained by weight (Nt)/total area of the wing (m^2). Wing loads are reported as Newtons per square meter (Nt/m^2) (Table A6).

Aspect ratio.—We followed Hartman (1963) in computing this variable: *overall aspect ratio*—2 (length of forearm plus length of digit III)^2/total area of the wing. We partitioned the aspect ratio into two additional ratios as follows: 1) *aspect ratio of the plagiopatagium*—(length of the forearm $\times$ 2)^2/area of the plagiopatagium, and 2) *aspect ratio of the wing tip*—(length of digit III $\times$ 2)^2/area of the wing tip. These ratios are presented in Tables A3-A5.

Tip index.—The tip of the chiropatagium is the principal propulsive portion of the chiropteran wing (Vaughan, 1970*c*). The *tip index* (Findley *et al.*, 1972) is the ratio of length of digit III/length of forearm. A high tip index (2.00) indicates a proportionately long third digit, whereas a low index (1.00) reflects a relatively short wing tip (Table A2).

Relative lengths of the wing elements.—We followed Findley *et al.* (1972) in computing the *relative length of the wing*, which is (length of forearm plus length of digit III)/length of the head and body. In similar fashion, we computed the relative lengths of the forearm and digits III-V (Tables A7-A11).

Percentage of digital composition.—In an *a priori* effort to characterize the varying composition of digits III-V, we computed the percentage that each digital element contributed to the total length of its respective digit. These values proved *a posteriori* to be useful guidelines in the interpretation of the discriminant analysis (Tables A12-A21).

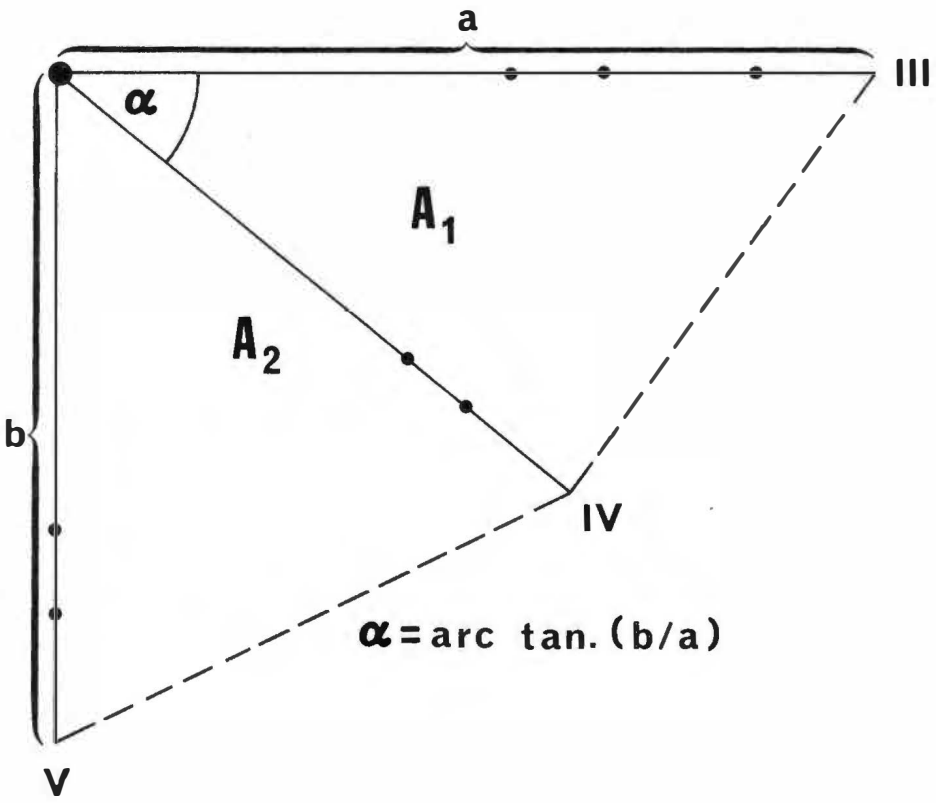

FIG. 2.—Diagrammatic representation of the derivation of the alpha angle. See text (methods) for discussion.

STATISTICAL PROCEDURE

Past studies of the morphometrics of chiropteran wings have been rather limited in the sophistication of their statistical analysis. Most report only simple descriptive statistics such as mean, range, standard deviation, and in some cases, coefficient of variation. As noted earlier, Bader and Hall (1960) and Findley *et al.* (1972) have applied more detailed statistical procedures; the latter employed both correlation and regression statistics as well as factor analysis.

In our initial statistical analysis of the morphometric properties of bat wings, we computed such simple statistics as mean, range, one standard error of the mean, and coefficient of variation for all variables. As noted above, these descriptive statistics for selected derived variables are presented in the Appendix (Tables A1-A21). In these tables, taxonomic groups are ranked by the magnitude of their variable means (largest to smallest) rather than in phylogenetic order. Within the family Phyllostomatidae, subfamilies were allowed to rank in this fashion as were genera within subfamilies. The mean for "all bats" also was allowed to take its appropriate position within the familial ranking.

We used regression and correlation analyses from BIOMED (Dixon, 1973) and SPSS (Nie *et al.*, 1975) in our examination of the relationships between head and body length and weight. However, in the main portion of our study, we employed the multivariate procedures of principal components (PCA) and discriminant analyses to assess the morphometric interactions among the twelve original variables and their effects on size and shape of chiropteran wings. Descriptions of these multivariate procedures may be found in Koons (1962), Cooley and Lohnes (1971), and Pimentel (1978). The computations of these procedures were accomplished in the Computer Center, California Polytechnic University, San Luis Obispo, using an unpublished program (DISANAL) written by Richard A. Pimentel.

Interpretation of the component graphs and variable vectors.—We suspect that many readers might not be completely familiar with the graphical representations that we have employed in this study. It is difficult to portray visually the multidimensional patterns of variation computed by the multivariate statistical procedures used in this study, which assess variation among all p-variables in p-dimensional space. We have used component graphs that are two dimensional views of portions of these multidimensional spaces. In the figures beyond, we have plotted the first and second (1×2) axes to show the length/width character of the dispersion. Height of the dispersion is shown in the graphs in which axes one and three (1×3) are plotted. Viewed together, each set of component graphs depicts the dispersion of centroids in three dimensions. The coordinates used to plot these graphs (Figs. 3, 5, 6) are given in Tables 3 and 5, respectively.

In Fig. 4, we have plotted the direction cosines (PCA) and canonical vectors for the twelve original variables in much the same manner as described for the component graphs. The coordinates used to plot these vectors are given in Tables 2 and 4, respectively. To avoid confusion, only the positive end of each vector is shown. The tail or negative end of a vector passes through the ordinate of each graph for an equal length in the opposite direction. The influence that any one vector has on the location of the group centroids is determined by the magnitude or length of that vector and the proximity of its point (positive end) or tail (negative end) to the various centroids. Long vectors exert a strong influence on the location, whereas shorter vectors exhibit weaker effects. In these analyses, an association with the positive end of a vector implies large size (longness) and proximity to the tail of a vector indicates small size (shortness).

It is important to bear in mind continually the fact that the overall ordination of groups (Figs. 3, 5, 6) is the result of synergistic interplay among variables (Fig. 4) and not the result of any one or two of these. We have attempted to illustrate and set these figures in such a way as to facilitate the reader's perception of the dimensionality of the variation on the dispersion of groups. To facilitate further an interpretation of the component graphs, the reader may wish to make a xerox transparency of Fig. 4 and overlay this on the corresponding component graphs. In addition, this overlay may be used to interpret Figs. 11 to 16.

For those readers who wish to see the finer aspects of the ordination, we strongly encourage the construction of three-dimensional models. This may be accomplished easily by xeroxing the 1×2 component graphs and attaching these to a styrofoam base. Sticks may be cut to an appropriate length by using the 1×3 component graphs to determine the height of particular centroids. Leave a sufficient excess on these sticks to allow placement in the styrofoam base at their respective (1×2) centroid positions. A three-dimensional model of the variable vectors may be constructed by pushing wires through a styrofoam ball and using Fig. 4 for proper orientation.

Specimens Examined

In the following list of specimens examined, a total of 1456, bold-faced letters preceding the familial or subfamilial name will be used to identify the respective group centroids in the component graphs (Figs. 5, 6, 10). Within the Phyllostomatidae, bold-faced numbers indicate the species identity in the component graphs (Figs. 11-16). Any variations from this scheme will be noted in the respective legends. Numbers following scientific names indicate sample size. The mnemonic acronyms (for example, PTEROP for Pteropodidae and PHYNYC for Phyllonycterinae) used in the figures are sufficiently phonetic to provide easy interpretation.

A. Pteropodidae (172); *Aethalops alecto*, 5; *Chironax melanocephalus*, 4; *Cynopterus archipelagus*, 4; *C. brachyotis*, 5; *C. sphinx*, 4; *Dobsonia inermis*, 2; *D. minor*, 2; *D. moluccensis*, 1; *D. praedatrix*, 1; *Dyacopterus spadiceus*, 3; *Eidolon helvum*, 2; *Epomophorus labiatus*, 1; *E. minor*, 4; *E. wahlbergi*, 1; *Balionycteris maculata*, 5; *Epomops dobsoni*, 1; *Haplonycteris fisheri*, 3; *Hypsignathus monstrosus*, 1; *Megaerops ecaudatus*, 3; *M. wetmorei*, 3; *Micropteropus pusillus*, 3; *Myonycteris torquata*, 2; *Nanonycteris veldkampi*, 1; *Penthetor lucasi*, 7; *Ptenochirus jagori*, 6; *Pteropus alecto*, 2; *P. anetianus*, 1; *P. giganteus*, 3; *P. hypomelanus*, 4; *P. lylei*, 1; *P. melanotus*, 1; *P. rufus*, 1; *P. tonganus*, 5; *P. woodfordi*, 7; *Rousettus amplexicaudatus*, 1; *R. angolensis*, 1; *R. arabicus*, 2; *R. leschenaulti*, 3; *R. obliviosus*, 1; *Scotonycteris zenkeri*, 1; *Eonycteris spelaea*, 3; *Macroglossus lagochilus*, 4; *M. minimus*, 3; *Megaloglossus woermanni*, 8; *Melonycteris melanops*, 2; *M. woodfordi*, 4; *Notonycteris macdonaldi*, 11; *Syconycteris crassa*, 4; *Nyctimene albiventer*, 6; *N. cephalotes*, 3; *N. major*, 6; *N. robinsoni*, 6; *Paranyctimene raptor*, 3; *Harpionycteris whiteheadi*, 1.

B. Rhinopomatidae (9): *Rhinopoma hardwickei*, 5; *R. microphyllum*, 1; *R. muscatellum*, 3.

C. Craseonycteridae (5): *Craseonycteris thonglongyai*, 5.

D. Emballonuridae (90): *Centronycteris maximilliani*, 1; *Coleura afra*, 5; *Cormura brevirostris*, 2; *Emballonura atrata*, 1; *E. beccarii*, 6; *E. monticola*, 3; *E. nigrescens*, 3; *E. raffrayana*, 2; *E. semicaudata*, 5; *Peropteryx kappleri*, 1; *P. macrotis*, 2; *P. leucopterus*, 2; *Rhynchonycteris naso*, 2; *Saccopteryx bilineata*, 3; *Taphozous australis*, 2; *T. flaviventris*, 3; *T. hamiltoni*, 2; *T. hildegardeae*, 2; *T. longimanus*, 2; *T. mauritianus*, 3; *T. melanopogon*, 8; *T. nudiventris*, 4; *T. peli*, 3; *T. perforatus*, 9; *T. pluto*, 5; *T. saccolaimus*, 5; *Cyttarops alecto*, 1; *Depanycteris isabella*, 1; *Diclidurus scutatus*, 1; *D. albus*, 1.

E. Rhinolophidae (140): *Rhinolophus acuminatus*, 2; *R. affinis*, 2; *R. alcyone*, 6; *R. arcuatus*, 2; *R. blassi*, 2; *R. borneensis*, 1; *R. creaghi*, 2; *R. capensis*, 2; *R. clivosus*, 4; *R. cornutus*, 2; *R. deckeni*, 2; *R. denti*, 2; *R. euryale*, 3; *R. euryotis*, 2; *R. ferrumequinum*, 4; *R. fumigatus*, 2; *R. hildebrandti*, 2; *R. hipposideros*, 5; *R. keyensis*, 3; *R. landeri*, 3; *R. lepidus*, 2; *R. luctus*, 2; *R. macrotis*, 1; *R. madurensis*, 1; *R. malayanus*, 1; *R. megaphyllus*, 2; *R.*

mehelyi, 1; *R. pearsoni*, 2; *R. philippinensis*, 2; *R. pusillus*, 2; *refulgens*, 4; *R. rouxi*, 2; *R. shameli*, 1; *R. simulator*, 1; *R. stheno*, 2; *R. subbadius*, 2; *R. swinnyi*, 2; *Hipposideros armiger*, 3; *H. bicolor*, 4; *H. caffer*, 8; *H. camerunensis*, 2; *H. cineraceous*, 2; *H. commersoni*, 4; *H. cyclops*, 4; *H. diadema*, 2; *H. galeritus*, 1; *H. lankadiva*, 3; *H. larvatus*, 3; *H. lylei*, 2; *H. pratti*, 1; *H. speoris*, 2; *Aselliscus tricuspidatus*, 2; *Asellia tridens*, 3; *Cloeotis percivali*, 5; *Coelops frithii*, 2; *Triaenops persicus*, 2.

F. NYCTERIDAE (26): *Nycteris arge*, 2; *N. grandis*, 2; *N. hispida*, 4; *N. javanica*, 3; *N. macrotis*, 6; *N. thebaica*, 5; *N. tragata*, 1; *N. woodi*, 3.

G. MEGADERMATIDAE (14): *Cardioderma cor*, 4; *Lavia frons*, 2; *Macroderma gigas*, 1; *Megaderma lyra*, 5; *M. spasma*, 2.

H. NOCTILIONIDAE (6): *Noctilio albiventris*, 4; *N. leporinus*, 2.

I. MORMOOPIDAE (8): *Pteronotus parnellii*, 2; *P. davyi*, 2; *P. gymnonotus*, 2; *Mormoops blainvillii*, 1; *M. megalophylla*, 1.

J. PHYLLOSTOMATINAE (183): **1-2** *Micronycteris megalotis*, 14; **3** *M. schmidtorum*, 8; **4** *M. minuta*, 8; **5** *M. hirsuta*, 4; **6-7** *M. brachyotis*, 6; **8** *M. pusilla*, 1; **9** *M. nicefori*, 8; **10** *M. sylvestris*, 4; **11** *M. behni*, 2; **12** *M. daviesi*, 5; **13** *Macrotus waterhousii*, 4; **14** *M. californicus*, 10; **15-16** *Lonchorhina aurita*, 13; **17** *L. orinocensis*, 1; **18-19** *Macrophyllum macrophyllum*, 8; **20-21** *Tonatia bidens*, 7; **22** *T. brasiliensis*, 3; **23** *T. carrikeri*, 3; **24** *T. nicaraguae*, 5; **25** *T. silvicola*, 8; **26** *T. venezuelae*, 3; **27** *Mimon bennetti*, 1; **28** *M. cozumelae*, 4; **29-30** *M. crenulatum*, 12; **31** *M. koepckeae*, 1; **32-33** *Phyllostomus discolor*, 10; **34** *P. hastatus*, 6; **35** *P. elongatus*, 4; **36** *P. latifolius*, 2; **37** *Phylloderma stenops*, 2; **38** *Trachops cirrhosus*, 10; **39** *Chrotopterus auritus*, 3; **40** *Vampyrum spectrum*, 5.

K. GLOSSOPHAGINAE (156): **1** *Glossophaga soricina*, 6; **2** *G. alticola*, 5; **3** *G. commissarisi*, 10; **4** *G. longirostris*, 5; **5** *Monophyllus redmani*, 6; **6** *M. plethodon*, 5; **7** *Leptonycteris nivalis*, 10; **8** *L. sanborni*, 3; **9** *L. curasoae*, 5; **10** *Lonchophylla hesperia*, 8; **11** *L. mordax*, 10; **12** *L. concava*, 2; **13** *L. robusta*, 7; **14** *L. thomasi*, 10; **15** *Lionycteris spurrelli*, 4; **16** *Anoura geoffroyi*, 5; **17** *A. caudifera*, 3; **18** *A. cultrata*, 5; **19** *A. werckleae*, 2; **20** *A. brevirostrum*, 2; **21** *Scleronycteris ega*, 1; **22** *Lichonycteris degener*, 1; **23-24** *L. obscura*, 7; **25** *Hylonycteris underwoodi*, 5; **26** *Platalina genovensium*, 6; **27** *Choeroniscus godmani*, 3; **28** *C. minor*, 3; **29** *C. intermedius*, 6; **30** *C. inca*, 3; **31** *C. periosus*, 1; **32** *Choeronycteris mexicana*, 10; **33** *Musonycteris harrisoni*, 3.

L. CAROLLIINAE (23): **41** *Carollia castanea*, 6; **42** *C. subrufa*, 2; **43** *c. brevicauda*, 4; **44** *C. perspicillata*, 4; **45** *Rhinophylla pumilio*, 2; **46** *R. alethina*, 2; **47** *R. fischerae*, 3.

M. STENODERMINAE (276): **1** *Sturnira lilium*, 5; **2** *S. thomasi*, 3; **3** *S. tildae*, 5; **4** *S. magna*, 6; **5** *S. mordax*, 1; **6** *S. bidens*, 6; **7** *S. nana*, 5; **8** *S. aratathomasi*, 3; **9** *S. ludovici*, 10; **10** *S. erythromos*, 6; **11** *Uroderma bilobatum*, 10; **12** *U. magnirostrum*, 2; **13** *Vampyrops infuscus*, 5; **14** *V. vittatus*, 4; **15** *V. dorsalis*, 6; **16** *V. aurarius*, 6; **17** *V. nigellus*, 2; **18** *V. brachycephalus*, 1; **19** *V. helleri*, 6; **20** *V. lineatus*, 5; **21** *V. recifinus*, 2; **22** *Vampyrops sp.* (new species, *fide* Gardner and Handley), 5; **23** *Vampyrodes caraccioli*, 5; **24** *Vampyressa pusilla*, 4; **25** *V. melissa*, 6; **26** *V. nymphaea*, 3; **27** *V. brocki*, 1; **28** *V. bidens*, 3; **29** *Chiroderma doriae*, 2; **30** *C. villosum*, 6; **31** *C. salvini*, 4; **32** *C. trinatatum*, 6; **33** *C. improvisum*, 1; **34** *Ectophylla macconnelli*, 6; **35** *Artibeus cinereus*, 6; **36** *A. glaucus*, 2; **37** *A. watsoni*, 4; **38** *A. phaeotis*, 6; **39** *A. toltecus*, 5; **40** *A. aztecus*, 5; **41** *A. hirsutus*, 6; **42** *A. inopinatus*, 5; **43** *A. concolor*, 5; **44** *A. jamaicensis*, 8; **45** *A. planirostris*, 10; **46** *A. lituratus*, 8; **47** *Artibeus sp.* (undescribed species, *fide* D. R. Patten), 10; **48** *Enchisthenes harti*, 6; **49** *Ardops nichollsi*, 6; **50** *Phyllops falcatus*, 1; **51** *P. haitiensis*, 4; **52** *Ariteus flavescens*, 6; **53** *Stenoderma rufum*, 6; **54** *Pygoderma bilabiatum*, 1; **55** *Ametrida centurio*, 8; **56** *Sphaeronycteris toxophyllum*, 2; **57** *Centurio senex*, 5.

N. PHYLLONYCTERINAE (27): **58** *Brachyphylla cavernarum*, 6; **59** *B. nana*, 3; **60** *Erophylla bombifrons*, 3; **61** *E. sezekorni*, 5; **62** *Phyllonycteris poeyi*, 4; **63** *P. aphylla*, 6.

O. DESMODONTINAE (13): **48-49** *Desmodus rotundus*, 5; **50** *Diaemus youngi*, 5; **51** *Diphylla ecaudata*, 3.

P. NATALIDAE (4): *Natalus stramineus*, 3; *N. micropus*, 1.

Q. THYROPTERIDAE (3): *Thyroptera discifera*, 2; *T. tricolor*, 1.
FURIPTERIDAE (1): *Furipterus horrens*, 1; sample too small for analysis.

R. MYZAPODIDAE (2): *Myzapoda aurita*, 2.

S. VESPERTILIONIDAE (178): *Barbastella barbastellus*, 5; *Chalinolobus gouldi*, 1; *C. tuberculatus*, 2; *C. variegatus*, 2; *Eptesicus bottae*, 6; *E. hottentotus*, 1; *E. serotinus*, 4; *E. somaliscus*, 1; *E. tenuipinnis*, 3; *Euderma maculatum*, 2; *Endiscopus denticulus*, 1; *Hesperoptenus tickelli*, 2; *Histiotus montanus*, 1; *Laephotis botswanae*, 2; *Lasionycteris noctivagans*, 1; *Lasiurus borealis*, 3; *L. cinereus*, 2; *L. egregius*, 1; *L. intermedius*, 2; *L. seminolus*, 2; *Minetillus moloneyi*, 3; *Myotis adversus*, 2; *M. austroriparius*, 2; *M. bechsteini*, 3; *M. blythi*, 3; *M. brandti*, 1; *M. capaccinii*, 3; *M. daubentonii*, 3; *M. evotis*, 1; *M. formosus*, 2; *M. muricola*, 3; *M. myotis*, 3; *M. mystacinus*, 4; *M. nattereri*, 2; *M. emarginatus*, 3; *M. ricketti*, 1; *M. scotti*, 4; *M. welwitschii*, 2; *Nycticeius humeralis*, 2; *N. schliefeni*, 1; *Nycatalus aviator*, 3; *N. azoreum*, 1; *N. lasiopterus*, 4; *N. leisleri*, 2; *N. noctula*, 5; *Otonycteris hemprichi*, 5; *Scotoecus hirundo*, 2; *Philetor brachypterus*, 4; *Pipistrellus imbricatus*, 4; *P. kuhlii*, 1; *P. nanulus*, 1; *P. pipistrellus*, 5; *P. savii*, 1; *P. subflavus*, 3; *Plecotus auritus*, 5; *P. phyllotis*, 2; *P. townsendii*, 2; *Scotomanes ornatus*, 1; *Scotophilus gigas*, 2; *S. heathi*, 3; *S. leucogaster*, 2; *Tylonycteris pachypus*, 3; *T. robustula*, 10; *Vespertilio superans*, 1; *Miniopterus medius*, 2; *M. schreibersi*, 4; *Harpiocephalus harpia*, 1; *Murina aurata*, 3; *M. cyclotis*, 2; *M. huttoni*, 1; *M. leucogaster*, 1; *Kerivoula cuprosa*, 1; *K. hardwickei*, 2; *K. picta*, 1; *Nyctophilus geoffroyi*, 1.

T. MYSTACINIDAE (8): *Mystacina tuberculata*, 8.

U. MOLOSSIDAE (112): *Cheiromeles torquatus*, 3; *Eomops albatus*, 1; *Eumops auripendulus*, 3; *E. bonariensis*, 1; *E. glaucinus*, 1; *E. hansae*, 1; *E. trumbulli*, 1; *E. underwoodi*, 1; *Molossops brachymeles*, 1; *M. temmincki*, 1; *M. greenhalli*, 1; *Molossus ater*, 4; *M. bondae*, 1; *M. crassicaudatus*, 1; *M. molossus*, 6; *Otomops martiensseni*, 4; *O. wroughtoni*, 2; *Sauromys petrophilus*, 3; *Promops centralis*, 1; *P. davisoni*, 1; *P. nasutus*, 6; *Tadarida aegyptiaca*, 2; *T. africana*, 2; *T. aloysiisabaudiae*, 2; *T. ansorgei*, 3; *T. aurispinosa*, 2; *T. australis*, 2; *T. bivittata*, 2; *T. condylura*, 3; *T. congicus*, 2; *T. demonstrator*, 2; *T. doriae*, 4; *T. femorosacca*, 1; *T. gallagheri*, 1; *T. jobensis*, 4; *T. jugularis*, 2; *T. laticaudata*, 3; *T. leonis*, 1; *T. lobata*, 2; *T. macrotis*, 2; *T. major*, 1; *T. midas*, 2; *T. nanulus*, 2; *T. nigeriae*, 4; *T. norfolkensis*, 2; *T. plicata*, 1; *T. pumila*, 3; *T. russata*, 2; *T. sarasinorum*, 5; *T. spurrelli*, 2; *T. teniotus*, 3; *T. thersites*, 1.

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Finally, we wish to express our gratitude to Susan E. Smith who sat for many hours recording measurements, keypunched data, helped with the illustrations, and most of all provided moral support and companionship to the senior author.

RESULTS AND DISCUSSION

The mean (range in parentheses), one standard error, and coefficient of variation for the raw variables and selected derived variables are given in the Appendix (Tables A1-A21). A pooled correlation matrix for raw variables was computed, and all coefficients, except those for the third phalanx of digit III, were strongly and positively correlated ($P<0.001$). This was to be expected owing to the size/growth nature of these variables. The coefficients for the third phalanx of digit III were low because this phalanx is not present in all groups of bats (for example, pteropodids, emballonuroids, rhinolophoids, see Miller, 1907). The largest coefficients of correlation for this phalanx were shown with the metacarpal and two phalanges of digit V, 0.405 ($P<0.05$) and 0.325 ($P<0.05$), respectively.

Principal components analysis.—The results of the principal components analysis are given in Figs. 3 and 4 and Tables 2 and 3. Because of the notorious susceptibility of the first component axis to size factors, this analysis yields only broad generalizations concerning the shape of bat wings. The first component, usually designated the "size component," exhibits 91.8 per cent of the total variation (Table 2). Also, the component correlations for all variables are high for this component. The first three components account for 96.7 per cent of the total variation. Although component loading extends to the twelfth component, 99.1 per cent is accumulated by the sixth. The majority of the loading, past the first three components, is contributed by the third phalanx of digit III, which exhibits high loading in the fourth and seventh component (51.36 and 13.75 per cent, respectively).

As noted above, the first component contains high loading as the result of general size. This is illustrated by the complete agreement of signs by all coefficients in this component (Table 2). The direction of the sign (negative, in this case) is irrelevant and simply indicates that all variables increase (+) or decrease (−) in the same direction (for example, length of the head and body decreases in consort with length of the forearm or any of the other raw variables). The fact that the component scores for each variable are of different magnitude indicates general positive allometry among the variables. The effect of size in the first component also can be seen in Figs. 3 and 4. In figure 4A-B, the agree-

TABLE 2.—*Eigenvectors (direction cosines) of principal components for lengths of head and body and selected wing elements. Only the first three components are shown because most of the variation is exhibited in these components. The numbers in parentheses following each component score indicates the percentage of variance contributed by each variable to a particular component.*

Variable	Component Axes 1	2	3	Cumulative per cent
Head and body	−0.626 (96.07)	0.701 (3.53)	−0.075 (0.03)	99.63
Forearm	−0.427 (96.77)	−0.173 (0.46)	0.176 (0.38)	97.61
Metacarpal III	−0.313 (92.52)	−0.124 (0.42)	0.485 (5.13)	98.07
Digit III, phalanx 1	−0.186 (89.16)	−0.038 (0.11)	−0.130 (1.00)	90.27
Digit III, phalanx 2	−0.244 (84.53)	−0.165 (1.13)	−0.525 (9.03)	94.32
Digit III, phalanx 3	−0.022 (6.03)	−0.247 (21.63)	0.014 (0.05)	27.71
Metacarpal IV	−0.303 (93.16)	−0.261 (2.02)	0.362 (3.08)	98.26
Digit IV, phalanx 1	−0.150 (86.65)	−0.069 (0.53)	−0.139 (1.70)	88.88
Digit IV, phalanx 2	−0.133 (70.89)	−0.150 (2.62)	−0.440 (17.89)	91.40
Metacarpal V	−0.276 (86.51)	−0.505 (8.51)	−0.064 (0.11)	95.13
Digit V, phalanx 1	−0.116 (82.78)	−0.106 (2.04)	−0.094 (1.26)	86.08
Digit V, phalanx 2	−0.107 (75.09)	−0.114 (2.50)	−0.280 (11.90)	89.49
Per cent trace	91.8	2.7	2.1	
Cumulative per cent	91.8	94.5	96.7	

ment among the signs of the first component scores is manifested by all vectors of variables (direction cosines) orienting toward the left. Likewise, the ordination of group centroids along the first component axis (Fig. 3) aligns large-sized bats (Pteropodidae, A) to the left, and small-sized bats (Craseonycteridae, C) to the right. Also, it should be noted that the nature of the ordination of groups (Fig. 3) is greatly influenced, especially in the first two component axes, by the magnitude of the eigenvalues for head and body length (−0.626 and 0.701, Table 2 and Fig. 4A-C). Other vectors of variables that markedly affect the ordination along the first component are the lengths of the forearm (B) and the metacarpals of digits III-V (C, G, J) (−0.427, −0.313, and −0.276, respectively).

In the second component, all coefficients, except that for the length of the head and body, agree in sign (Table 2). This strongly suggests that the size and shape of bat wings are essentially independent of body size and, presumably, weight. The fact that all of the coefficients for intrinsic wing elements vary in magnitude continues to indicate a level of positive allometry. Other than head and body length, the strongest eigenvalue in this component axis is that for the fifth metacarpal (−0.505). It is difficult to evaluate the shape tendencies in the second component because the correlation structure is rather weak in both this and the third component. In addition, a minor portion of the variation is shown in these two components compared to the overwhelming nature of the first. A cautious interpretation of the shape trends in the second component might be that shape is modified by a factor of size.

Influence attributable to shape are much more distinct, albeit weak, among the coefficients of the third component. Body size, as expressed by the length of

TABLE 3.—*Mean coordinates of group centroids from the principal components analysis. These centroids are plotted in Fig. 3.*

Taxon	Code	Component axes 1	2	3
Pteropodidae	A	−68.73	9.16	−21.46
Rhinopomatidae	B	16.06	1.95	5.81
Craseonycteridae	C	60.81	−1.68	−9.15
Emballonuridae	D	2.23	1.05	10.75
Rhinolophidae	E	9.84	−2.62	−1.56
Nycteridae	F	13.07	−4.78	−5.53
Megadermatidae	G	−17.38	−6.65	−11.30
Noctilionidae	H	−24.10	−17.87	2.90
Mormoopidae	I	8.07	−4.62	10.09
Phyllostomatinae	J	−0.64	−7.09	0.27
Glossophaginae	K	19.63	2.86	−1.17
Carolliinae	L	24.47	−4.63	−4.36
Stenoderminae	M	4.14	−6.08	−1.59
Phyllonycterinae	N	−2.26	−0.75	3.41
Desmodontinae	O	−15.05	−5.44	7.14
Natalidae	P	32.07	−9.13	0.37
Thyropteridae	Q	40.68	−4.96	6.70
Myzapodidae	R	13.70	−9.45	1.06
Vespertilionidae	S	19.24	−2.43	6.15
Mystacinidae	T	18.16	−0.76	6.14
Molossidae	U	2.35	9.66	9.51

head and body, has little influence in this component, having expended most of its force in the ordination of the first and second component axes. It will be noted (Table 2) that several of the wing elements, notably the third and fourth metacarpals (C,G) and the second phalanges of digits III-V (E,I,L), have their largest eigenvalues in the third component. The divergence of variable vectors, caused by differential signs in the third component axis, further substantiates the shape trends of this component (Fig. 4B-C). Bearing in mind that only a small portion of the variation is expressed and the weak correlation structure of the third component, we cautiously direct attention to several interesting associations among the variables in this component.

In Figure 4B-C, the vectors for variables of all intrinsic wing elements (B-L) are directed to the left; the vector for head and body length (A) projects to the right in the 2×3 graph (Fig. 4C) again indicating the independent nature of this variable. As noted previously, the general similarity in the direction of orientation of all vectors for wing elements postulates a general allometric relationship among wing components in terms of size. However, in the two graphs (1×3 and 2×3), the vectors for wing components diverge into different regions of the graphs (that is, some orient upward and others are directed downward). This signifies differences in relative independence that ultimately are expressed as shape.

The vectors for the third and fourth metacarpals (C, G) project in the same general direction and are nearly equal in length (Fig. 4B-C), indicating that their

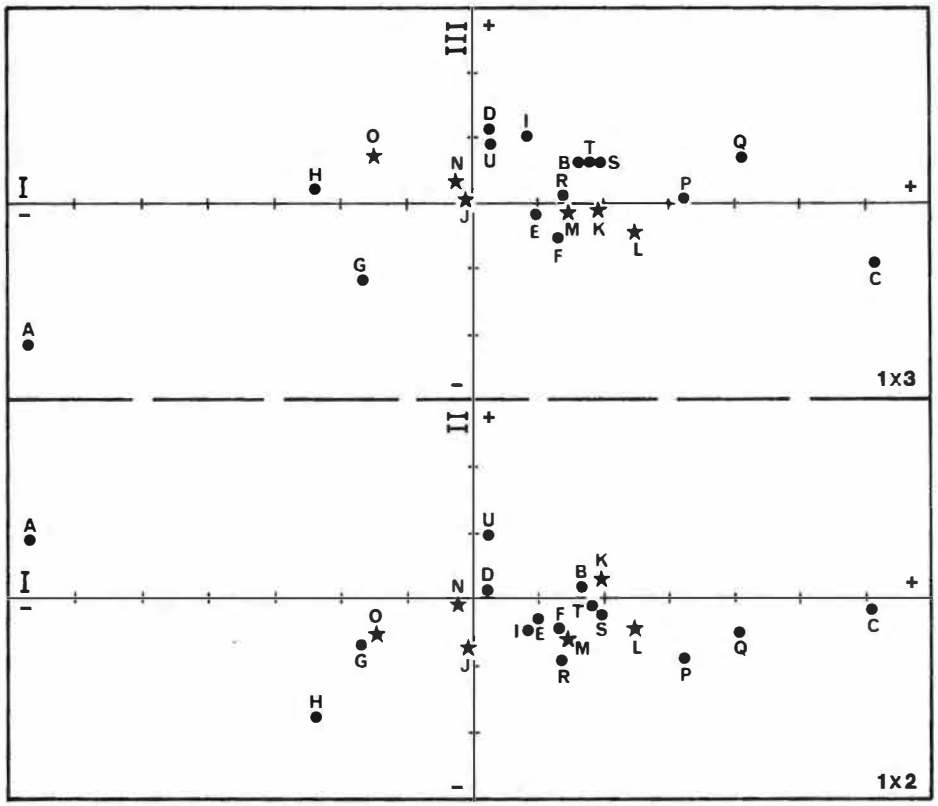
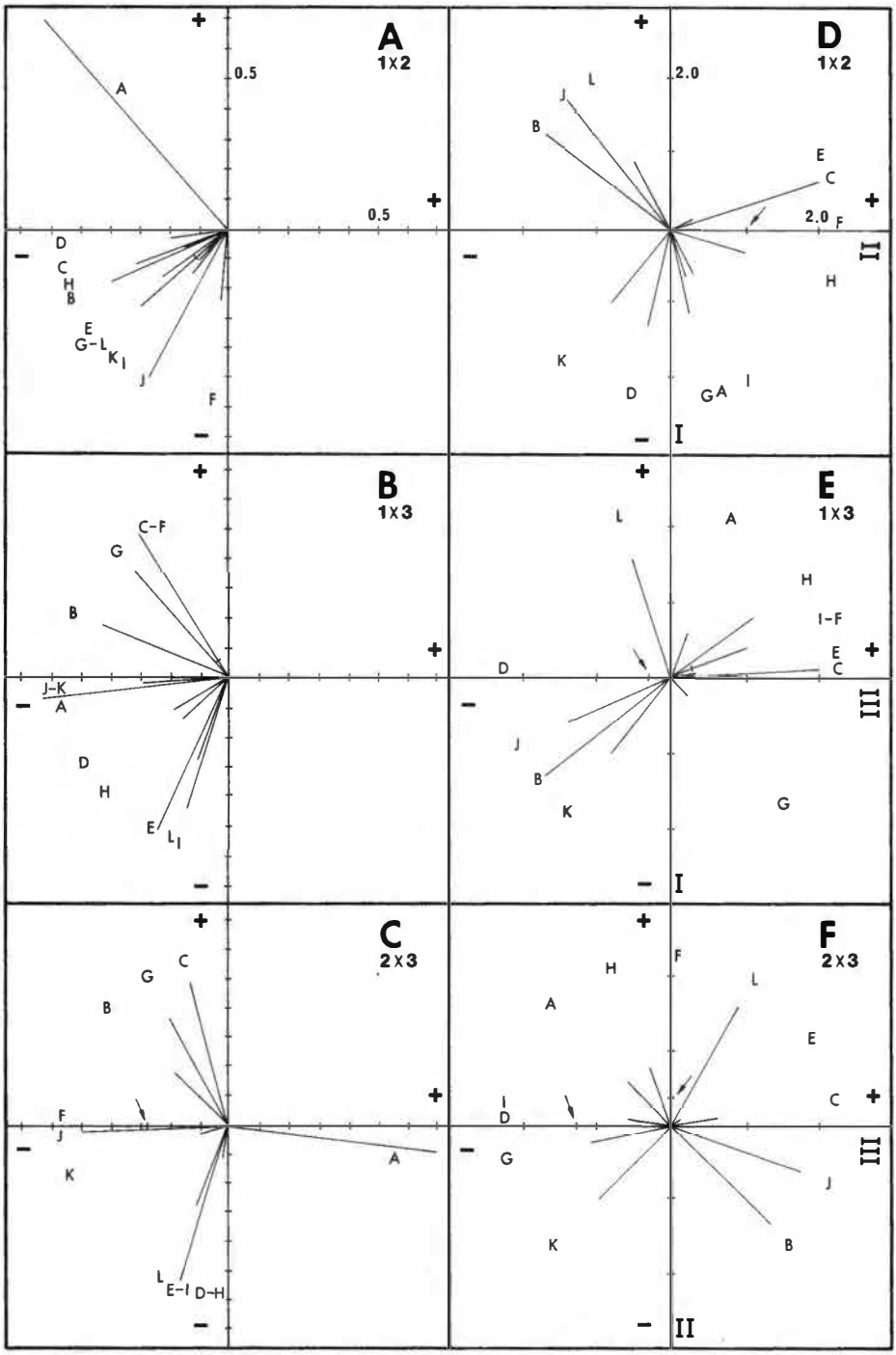


FIG. 3.—Component graph from principal component analysis. Group centroids are plotted on the 1 × 2 axes and 1 × 3 axes to illustrate their position in Euclidean three-space. Coordinates for these centroids are given in Table 3. Stars represent phyllostomatid centroids (see list of specimens examined or Table 3 for key to alphabetic code). This figure may be xeroxed and folded on the dotted line to help visualize the three-dimensionality of the dispersion of centroids.

variation is associated. Although somewhat removed, the vector for the forearm (B) tends to share this same general relationship. It is interesting to note that the vector for the fifth metacarpal (J) is rather far removed from the third and fourth metacarpals thereby suggesting a marked divergence in its pattern of variation. This suggests that the forearm and metacarpals of digits III and IV vary as a unit, whereas the metacarpal of the fifth digit is somewhat independent. Following these examples, we can point to several additional interesting sets of vectors that

FIG. 4.—Positive eigenvectors (A-C) and variable vectors (D-F) for the raw variables computed in the principal components analysis and discriminant analysis, respectively. Coordinates for these vectors are given in Tables 2 and 4, respectively. Corresponding sets of vectors from these two analyses are shown side-by-side to allow easy comparison. The negative portions of the vectors were omitted to avoid confusing the diagram. If shown, they would project an equal distance in the opposite direction past the zero-zero point. Letters at the ends of vectors refer to the respective lengths of variables: A, head and body; B, forearm; C, metacarpal III; D, first phalanx III; E, second phalanx III; F, third phalanx III; G,



metacarpal IV; H, first phalanx IV; I, second phalanx IV; J, metacarpal V; K, first phalanx V; L, second phalanx V. See text for discussion.

have generally associated patterns of variation. The first phalanges of digits III and IV (D, H) appear to have a similarly related effect on wing shape. Likewise, the vectors for the second phalanges of digits III to V (E, I, L) suggest a similar relationship among these phalangeal elements. These two sets of variables, together, diverge markedly from the metacarpal elements (C, G, J) of their respective digits. The vector for the first phalanx of digit V (K) tends to associate with the fifth metacarpal (J). These patterns of positive allometry generally indicate the complexities of wing shape.

As we have seen, size greatly influences the ordination of groups in the principal components analysis. This is exerted strongly in the first component and hardly at all in subsequent components. The overwhelming effect of size has led many investigators to attempt to eliminate size as an ordinating factor and thereby increase the component loading by the "inherent" shaping qualities of their raw variables. The product of these efforts has been the mathematical adulteration of raw variables into ratios, indices, and proportions, which may appear to eliminate size, but which actually obscure or otherwise confound the recognition of independent patterns of variation. Simply ignoring the first component and considering components 2-4 is not a satisfactory means of eliminating size, because the component correlations are usually even weaker in the fourth component. We submit that in a morphometric analysis such as this, and in fact in all analyses based on absolute measures of continuous variables, size reflects the essence of variation. By this, we do not mean absolute size in itself, but the allometric and isometric aspects of size that ultimately are expressed as synergistic relationships among variables. Therefore, any attempt to strip away the effects of size seriously risks masking or totally eliminating the interactive relationships between size and shape.

The centroids computed for each group in the principal components analysis are given in Table 3 and plotted in Fig. 3. The cigar-shaped dispersion, as noted earlier, is oriented with the longest axis more or less corresponding to the first component axis. The shape of this cluster is caused mostly by the effects of gross size. Most taxa, including the six subfamilies of phyllostomatids (J to O), are packed in the midregion of the dispersion. By examining the vectors of variables shown in Fig. 4A-C and the group centroids plotted in Fig. 3, the reader can begin to appreciate the ordinating effects exerted by the various characters. In the lower diagram of Fig. 3 (axes 1×2), the pteropodids (A) are pushed to the far left and into the upper quadrant, primarily on the basis of large head and body length. The noctilionids (H), megadermatids (G), and, to a lesser extent, the desmodontines (O) also are influenced by the positive force of this vector. The craseonycterids (C), on the other hand, ordinate into the lower right-hand quadrant by the opposite (negative) effect of the vector for head and body length. The taxa in the lower left-hand quadrant are ordinated by the positive (large size) effects of all vectors of variables for wing elements; especially lengths of the forearm, second phalanx of digit III, third and fourth metacarpals, and second phalanx of digit V. The taxa in the upper right-hand quadrant ordinate by the negative (small size) effects of these wing elements. Note that the phyllostomatines (Fig. 3J)

are pushed, almost directly, by the vector for the fifth metacarpal (Fig. 4J), whereas the molossids (U) and emballonurids (D) lie along the tail end of this vector. The majority of the taxa are ordinated into the lower right-hand quadrant, which results from a complex synergistic interaction among the intrinsic elements of the wing.

The effects of the vector for variables in the third component may be seen in the upper diagram of Fig. 3 (axes 1×3). In this component graph, the pteropodids (A) and megadermatids (G) are ordinated into the lower left-hand quadrant by large-sized, distal phalangeal elements (E, I, L). In these two groups, the metacarpals constitute a relatively smaller portion of the total length of the various digits (Fig. 7; Tables A12, A15, A16). On the other hand, noctilionids (H), desmodontines (O), and, to a lesser extent, carolliines (N) are characterized by a generally long forearm (B), third and fourth metacarpal (C, G), and third phalanx of digit III (F). The taxa positioned in the upper right-hand quadrant generally reflect a complex synergism among variables.

In summary to this point, principal components analysis is an effective screening procedure that allows some general insights into the interactive relationships of size and shape exhibited by the wings of bats. However, this procedure, because of its sensitivity to gross size, is not well suited to the detection of subtle nuances in the variation of wing shape among chiropterans. It provides a generalized view of the tip of the iceberg, so to speak, but does not give a clear perspective of the underlying complexity of shape. With regard to the phyllostomatids as a group, little can be said other than that they tend to ordinate amongst the medium to large-sized bats near the grand centroid.

Discriminant analysis.—The transformation from Euclidean space into discriminant space effectively reduces the overwhelming influence of general size on the ordination of group centroids without otherwise adulterating the intrinsic variation of the raw variables. In Table 4, there is a more equitable dispersal of the variation across the first six canonical axes. There is much more symmetry shown by the canonical vectors of variables in Fig. 4D-F than by vectors from the component analysis (Fig. 4A-C). In addition, the correlations of canonical vectors and variables are more evenly dispersed across the various canonical axes rather than being heavily focused in the first axis as was the case in the principal components analysis.

It should be pointed out that, although the variable vector for the third phalanx of digit III (F) is not particularly strong as compared to other vectors, its influence on the dispersion in the first canonical axis essentially segregates taxa into two groups—those that possess this element and those that do not. The correlation coefficient for this variable with the first canonical axis is comparatively high (0.540). This is equalled by the correlation coefficients for the fifth metacapal (J) and second phalanx of digit V (L), which have their greatest affinity with the third canonical axis (0.489 and 0.582, respectively). A more detailed discussion of the effects of these various variable vectors on the size and shape of chiropteran wings will be presented in the following accounts.

TABLE 4.—*Standardized vectors (z-scores) for the lengths of the head and body and selected wing elements. The numbers in parentheses following each z-score is the percentage of the variance contributed by each varaible to a particular canonical axis.*

Variable	Canonical axes						Cumulative per cent
	1	2	3	4	5	6	
Head and body	0.225(9.41)	−0.594(41.19)	0.578(26.68)	0.016(0.04)	−0.218(0.78)	−0.406(2.58)	80.68
Forearm	−1.729(50.27)	1.282(17.36)	−1.269(11.66)	−0.614(0.54)	−0.439(0.29)	−3.302(15.48)	95.60
Metacarpal III	2.040(55.08)	0.631(3.31)	0.135(0.10)	4.878(26.92)	−1.725(3.47)	2.925(9.56)	98.44
Digit III, phalanx 1	−0.304(4.24)	−1.329(50.98)	−0.030(0.20)	−2.007(15.83)	0.701(1.99)	2.063(16.52)	89.29
Digit III, phalanx 2	0.325(10.08)	0.096(0.55)	0.046(0.90)	−1.178(11.31)	−2.729(62.51)	0.405(1.32)	85.86
Digit III, phalanx 3	1.000(89.40)	−0.011(0.01)	0.370(5.27)	−0.366(1.02)	−0.588(2.73)	−0.185(0.26)	98.69
Metacarpal IV	0.252(1.66)	−1.062(18.52)	−0.186(0.39)	−4.803(51.55)	2.045(9.63)	−1.857(7.61)	89.36
Digit IV, phalanx 1	1.125(46.36)	−0.277(1.77)	0.802(10.14)	2.521(19.92)	1.885(11.48)	−1.196(4.43)	94.10
Digit IV, phalanx 2	0.320(12.35)	−0.643(31.25)	0.132(0.91)	0.701(5.05)	1.039(11.44)	−1.095(12.19)	73.19
Metacarpal V	−1.369(40.50)	1.747(41.44)	−0.622(3.60)	0.800(1.18)	0.963(1.77)	1.464(3.91)	92.40
Digit V, phalanx 1	−0.773(30.55)	−1.006(32.52)	−0.961(20.34)	−0.083(0.03)	−1.442(9.38)	0.290(0.36)	93.18
Digit V, phalanx 2	−0.508(11.15)	0.915(22.72)	1.652(50.79)	0.147(0.08)	−0.049(0.09)	0.698(1.78)	86.61
Per cent trace	37.99	18.71	15.52	9.78	5.96	4.72	
Cumulative per cent	37.99	56.70	72.22	81.39	87.35	92.07	

TABLE 5.—*Group centroids for the first six canonical axes. The first three axes are plotted in Figs. 5 and 6.*

Taxon	Code	Canonical axes 1	2	3	4	5	6
Pteropodidae	A	−3.738	−2.621	2.456	0.992	−0.101	−0.294
Rhinopomatidae	B	−2.791	3.379	−2.446	4.291	0.374	−3.076
Craseonycteridae	C	−1.660	0.525	−0.725	−2.080	−1.265	−0.199
Emballonuridae	D	−0.733	0.376	−2.779	2.421	−1.728	1.512
Rhinolophidae	E	−3.741	1.106	−1.076	−1.379	0.010	−0.547
Nycteridae	F	−3.711	−0.434	−0.739	−3.183	0.863	2.374
Megadermatidae	G	−4.678	1.284	−0.556	−4.321	−2.089	1.244
Noctilionidae	H	3.106	1.231	−3.222	−2.933	−3.010	−3.535
Mormoopidae	I	2.203	1.986	−0.166	1.015	−2.226	−1.714
Phyllostomatinae	J	1.364	1.412	1.114	−0.510	−0.535	−0.170
Glossophaginae	K	1.778	0.770	1.622	−0.059	−0.792	0.518
Carolliinae	L	1.590	0.298	1.608	−0.233	−0.538	1.227
Stenoderminae	M	2.752	1.360	2.018	−0.124	−0.294	0.345
Phyllonycterinae	N	1.028	1.885	1.073	0.891	0.758	−0.912
Desmodontinae	O	2.207	3.805	1.199	−0.187	−0.700	−1.650
Natalidae	P	−2.076	1.060	−1.075	−0.762	0.158	2.415
Thyropteridae	Q	−0.024	0.323	−0.695	−0.636	2.004	1.694
Myzapodidae	R	1.146	0.288	0.051	−0.416	1.367	−1.053
Vespertilionidae	S	0.781	0.480	−0.843	0.423	1.813	0.291
Mystacinidae	T	2.315	2.132	1.447	0.774	1.658	−1.224
Molossidae	U	3.194	−3.510	−1.523	−0.585	−0.120	−0.474

Pteropodidae

Fruit bats are generally the largest chiropterans in terms of absolute size of all raw variables. We have observed that overall large size greatly effects the ordination in the principal components analysis. However, in discriminant space, these overwhelming effects of size are much reduced. Because of their large size, the pteropodids are especially well suited to illustrate the moderation of size in the discriminant analysis. The strongest vector in the principal component analysis was that for head and body length (A)—see Fig. 4A-C. This feature in the discriminant analysis is one of the least powerful (Fig. 4D-F; Tables 4 and 6). Not only is the length of the vector short as compared to others such as those for the lengths of the forearm (B), and third and fifth metacarpal (C, J), for example, but it is directed away (approximately 90 degrees) from the group centroid for pteropodids. The canonical coefficient (0.225) for head and body length in the first canonical axis (Table 4) is positive and near zero, suggesting the denial of large body size by pteropodids relative to this axis. Although comparatively minor, the greatest influence by this variable on the ordination of bats in discriminant space occurs in the second and third axes, but here too the vector generally orients away from the pteropodids. Furthermore, the contribution of this variable to the overall discriminant functions of the various centroids appears to be minor (Table 6).

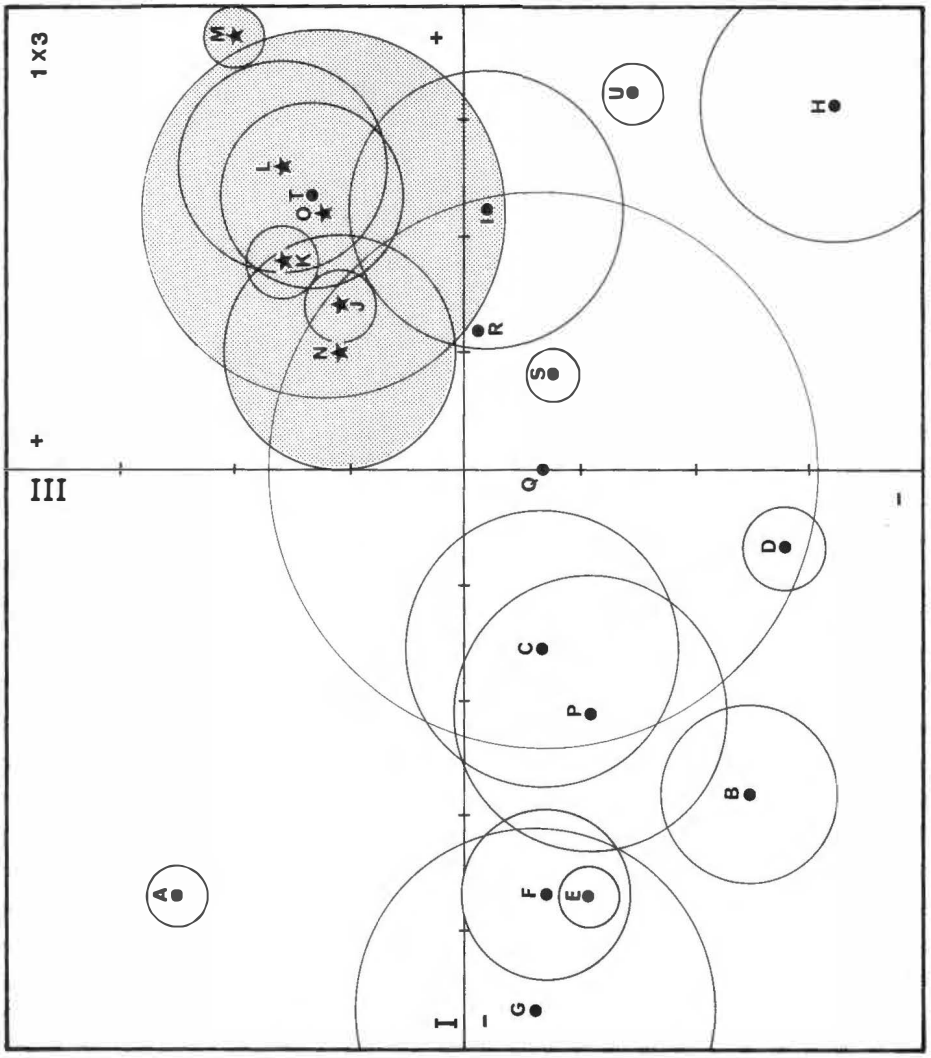


FIG. 5.—Canonical graph from discriminant analysis. Group centroids are plotted with their respective confidence circles (95 per cent) on 1 × 3 canonical axes of discriminant space and the coordinates for these are given in Table 5. Stars and stippled area indicate phyllostomatid centroids and confidence circles. The confidence circle for the Myzapodidae (R) is too large to plot. See list of specimens examined or Table 5 for key to alphabetic code and text for discussion.

The length of the forearm (B) is one of the more powerful forces in the overall ordination of groups (Tables 4, and 6). In the first two canonical axes, the vector for this variable lies approximately perpendicular to the pteropodid centroid. Relative to the molossid centroid (U), this vector may be interpreted as exerting a positive force on the pteropodid centroid. However, the peripheral position of this centroid to the vector suggests a weak influence by this variable. In the third

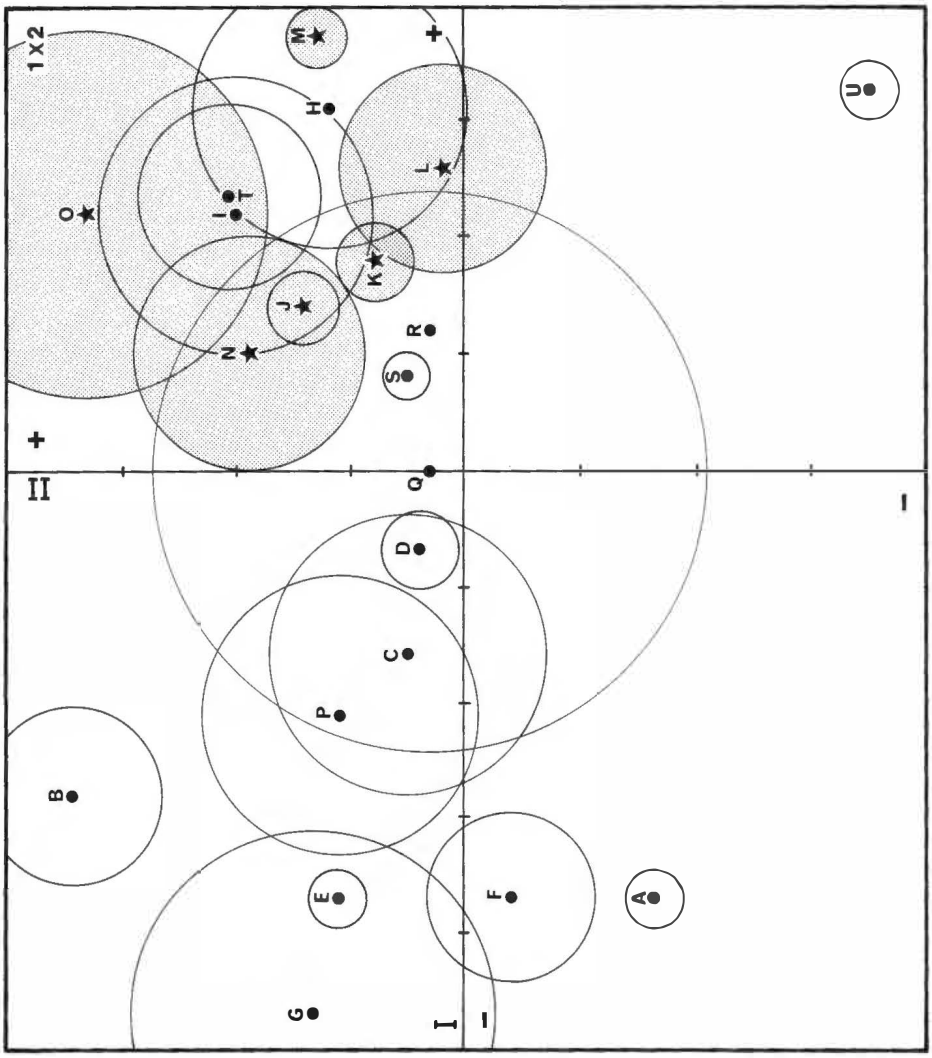


FIG. 6.—Canonical graph from discriminant analysis. Group centroids are plotted with their respective confidence circles (95 per cent) on 1×2 canonical axes of discriminant space and the coordinates for these are given in Table 5. Stars and stippled area indicate phyllostomatid centroids and confidence circles. The confidence circle for the Myzapodidae (R) is too large to plot. See list of specimens examined or Table 5 for key to alphabetic code and text for discussion.

canonical axis (Figs. 4E, 5), the effect of this variable is somewhat more direct (negative). A heuristic interpretation of this variable vector would suggest a medium to short forearm for the pteropodids.

An examination of the relative lengths of the wing and forearm (Tables A7, A8) clarify and substantiate this interpretation. Although the absolute lengths of all wing elements are large, the wings of pteropodids average proportionately

shorter than those of other chiropterans (1.80). The mean relative length of the forearm is second smallest for the order (0.65); only that of molossids is smaller (0.63). In terms of the composition of wing span, the forearm of pteropodids contributes an average of 35.98 per cent (range, 32.69-38.84) to the length of the wing.

The canonical coefficients for the metacarpals of digits III-V (C, G, J) illustrate the simultaneous nature of the interactive relationships among these variables. By comparing Fig. 4D with Fig. 6, it will be noted that the negative end (smallness) of the variable vector for the third metacarpal (C) passes in proximity to the centroid of pteropodids. This indicates a rather strong tendency in the direction of small size, especially in the first and second canonical axes. The variable vectors for the fourth and fifth metacarpals (G, J) orient in nearly opposite directions from each other, and both orient almost perpendicularly to the centroid for pteropodids. It will be noted that the latter vector (J) is the stronger of the two (Table 4) and it is oriented directly toward the rhinopomatids. The vector for the fourth metacarpal (G) is of a lesser magnitude and is oriented generally toward the centroid of the Molossidae. The influences of these two variable vectors on these two centroids will be discussed beyond and are mentioned here only for orientation by the reader. It is difficult to assess the nature of the effect these two vectors have on the pteropodid centroid in the first and second canonical axes; suffice it to say that it is synergistic. In the third canonical axis (Figs. 4E, 5), the interaction of these three vectors is somewhat clearer. The vector for the third metacarpal (C) continues in its implication of small size. The vectors for the fourth and fifth metacarpals (C, J) maintain their opposite orientation, but their negative (smallness) ends are closer to the centroid of the Pteropodidae than before. The net effect of all three of these vectors is to carry the centroid in an upward direction in three-dimensional space and, because it is the tail end of these vectors that effects this lifting, the implication is small size for all three metacarpals. An examination of Tables A12, A16, and A19 reveals that these manal elements of the pteropodid wing contribute the smallest percentage to the overall lengths of digits III to V as compared to other chiropteran taxa. Norberg (1972) also noted the general shortness of the metacarpals of the megachiropterans.

A long first phalanx of digits III and V (D, K) is strongly implicated in the discrimination of pteropodidis in all three canonical axes. The vector for this phalanx in the fourth digit (H) is most influential in the third canonical axis (Figs. 4E-F, 5, 6; Table 4) and here also suggests relatively long length. The vectors for the second phalanx of digits IV and V (I, L) share a similar orientation as described above for the fourth and fifth metacarpals (G, J) except that the positive ends of these variable vectors, rather than the negative ends, carry the centroid aloft. An examination of the percentages contributed to the discrimination of each group (Table 6) generally substantiates the characteristically long phalangeal elements of pteropodids. In addition, Tables A13, A17, A18, A20, and A21 show the mean percentages contributed by these phalanges to the overall lengths of digits III to V, respectively, and further support the above interpretations by

ranking the pteropodids as the largest, or nearly so, with respect to these wing elements.

The vector for the second phalanx of digit III (E) presents an interesting paradox in that it nearly parallels, in both direction and sign, the orientation of the variable vector for the third metacarpal (C). This seems to suggest short length of this feature in the first two canonical axes. However, there is a slight elevating quality by the point of this vector on the centroid in the third dimension of discriminant space. Those familiar with pteropodid wings should be duly impressed by the extraordinary length and massive structural nature of this phalanx. However, though this wing element is outwardly large-sized in appearance, pteropodids rank fourth largest in terms of the average percentage contributed by this element to the overall length of digit III, as compared to the Craseonycteridae, Megadermatidae, and Furipteridae (Table A14). (The latter group was not included in the multivariate analyses because the sample size was too small.)

Therefore, pteropodids are characterized by having a relatively short wing as the combined result of a relatively short forearm and third metacarpal (Fig. 7). Although the two phalangeal elements of the third digit are long, the shortness of the metacarpal tends to suppress the overall length of the digit. The total length of digit III contributes between 61 and 67 per cent to the wingspan, shown by a mean tip index of 1.78 (2.06-1.57), which ranks in the middle to upper range of all bats (Table A2). The wings of pteropodids are further characterized by their generally broad aspect (Fig. 10; Tables A3-A5). Although the shortness of the fourth and fifth metacarpals would tend to cause a narrow wing, apparently the combined lengthening of the phalangeal elements of digits III to V maintains the proportional breadth.

Contrary to Findley *et al.* (1972), such a wing should have an excellent lift potential at slow speeds. In addition, the relatively long phalanges of all three digits, especially those of digits IV and V, should facilitate increased camberability with relatively little digital flexion and thereby further augment lift potential at slow speeds. Whereas the nearly equal (isometric) partitioning of the respective digits may contribute, in a crude sort of way, to the slow-flight characteristics of pteropodid wings, the fine adjustments necessary for maneuverability in slow flight, such as hovering, apparently are not possible. In the following accounts we will show that all other chiropteran families depart from the general isometric construction of the wing as exhibited by the Pteropodidae.

Rhinopomatidae

As in the pteropodids, the mouse-tailed bats possess a morphometrically unique and interesting wing (Fig. 7). Whereas the pteropodids are in a generally peripheral location relative to the variable vector for head and body length (A), the rhinopomatids receive nearly the full negative (shortness) force of this vector in the ordination of their centroid. This vector is discriminatory in all three canonical axes (Figs. 4D-E, 5, 6). The variable vector for the length of the forearm (B) is closely aligned with that for head and body length, but the ordinating effect of this vector is more direct and positive (large-sized) rather than negative, and its

influence in discrimination is more important (Table 6). The relative length of the forearm approaches unity (0.94; Table A8), which may or may not reflect an interactive relationship between these two variables. It is interesting to note that this relationship is maintained through the sixth canonical axis (Table 4), although the position of the centroid shifts slightly into a more peripheral location.

A much more complex, extra-dimensional interaction exists for the combined variation of the metacarpal elements of digits III-V (C, G, J) (Figs. 4D-E, 5, 6; Table 4). In the first three canonical axes, and similar to the vector for the forearm (B), the vector for the fifth metacarpal (J) is a strong positive discriminator (Table 6). This manal element comprises 68.10 per cent of the total length of the fifth digit (Table A19), and this percentage is exceeded only by some vespertilionids and *Noctilio*. The tail (shortness) of the variable vector for the length of the fourth metacarpal (G) also is directed toward the centroid for rhinopomatids in the first two canonical axes. However, in the third canonical axis, the tail of this vector is directed upward, and, although it seems to interact synergistically with other vectors to carry some centroids aloft, its effect seems minimal in this regard to the rhinopomatids. This is interesting in light of the apparent importance of this variable in the discrimination of the group (Table 6). In Table 4, it will be noted that the cumulative percentage of the variance contributed by the fourth metacarpal to the first three canonical axes is low—20.57 (1.66, 18.52, and 0.39, respectively), whereas the percentage contributed in the fourth axis of discriminant space is markedly increased—51.55 (72.12 cumulative per cent). In addition, this vector becomes a strong discriminator for shortness of the fourth metacarpal and is again oriented more directly toward the centroid of the rhinopomatids. This metacarpal contributes 59.77 per cent to the total length of the fourth digit (Table A16). The length of the third metacarpal of rhinopomatids is particularly striking (61.70 per cent of the length of digit III) compared to that of other bats. In Table A12, it is exceeded only by the emballonurid *Depanycteris* (63.21). However, the influence of this variable on the dispersion in the first three canonical axes is not readily apparent (Figs. 4D-E, 5, 6). An examination of Table 4 will show that there exists an extradimensional effect similar to that described for the fourth metacarpal. Whereas the orientation of this variable vector is oblique to the rhinopomatid centroid in the first three canonical axes, its point (longness) directly ordinates this group in the fourth through sixth dimensions of discriminant space.

The vectors for the lengths of the first and second phalanges of digit III (D, E) generally indicate small size, although the interaction between these variables results in vectors that tangentially effect the centroid for rhinopomatids. Again, this effect becomes more direct in extradimensional space. The variable vectors for these two phalanges of the fourth digit (H, I) directly indicate shortness in the first three canonical axes. The effect is strongest for the distalmost member (I) of this pair of phalanges. Table 6 indicates a rather minor role for the first and second phalanges of digit V (K, L) in the discrimination of the rhinopomatids. Nonetheless, the vector for the proximal member of this pair (K) is oriented

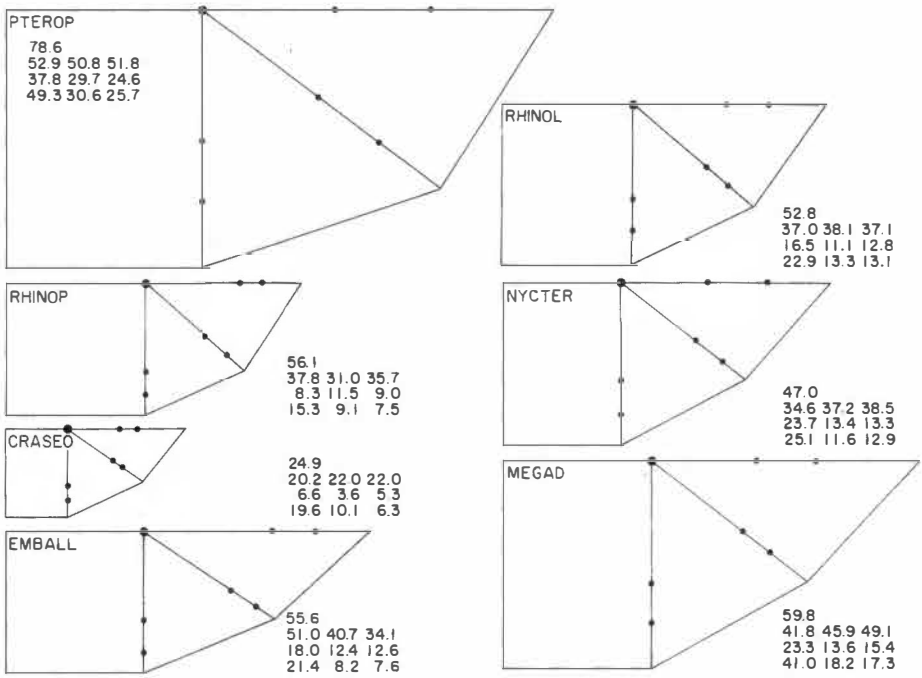


FIG. 7.—Diagrammatic representation of the wing construct based on the mean lengths of variables for the Pteropodidae, Emballonuroidea, and Rhinolophoidea. Columns of numbers associated with each construct are, from left to right: length of forearm, metacarpal, and phalanges of digit III; length of metacarpal and phalanges of digit IV; and length of metacarpal and phalanges of digit V. Digit IV is projected at the mean alpha angle computed for each taxon (see Table A1).

positively toward the group centroid in the first two canonical axes (Figs. 4D, 6). In the third canonical axis, the effect of this variable is reduced. Similarly, the vector for the terminal phalanx of digit V (L) is oriented toward the centroid for rhinopomatids, but in the third dimension this vector stands far above the centroid. This further indicates the complexity of the variation and interactive associations among variables.

The overall effect of the interplay among the wing elements of rhinopomatids is to produce a wing with a below average overall aspect ratio of 5.57 (Figs. 7, 10; Table A3). Findley *et al.* (1972) noted the shortness of the wing tip and indicated that rhinopomatids had the lowest tip index of all bats examined by them. We computed an average tip index of 1.09, which agrees with 1.19 reported by these authors for *Rhinopoma hardwickei.* In addition, they commented on the relatively short wings possessed by these bats. Although these indices and ratios provide a vague impression of the rhinopomatid wing, they do not clearly delineate the uniqueness of its shape or the causative aspects of this shape.

The shortness of digits III to V is most greatly effected by short phalangeal elements and a relatively short fourth metacarpal; the third and fifth metacarpals are among the longest for all bats (Tables A16, A19). As noted above,

rhinopomatids possess nearly the longest forearm relative to their head and body length (the relationship is almost 1:1). Whereas pteropodids, and to a greater extent molossids, have much higher tip indices, the relative length of digit III for both is only slightly higher than that shown for rhinopomatids (Tables A2, A9). The long forearm, in combination with a relatively short fifth digit (0.92 as compared to 1.00 for molossids) produces a plagiopatagium with an extremely high aspect ratio (2.16) (Figs. 7, 10; Table A5). This mean value is the largest among bats and is exceeded in range only by molossids and emballonurids.

According to Harrison (1964:62), the flight of *Rhinopoma hardwickei* is peculiar and distinctive, consisting of a "series of alternating flutters and glides, with a rising and falling motion. . . ." Dr. Gamal Madkour, who is familiar with *R. microphylum* of Egypt, indicated to us (personal communication) that these bats are rather swift-flyers that forage in open country. In view of these apparent conflicting observations, we hesitate to comment on the functionality of the wing of rhinopomatids other than to say that it should be capable of producing moderate speed as well as maneuverability. We see little basis for a close functional relationship between the Rhinopomatidae and the rhinolophoids, the wings of which are constructed differently. Finally, mouse-tailed bats share the closest resemblance with the family Emballonuridae—generalized (not taxonomic) distance 6.94. This resemblance is founded on similarity of variable vectors for the lengths of the forearm, first phalanx of digit IV, second phalanx of digits IV and V, and the fifth metacarpal.

Craseonycteridae

Craseonycteris thonglongyai represents the small extreme in the size variation among the Chiroptera. These bats, recently described as a monotypic family (Hill, 1974), can truly be thought of as "bumble-bee bats," as they are scarcely larger than their hymenopteran namesake. Because of their extreme small size, we can reemphasize the rather minor effect that general size has on ordination in discriminant space. In the principal components analysis (Fig. 3), this family was strongly ordinated along the first component axis by the tail (smallness) of the variable vector for head and body length (A). As we noted, the pteropodids were ordinated in the opposite direction and the remaining taxa disperse between these two extremes. In terms of distance coefficients, this spread (PCA) constitutes a taxonomic (Euclidean) distance value of 131.18. Similarly large taxonomic distances were computed between pteropodids and other small-sized taxa such as the Natalidae and Thyropteridae (105.11 and 114.12, respectively). However, in discriminant space, these general size effects are markedly moderated and the generalized distances between pteropodids and these three small-sized taxa (9.23, 6.43, and 6.72, respectively) are suggestive of shape rather than size differences. Whereas the vectors for nearly all variables effect the ordination of the pteropodids by pushing them away from the centroid of the craseonycterids, that for head and body length contributes the least percentage to the group discrimination vector of the latter (0.36, Table 6). Therefore, again we see that in

TABLE 6.—*Percentage contributed by each direction cosine to the discriminant function of each group. These values may be compared with the canonical coefficients (Table 4) in an interpretation of the overall effect a variable or set of variables has on the ordination of a group(s).*

Taxon	Code	Head and body	Forearm	Metacarpal III	Digit III, phalanx 1	Digit III, phalanx 2	Digit III, phalanx 3	Metacarpal IV	Digit IV, phalanx 1	Digit IV, phalanx 2	Metacarpal V	Digit V, phalanx 1	Digit V, phalanx 2
Pteropidae	A	1.43	4.46	5.66	3.43	9.40	16.06	7.65	5.81	10.22	6.77	16.95	12.15
Rhinopomatidae	B	0.52	9.38	8.08	22.82	5.91	10.94	14.88	12.68	0.34	11.62	2.35	0.44
Craseonycteridae	C	0.36	1.84	4.26	5.12	12.42	9.78	8.11	28.52	6.24	10.25	11.34	1.74
Emballonuridae	D	1.03	3.15	22.96	4.70	2.27	7.28	17.86	9.93	1.10	9.88	16.78	3.17
Rhinolophidae	E	1.06	6.20	7.20	0.52	5.46	14.92	6.11	22.92	3.84	9.58	12.41	9.76
Nycteridae	F	0.62	0.18	8.41	19.33	1.65	8.64	5.46	27.16	7.02	10.45	9.65	1.41
Megadermatidae	G	0.33	1.66	9.70	6.60	8.17	6.14	5.59	27.27	13.12	8.97	9.01	3.42
Noctilionidae	H	0.45	2.14	1.50	2.72	5.39	9.01	0.42	19.76	13.64	4.36	8.94	31.67
Mormoopidae	I	0.49	0.54	20.56	26.30	2.17	11.65	6.42	0.23	1.75	3.12	11.44	15.33
Phyllostomatinae	J	0.09	5.58	18.44	6.29	4.51	15.53	5.43	14.64	1.23	7.97	4.24	16.05
Glossophaginae	K	2.13	12.28	23.65	7.14	1.49	10.95	5.12	7.23	0.83	0.86	5.56	22.75
Carolliinae	L	0.12	15.65	26.01	0.46	0.70	12.50	9.54	7.23	1.15	6.13	4.13	16.39
Stenoderminae	M	0.31	10.89	22.44	6.18	0.63	17.13	6.15	2.41	1.41	3.96	13.76	14.74
Phyllonycterinae	N	1.43	0.90	17.18	7.68	17.26	5.05	10.37	3.23	9.96	9.27	4.58	13.08
Desmodontinae	O	1.37	4.87	15.53	24.97	4.64	4.87	3.13	2.51	3.51	3.80	9.21	21.58
Natalidae	P	2.83	7.14	10.64	3.79	2.10	15.64	1.55	17.52	4.83	14.84	9.18	9.92
Thyropteridae	Q	2.74	7.40	10.63	13.95	16.24	8.53	4.02	10.90	3.67	11.24	0.97	9.70
Myzapodidae	R	4.53	3.77	7.20	6.93	17.78	10.05	2.97	2.00	21.88	5.02	8.93	8.93
Vespertilionidae	S	0.66	9.53	18.60	0.55	18.07	8.61	3.73	2.07	14.18	16.53	1.65	5.83
Mystacinidae	T	0.46	2.16	10.21	12.37	9.02	2.62	3.60	14.21	6.70	1.15	20.80	16.69
Molossidae	U	1.57	9.28	9.98	4.40	3.20	12.16	9.90	0.32	7.93	10.37	13.34	17.54

discriminant space the quantitative effects of general size are much reduced in lieu of the more complicated synergistic interactions among variables that reflect the qualitative aspects of size.

The variable vector for the length of the forearm (B) appears to have a moderately strong influence on the ordination of the craseonycterids (Figs. 4D-E, 5, 6; Tables 4, 6). Although this variable is the shortest, in terms of absolute length, among all bats, the vector suggests longness of the forearm. In Table A8, the mean relative length of the forearm (0.82) is somewhat larger than that of all bats (0.73), further substantiating the interpretation of this vector. The combined effect of the lengths of digit III and the forearm is the production of a relatively long wing for the craseonycterids (Tables A2, A7).

Hill (1974), in his detailed comparison of the structure of the wing of *Craseonycteris* with those of other bats, noted a rather peculiar variation among the metacarpal elements. The third metacarpal of *Craseonycteris* is relatively short as compared to the fourth and fifth, which are somewhat longer and approximately equal in length. The relationship of the vector for the length of the third metacarpal (C) to the centroid of craseonycterids is similar to that discussed for pteropodids. The contribution of this element to the length of digit III (43.44, Table A12) is below the average of other bats. The qualitative shortness of the fourth metacarpal is suggested by the vector for this variable (G) in the first and second canonical axes (Figs. 4D, 6). In the third axis (Figs. 4E, 5), the group centroid is located somewhat to the side of this variable vector, although the implication of shortness persists. The relationship of the variable vector for the fifth metacarpal (J), in all three axes, implies longness. The contribution of the fourth and fifth metacarpal elements to the lengths of their respective digits is above average for all bats (Tables A16, A19).

Perhaps the most striking feature of the third digit is the relatively long second phalanx (Fig. 7). This phalanx is nearly equal to the metacarpal in length (Tables A12, A14) and its contribution to the length of the digit is largest among all bats. Although the percentage contributed to the discrimination vector of the group (12.42, Table 6) is relatively high, the implication of this variable vector (E) in the first three canonical axes (Figs. 4D-E, 5, 6) is toward shortness. However, in the fourth and fifth canonical axes, the positive end (longness) of the vector is strongly oriented toward the centroid of craseonycterids. Again, this emphasizes the multidimensional and synergistic nature of the interaction among variables on alar shape.

A similar relationship for the distal phalanx of digit III exists for the rhinolophids, megadermatids, and, to a lesser extent, nycterids. The actual structure of the tip portion of the wing in these bats is rather curious and is not found in any other group. The middle and distal portion of the shaft of the second phalanx of digit III is arched in such a way as to trap, and maintain taut, a small section of the alar membrane in much the same fashion as the string of a bow. The joint between the distal phalanx and the first phalanx of digit III is broad, and there appears to be a great deal of mobility at this joint, judging from specimens preserved in alcohol. Although we are not prepared to discuss the functional

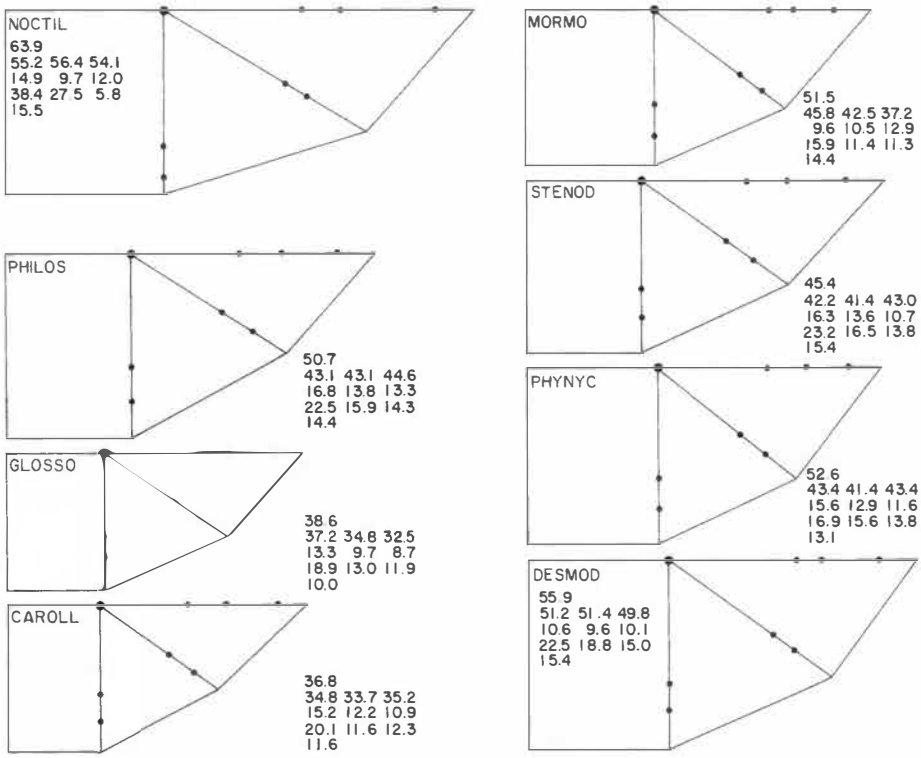


FIG. 8.—Diagrammatic representation of the wing construct based on the mean lengths of variables for the Phyllostomatoidea. Columns of numbers associated with each construct are, from left to right: length of forearm, metacarpal, and phalanges of digit III; length of metacarpal and phalanges of digit IV; and length of metacarpal and phalanges of digit V. Digit IV is projected at the mean alpha angle computed for each taxon (see Table A1).

ramifications of this anatomical configuration, we suggest that the apparent emphasis in the ordination of these families by this feature implies not only similarity in shape, but also functional similarity. Perhaps it is employed during the "flick phase" of the wing beat cycle, or it simply may be a device for furling this long wing element. Although the phylogenetic sources of shape are not our primary goal in this paper, we would point out that this feature suggests a close relationship among these families. The emballonurids possess a slightly different folding device in this distal region of their wings, and the rhinopomatids, which lack this feature, might represent the underived (primitive) condition for this characteristic.

Of all the variables employed in this study, the length of the first phalanx of digit IV appears to be the most distinctive of *Craseonycteris* (Table 6). This wing element is extremely short and constitutes only 10.2 per cent of the total length of the fourth digit and, in a relative sense, is the shortest observed in all bats (Table A17). The shortness of this wing element is emphasized in the discriminant analysis by the variable vector (H) in the first three canonical axes (Figs. 4D-E,

5, 6; Table 4). This vector is involved similarly, but to a slightly lesser degree, in the ordination of the Rhinolophidae, Nycteridae, Megadermatidae, Noctilionidae, and Natalidae. The second phalanx of digit IV is long and is second in size only to that of the Noctilionidae (Table A18). However, the interactive relationship of this variable is obscured by the synergistic complexity among all variables.

The variable vectors for both phalangeal elements of the fifth digit (K, L) also are difficult to interpret, although they indicate longness in the first three canonical axes. Of the two variables, the length of the first phalanx of this digit appears to be the most influential in the discrimination of the group (Table 6). The precentages contributed to the length of digit V by the first and second phalanges (15.79 and 18.64, respectively) are below the average for all bats (Tables A20, A21).

The overall aspect ratio of the wing of *Craseonycteris thonglongyai* is slightly below the mean for all bats (5.64, Table A3 and Fig. 10). The aspect of the plagiopatagial portion is not particularly distinctive (1.48) and falls in the middle to lower range for all bats (Table A5). In addition, the aspect ratio of the tip portion of the wing is approximately equal to the average for all bats (Table A4 and Fig. 10). On the other hand, the third digit is 1.86 times as long as the forearm, which is generally high compared to that of other bats (Table A2; Fig. 10).

The overall shape of the craseonycterid wing is the result of a rather unusual combination of interactions among the various wing elements. The length of the third digit appears to be most strongly influenced by the length of the distal phalanx, which tends to offset the shortness of the metacarpal. In the fourth digit, the relatively long metacarpal and distal phalanx appear to compensate for the markedly shortened first phalanx. The fifth digit is relatively long, owing to a generally isometric association with the metacarpal and second phalanx of digit IV, and tends to offset the length of the third digit. These interactions thereby contribute to the generally broad aspect of the wing tip.

Prompted by comments made by Findley *et al.* (1972) concerning an average or below average aspect ratio coupled with a high tip index, Hill (1974) suggested a hovering ability for these small bats. We agree that *Craseonycteris* may possess this flight potential, but our basis for this assumption lies more with the structural nature of the third digit, especially the long distal phalanx, rather than with the relationship between aspect ratio and tip index.

Emballonuridae

From the standpoint of wing diversity, the emballonurids represent one of the most intriguing families of bats. In terms of aspect ratios, they range from slightly above average (6.05) for the order to extremely high aspect ratios (7.93). Their forearms may be relatively short to long and, as a consequence, the tip indices for members of the family also vary from low to high. In these general descriptive terms, the wings of emballonurids most closely resemble those of bats of the family Molossidae and, in some respects the Noctilionidae and Mormoopidae. However,

this resemblance is merely superficial as these families acquire their extreme wing shapes through different morphometric modes. To draw attention to this misleading resemblance, we will draw comparisons between the emballonurids, molossids, and noctilionids in this account. The group centroids of these three families are located in separate regions of discriminant space (Figs. 5, 6).

Emballonurids are about average for bats in length of the head and body. The vector for this variable (A) is a minor force in the overall discrimination of the group (Table 6). Head and body length has a slightly stronger effect in the ordination of the Molossidae; this is particularly true in the first and second canonical axes (Figs. 4D, 6).

Length of forearm appears to be a moderately important variable in the ordination of the emballonurid centroid. This appears to be a general feature of those bats referred to the superfamilies Emballonuroidea and Rhinolophoidea, which are generally characterized by possessing relatively long forearms (Table A8). Within the Emballonuridae, the mean, relative length of the forearm approaches unity (0.93). Although most species range below this value, the exceptions are notable: *Centronycteris maximiliani* (1.14); *Cyttarops alecto* (1.10); *Emballonura solomonis* (1.11); *E. beccarii* (1.06); and *Cormura brevirostris* (1.04). The vector for the length of the forearm (B) contributes a moderately low percentage (3.15) to the discrimination vector of the emballonurids (Table 6). By comparison, the ordination of the molossids is more strongly influenced by the tail (shortness) end of this vector. This emphasis on short length of the forearm is reflected in the higher percentage contributed by this vector (9.28) to the group discrimination vector of molossids (Table 6). Therefore, although the absolute length of the forearm in these two groups is outwardly similar, there is a fundamental difference in their respective contribution to the shape of the wing (Table A8).

The variation of the dactylopatagial portion depicts even more striking differences in the wing construction of emballonurids and molossids (Figs. 7, 9). On the whole, the length of the third digit of emballonurids is not particularly impressive. The mean tip index (1.61) is well below the average for all bats (Table A2). *Centronycteris*, *Saccopteryx*, and several species of *Taphozous*, especially *T. peli*, have unusually large tip indices (1.70-1.90). On the contrary, molossids generally are characterized by larger than average tip length (Table A2).

The vectors for the various elements of digit III (C, D, E) are involved in the overall complex synergism among variables and their effect is not easily interpreted. In the first canonical axis (Figs. 4D-E, 5, 6), only the vector for the first phalanx (D) exerts a positive force on the ordination of emballonurids (Tables 4, 5); shortness is emphasized by the other vectors for this digit. The converse of these actions is implied for the ordination of the Molossidae with respect to the vectors associated with digit III. Also, the centroid for the Noctilionidae is closely associated with that of the Molossidae in this canonical axis.

Ordination along the second canonical axis illustrates a somewhat different picture (Tables 4, 5). Here the vectors for the metacarpal and second phalanx

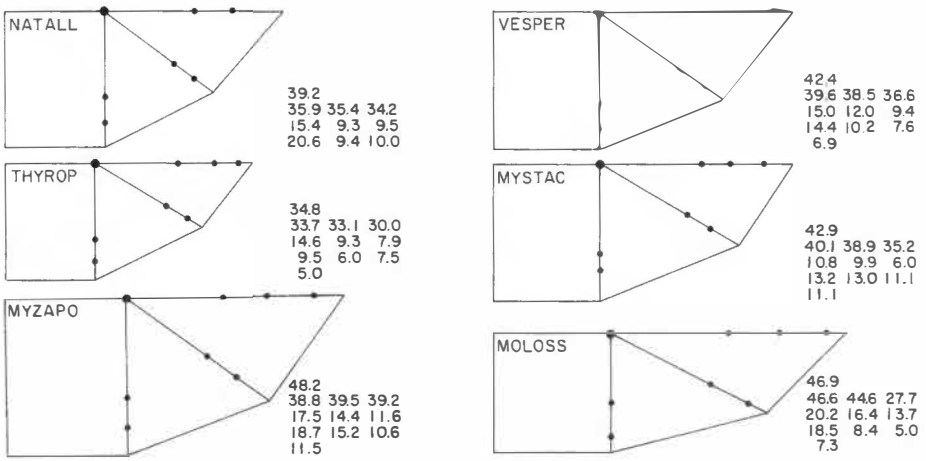


FIG. 9.—Diagrammatic representation of the wing construct based on the mean lengths of variables for the Vespertilionoidea. Columns of numbers associated with each construct are, from left to right: length of forearm, metacarpal, and phalanges of digit III; length of metacarpal and phalanges of digit IV; and length of metacarpal and phalanges of digit V. Digit IV is projected at the mean alpha angle computed for each taxon (see Table A1).

(C, E) exert a positive force and that for the first phalanx a negative effect on the ordination of emballonurids. Again, the molossids are ordinated in an opposite manner. Interestingly, the centroid for the noctilionids is not carried in association with the molossids, but is maintained in its same relative position in discriminant space. As will be noted later, the vectors for elements of the third digit are more directly involved in the ordination of noctilionids.

In the third canonical axis, the vectors for elements of digit III appear to be less important in the overall ordination of these three centroids. In this axis, vectors for the fourth and fifth digits are emphasized in a relative sense.

As stated above, variation of the third digit is difficult to describe because of its involvement in the complex synergistic interactions among variables. However, the net effect is a relatively long digit (Table A9). The metacarpal is particularly important in this regard, judging from the high percentage contributed to the discrimination vector of emballonurids (22.96, Table 6). The combined effect of a long digit III and forearm is the production of a relatively long wing as can be seen in Table A7. In fact, the high extremes in the range of variation are noteworthy. The relative length of the wing of *Centronycteris* is nearly three and a half times (3.34) longer than the head and body length, which greatly exceeds that for all bats. Likewise, *Cyttarops* exhibits an unusually long wing (2.91) as compared to other chiropterans. These two species also fall at the high extreme for relative length of digit III (Table A9).

Whereas the length of the third digit is important in the overall length of the wing, the lengths of the fourth and fifth digits combine to determine the overall aspect of the dactylopatagium. We have noted that in the rhinopomatids and craseonycterids the length of digit III is generally offset by a relatively long

fourth and fifth digit for the overall production of a short, broad tip. In the formation of high aspect tips, the trend is toward a relatively long fourth digit and a shortened fifth digit. The emballonurids, noctilionids, and molossids generally follow this trend, although the manner in which each responds is somethat different.

The vectors for elements of the fourth digit (G, H, I) of emballonurids defy easy interpretation because of their overall interaction with other variables. In the first two canonical axes, these vectors imply shortness of the fourth digit. However, in the third axis, a longish fourth metacarpal is suggested. The reader will recall that the elements of the fourth digit are not particularly strong factors in the ordination in the first three canonical axes, but that they gain strength in the extradimensional fourth through sixth axes. In the fourth and fifth axes (Table 4), the vector for the fourth metacarpal (G) is strong in its effect on the ordination of the emballonurids and suggests a relatively long length for this element. The contribution by this vector to the discrimination of the group also is high (17.86, Table 6). A similar implication applies to the molossids, but to a lesser extent—9.90 per cent contributed to the function. This variable appears to have only a minor role in the discrimination of noctilionids.

The vectors for the respective lengths of the two phalanges of digit IV do not appear to be important in the overall ordination of the emballonurids. The general implication is toward small size (Figs. 4D-E, 5, 6). However, the position of the centroid relative to these two canonical vectors suggests a null effect, or at least no significant elongation, when compared to the grand centroid for all bats. The ordination of both the molossids and noctilionids are effected by one or the other of these vectors. In the case of the molossids, a long first phalanx of digit IV is emphasized, whereas a long second phalanx, in combination with a short first phalanx, is suggested for the Noctilionidae.

The length of the fifth digit of emballonurids, as well as that of noctilionids and molossids, is relatively short as compared to the total length of digits III and IV, forearm, and head and body (Tables A7-A11). In a general sense, molossids represent the extreme of this variation. The most striking differences among these three groups is in the composition of this digit and specifically in the relative length of the metacarpal element (Table A19). The vector for this wing element (J) is directly involved in the ordination of the emballonurids and molossids, and, to a lesser extent, noctilionids (Figs. 4D-E, 5, 6). The percentage contributed by this vector to the discrimination of each of these groups is 9.88, 4.47, and 4.36, respectively (Table 6). This vector implies large size with respect to this variable for emballonurids and noctilionids, but suggests small size for molossids. The most important feature of the fifth digit of emballonurids is a relatively long proximal phalanx (Table 6). This phalanx contributes nearly a quarter of the total length of digit V (Table A20). Similarly, this phalanx is distinguished as long in the noctilionids, but the importance in discrimination of the group is slightly reduced (Table 6). The molossids, more than either of these two groups, emphasize the length of the first phalanx of digit V (Table 6). On the average, almost 30 per cent of the total length of the fifth digit is reflected

by the first phalanx, the largest contribution noted among all bats (Table A20). *Cheiromeles* and *Otomops* (both molossids) represent the high extremes with 39.13 and 35.30 per cent, respectively. The distalmost phalanx of the fifth digit is markedly shortened in the emballonurids and molossids. The significance of this reduction, in the overall ordination of these two families, is strongest for the molossids compared to emballonurids (Table 6). On the other hand, this wing element is markedly elongated in the Noctilionidae (Fig. 8), and the vector for this variable (L) contributes 31.67 per cent to the discrimination vector of this group. It is noteworthy to point out that this is the largest contribution by any variable vector to the group discrimination vector of any group.

Thus we have seen that emballonurids possess wings that may be characterized as relatively long and narrow (Fig. 7). An overall aspect ratio generally would reflect this shape (Table A3), but would reveal little in terms of the composition and interaction among the variables that produce such a shape. Outwardly, the short tip index, relatively long wing, and low wing loading tend to confuse any univariate or bivariate interpretation of this shape (Findley *et al.*, 1972). The multivariate approach does help to clarify the issue. The wings of emballonurids are truly high aspect in nature. However, a functional interpretation of this wing shape is liable to be confounded if the wings of emballonurids are compared to the high aspect wings of molossids. In such a comparison, one is likely to be biased and misled by the apparent high correlation between high aspect ratio and swiftness of flight, both attributes of molossids. In addition, generally high wing loading appears to accompany the high aspect ratio of the molossids and not that of emballonurids (Table A6).

We have shown that the construction of the wings of emballonurids differs greatly from those of molossids and noctilionids, albeit the end product is vaguely similar. Emballonurids appear to have modified a fundamentally short tip into a long, high aspect tip by maintaining relatively long metacarpal elements and elongating the terminal phalanx of digit III; the distalmost phalanges of digits IV and V appear to be shortened. The development of a high aspect wing in this manner may avoid allometric complexities associated with the modification of more proximal wing elements. In addition, to achieve a high aspect wing, such modifications might allow greater versatility. The highly maneuverable flight of emballonurids is suggestive of a wide range of flight potentials. Some species (notably those of *Taphozous*, *Emballonura*, Diclidurinae, and perhaps *Centronycteris*) appear to have capitalized on the speed qualities of high aspect wings.

Rhinolophidae

Horseshoe bats possess wings that average the lowest in overall aspect ratio (5.41) as compared to all other bats (Table A3, Fig. 7). The length of the third digit averages only slightly longer than the head and body (1.28). Also, the forearm nearly equals the length of head and body (Table A8). These attributes combine to produce a wing with next to the lowest average tip index (1.39) for all bats (Table A2 and Fig. 10); only the rhinopomatids average lower.

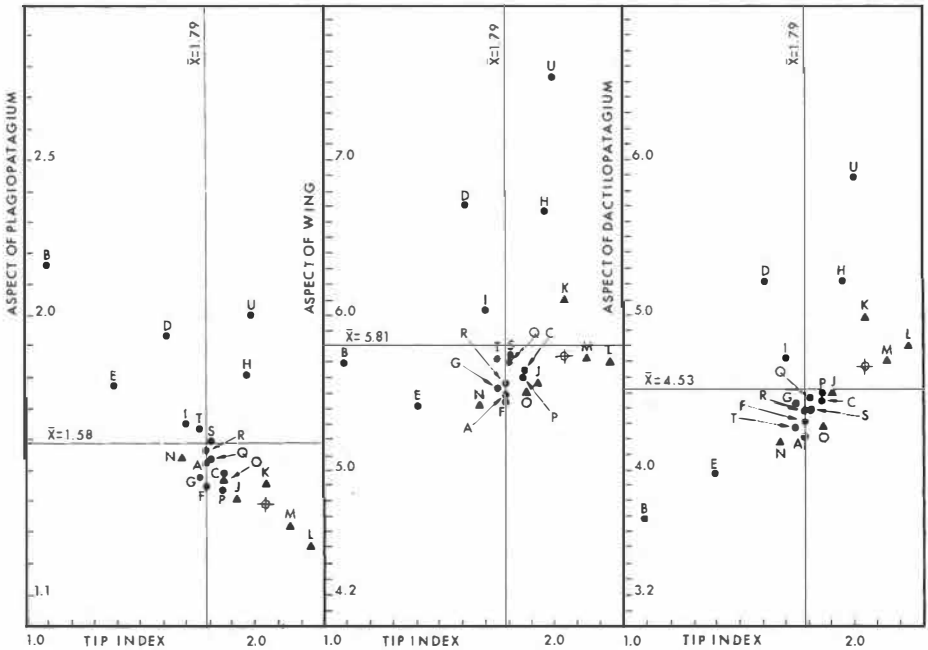


FIG. 10.—Bivariate graphs that illustrate the relationships between tip index and three aspect ratios of the wing. Triangles represent phyllostomatid centroids and the grand centroid for phyllostomatids is indicated by a circle with a plus. See list of specimens examined or Table 5 for key to alphabetic code and text for discussion.

The synergistic relationships among the raw variables, discussed above for the rhinopomatids and emballonurids, generally apply to the rhinolophids. A relatively long forearm is implied by the vector for this variable (B). The ordination of the group centroid for the rhinolophids, as well as that of the Nycteridae and Megadermatidae, appear to be more strongly effected by vectors associated with elements of the third digit. However, the relationships are difficult to characterize because they are involved in a complex interaction among all variables. In the first two canonical axes, the implication is toward shortness, whereas in the third axis there is a general, but weak, expression of large size. Our general impression is that these vectors describe the shortness of the digit as a whole, but the individual components are either not affected or show only slight elongation.

With regard to the fourth digit, all variable vectors for the elements of this digit (G, H, I) imply shortness in the first two canonical axes (Figs. 4D-E, 5, 6). In the third axis, the vector for the fourth metacarpal (G) further emphasizes shortness. However, in this third dimension of discriminant space, the vectors for both phalanges (H, I) of digit IV suggest large size. The percentage of the variance contributed to the discrimination vector of the group by the proximal element of this series is exceptionally high (22.92, Table 6).

The vectors for the components of the fifth digit (J, K, L) are somewhat more influential (Table 6) and all imply large size in the overall ordination of the

rhinolophids. The vector for the distalmost phalanx (L) tends to elevate the group centroid in the third dimension of discriminant space, but the combined effect of the vectors for the metacarpal and the proximal phalanx (J, K) act to suppress the elevation of the centroid.

The wings of rhinolophids, although perhaps not structurally as striking as those of the emballonurids, craseonycterids, or rhinopomatids, do agree in general structure and composition with wings of bats in these families. The generalized distance between rhinolophids and these other group centroids is relatively small—Rhinopomatidae (7.24), Craseonycteridae (4.23), and Emballonuridae (5.92). The most notable difference between the wing of rhinolophoids and that of emballonuroids, and a feature that appears to distinguish the former, is the short tip and generally broad aspect. The composition of the wing in these two superfamilies appears to be similar and to reveal a relatively close common ancestry.

Nycteridae and Megadermatidae

Because of their close association in discriminant space, (generalized distance 4.57), we will discuss these two families together. Although the megadermatids average somewhat larger in general size than do nycterids and rhinolophids, all three families are similar in general wing shape and composition (Fig. 7). The ordination of these two families is influenced by vectors of nearly the same direction and magnitude as discussed in the preceding account of the Rhinolophidae; major differences are mostly quantitative rather than qualitative.

The mean aspect ratio of the wings of nycterids and megadermatids is only slightly higher than that of rhinolophids (Table A3). The relative lengths of digit III, and consequently the tip indices also, are similar (Tables A9, A2). The agreement among these values further attests to the qualitative similarity of wing shape in these three families.

The major differences between the wings of these two families and the Rhinolophidae appear to involve the two phalanges of digit III. The nature of these quantitative differences is strong enough to produce a group discrimination vector capable of consistently classifying the respective members of each family (Fig. 17).

The first phalanx of the third digit is comparatively longer in nycterids than in either rhinolophids or megadermatids. The vector for this variable contributes 19.33 per cent to the discrimination of the group (Table 6). The vectors for the third and fourth metacarpal (C, G) of all three groups ordinate toward small size as discussed in the account of the Rhinolophidae. The vector for the fifth metacarpal (J) is slightly stronger in the ordination of the Nycteridae than it is in either the Rhinolophidae or Megadermatidae (Table 6).

In the ordination of the Megadermatidae, the vectors for the third metacarpal and second phalanx of this digit (C, E) are the strongest relative to these three families and contribute 9.69 and 8.17 per cent, respectively, to the discrimination of the group. The vector of the former implies shortness, whereas the latter in-

dicates large size. The combined effect appears to be elements of nearly equal length. The phalanges of the fourth digit are slightly longer, in a relative sense, and these vectors, likewise, are strong contributors to the discrimination vector of the group (27.23 and 13.12 per cent, respectively).

Noctilionidae

Many of the distinguishing features of the wings of *Noctilio* were discussed in the account of the Emballonuridae. The wings of both *Noctilio albiventris* and *N. leporinus* are essentially alike in shape even though they differ markedly in the absolute size of all raw variables. The wing of these two species are nearly two and a half times the length of the head and body and almost 65 per cent of the span is composed of the third digit. As a consequence, the tip index for the family is high for the order (1.92 for *N. albiventris* and 1.98 for *N. leporinus*). Although the overall aspect ratio of the wing is high and similar to that of molossids and emballonurids, we have noted that the acquisition of this aspect is achieved through different independent interactions among the elements that comprise the wing in these three families (Figs. 7, 8, 9).

All vectors relating to features of the third digit (C, D, E, F) weigh heavily in the ordination of the group. In addition, all but that for the first phalanx indicate large size. The vectors for the most proximal phalanx of the third digit (D) and fifth digit (K), as well as those for the fourth and fifth metacarpal (G, J), imply smallness and tend to suppress the ordination of the group centroid in the third canonical axis (Figs. 4E, 5).

Although the wings of *Noctilio* are high in aspect, we again caution comparisons with the apparent swift flying ability of molossids. We have observed both species in the field and would note that *N. leporinus* flies with a constant, but relatively slow and shallow wing beat. It does not appear to be a particularly fast flier. The smaller species, *N. albiventris*, is an insectivorous bat and from our observations is capable of faster flight judging from the force with which individuals strike a mist-net. *N. albiventris* also exhibits a fair amount of maneuverability in close quarters and is capable of avoiding obstacles.

In our discussion of the Pteropodidae, we suggested that the possession of wing elements of rather long span allowed for the control of large portions of the cambered surfaces. Slight flexion of these elements might greatly affect the camber of the wing, in a manner similar to the downward deflection of the hinged flaps on an airplane. This would contribute markedly to the lift potential at low speeds. We further suggested that the nearly equal lengths of the manal elements of pteropodids might allow for rather crude, yet effective, camber adjustments. We continue this argument here and suggest that the shortening of a proximal phalanx, especially in digits III and IV, would allow a greater range of variation as well as finer dexterous control of the camber of the wing.

With regard to *Noctilio*, and perhaps mormoopids, the shortened first phalanx in digits III and IV not only contributes to the high aspect construction, but might account for the apparent versatility of flight behavior. Furthermore,

in wings that have three phalangeal segments in the third digit, this means of differential elongation of elements also may allow an increase in dexterity during the "flick phase" of the wing beat cycle.

Mormoopidae

Bats of this family possess a relatively long wing, 63 per cent of which is contributed by the third digit (Fig. 8). As we observed in the Emballonuridae, the relatively long forearm may mask or otherwise offset the length of the tip. The tip index of mormoopids (1.70) is only slightly higher than that obtained for emballonurids and both values are well below average for all bats. Our data suggest that mormoopid wings are well above average in overall aspect ratio (Table A3) and that the tip can hardly be characterized as short. The mormoopids appear to be closest, in wing morphology, to the Phyllostomatidae; misclassification occurred with the least derived species, *Pteronotus parnellii*, being assigned to the Phyllonycterinae (Fig. 17).

The length of head and body is a relatively minor feature in the discrimination of mormoopids (Table 6). Also, the length of forearm appears to have little effect on the overall discrimination of the group.

The most important variable vectors in the ordination of the mormoopids appear to be those associated with elements of the third digit (C, D, E, F)—long metacarpal, short first phalanx, and long third phalanx are emphasized (Figs. 4D-E, 5, 6). The former two components of the mormoopid wing contribute the most to the discrimination of the group (20.56 and 26.30 per cent, respectively). Tables A12-A15 generally reflect these features. The percentage contributed to the length of digit III by the first phalanx is nearly the lowest for all bats (11.18), whereas that contributed by the distal phalanx is the highest (16.64). This appears to be a general phyllostomatoid feature.

The effects of the vectors for elements of the fourth digit (G, H, I) are difficult to interpret because of their apparent involvement in the overall synergistic interaction among all variables. In the first and second canonical axes (Figs. 4D, 6), the vector for the fourth metacarpal (G) is oriented away from the group centroid for the mormoopids and thereby implies shortness. However, in the third axis (Figs. 4E, 5), this vector exerts a more positive force in the ordination of the centroid. Both vectors for the phalanges of digit IV (H, I) indicate large size, with emphasis on the distalmost phalanx. This terminal phalanx is not nearly so long or apparently so important in the discrimination of the group as was observed in the Noctilionidae (Table 6). The vectors for the corresponding pair of phalanges in the fifth digit (K, L) also indicate large size with emphasis on the proximal member. These two phalanges weigh heavily in the discrimination of the group (Table 6) and appear to cause a lengthening of the fifth digit, which tends to broaden the wing.

Vaughan and Bateman (1970) presented an excellent discussion of the functional myology of this group. They noted the remarkable maneuverability of these bats and their rapid and sustained flight. *Mormoops megalophylla* is extreme in nearly

all aspects of the wing. *Mormoops blainvillii* is rather curious in that the aspect ratio of its wing is nearly equal to that of the larger-sized species *M. megalophylla* (6.32), whereas its wing loading is a third lower (4.99 Nt/m^2). Members of the genus *Pteronotus*, and especially *P. parnellii*, appear to be less specialized in most features of the wing.

Phyllostomatidae

The New World leaf-nosed bats, along with the noctilionids and mormoopids, tend to dominate the upper right-hand quadrant of discriminant space (Figs. 5, 6). Within this portion of space, each of the phyllostomatid subfamilies tends to occupy a discrete region and group discrimination vectors generally distinguished each of their centroids. There is a rather high percentage (22.30) of "misclassifications" (Fig. 17), which reflect a considerable amount of variation within the family. The majority of these "misclassifications" involves species that occupy a position near the grand centroid. Misclassifications outside of the family limits, although fewer in number, also tend to occur in this region. Among phyllostomatids, the desmodontines exhibit the most fidelity to their group discrimination vectors, whereas the carolliines show the least. We will consider the general nature of phyllostomatid wing morphology before dealing with that of each of the subfamilies.

As has been the case in previous accounts, the length of head and body of phyllostomatids is of minor importance in the discrimination of the family (Table 6). The range of variation of this variable is large and ranges from such small-sized species as *Ametrida centurio* to the large-sized *Vampyrum spectrum.* This variation nearly encompasses the range of variation observed for the order.

The vector for the length of the forearm indicates small size with respect to this variable for all phyllostomatid subfamilies (Figs. 4D-E, 5, 6). The absolute length of the forearm averages slightly below the mean computed for all bats as does the relative length of the forearm (Table A8). Table 6 indicates a rather strong importance of the shortness of the forearm in the discrimination of most subfamilies. This is strongest for the glossophagines, carolliines, and stenodermines, but it is rather minor with regard to the phyllonycterines.

Although the dispersion of centroids is caused by the overall interaction among all variables, the vectors that appear to influence most directly the ordination of phyllostomatid centroids are those associated with features of the third digit; most imply large size. The vector for length of the third metacarpal (C) apparently is a strong factor in the discrimination of all subfamilies (Table 6). The tail end of the vector for the first phalanx of digit III (D) is oriented toward the phyllostomatid centroids (Figs. 4D-E, 5, 6) and implies shortness (see also Fig. 8). This vector is a moderately strong discriminator of the family (Table 6), although it does not appear to be so important in the discrimination of the Carolliinae. The proportionately long third phalanx (F) is a strong discriminator of nearly all phyllostomatid subfamilies (Table 6); phyllonycterines and desmodontines appear to be less characterized by this variable.

The overall effect of interplay among the elements of the third digit is the production of a span that generally averages longer than that of any other group of bats (Table A9). The length of this digit contributes nearly 67 per cent (range, 61.31-70.10) to the overall length of the wing, which is larger than in any other chiropteran family. This is of interest in that the third digit of the molossid wing, which is generally long-tipped and of high aspect, contributes a somewhat lower average of 66.40 percent (range, 64.36-69.70) to the overall span of the wing. The combined effect of the relatively short forearm of phyllostomatids and their long third digits results in the highest tip indices of any group of chiropterans (Fig. 10; Table A2), as also noted by Findley *et al.* (1972).

The vectors for elements of the fourth digit (G, H, I) pass tangentially to the position of phyllostomatid centroids and a precise interpretation of their effect on alar shape is difficult. The vector for the fourth metacarpal (G) suggests large size in all three canonical axes (Figs. 4D-E, 5, 6). The vectors for the two phalangeal elements of digit IV (H, I) appear to exert their greatest force on the ordination of phyllostomatid centroids in the third canonical axis and here also imply large size. Although there is variation within the family, as will be discussed below, the second phalanx of the fourth digit tends to be proportionately longer than the first (Tables A17, A18). Relative to the span of the wing, the fourth digit of phyllostomatids averages longer (60.11 per cent of span) than does that of most other groups of bats; only the molossids are larger in this respect (60.28 per cent of span). In addition, the total length of this digit in phyllostomatids averages nearly one and a half times the length of the forearm (range, 1.23-1.83).

Whereas phyllostomatids and molossids exhibit some similarities relative to the lengths of digits III and IV, these two families are markedly dissimilar with regard to the length of digit V. Indicative of the generally low aspect nature of phyllostomatid wings, the fifth digit is long and averages 1.44 (range, 1.26-1.68) times the length of the forearm. The vector for the second phalanx of this digit (L) appears to be an important feature in the discrimination of all subfamilies of phyllostomatids (Table 6). This variable has its strongest effect on the ordination of phyllostomatid centroids in the third canonical axis where it implies large size (Figs. 4E, 5). The vector for the fifth metacarpal (J), as that of the fourth metacarpal, is difficult to interpret because it is oriented tangentially to the phyllostomatid centroids (Figs. 4D-E, 5, 6). In the first and second axes, the implication is large size, but shortness is emphasized in the third axis. The effect of the first phalanx of digit V (K) on the ordination of phyllostomatids is somewhat clearer, and it implies shortness in all three axes. The vector for the second phalanx of digit V (L) suggests large size. The relative importance of these two proximal elements in the discrimination of the phyllostomatid subfamilies is variable but generally high (Table 6).

Finally, the structural, and perhaps phylogenetic, similarity of wing morphology among phyllostomatids may be summarized by examining the angles between the discrimination vectors of each subfamily (Table 7). In this table, the phyllostomatines are nearest the carolliines and glossophagines. The latter two subfamilies are relatively close to each other as indicated by a 23.08 degree

TABLE 7.—*Angles between the group discriminant functions for the subfamilies of the Phyllostomatidae.*

	Phyllostomatinae	Glossophaginae	Carolliinae	Stenoderminae	Phyllonycterinae	Desmodontinae
Phyllostomatinae	00.00	28.80	26.30	42.32	43.47	48.41
Glossophaginae	28.80	00.00	23.98	25.46	44.30	37.17
Carolliinae	26.30	23.98	00.00	35.02	48.38	56.18
Stenoderminae	42.32	25.46	35.02	00.00	45.68	42.78
Phyllonycterinae	43.47	44.30	48.38	45.68	00.00	45.48
Desmodontinae	48.41	37.17	56.18	42.78	45.48	00.00

divergence between their respective discrimination vectors. The stenodermines fall nearest the discrimination vectors of glossophagines, carolliines, and phyllostomatines, respectively. The most divergent angles between group discrimination vectors occur between phyllonycterines and desmodontines, and all other subfamilies. The angle between the discrimination vectors of these two subfamilies also is rather large (45.48 degrees). These relationships suggest that the phyllostomatines form the nucleus of the family, which is rooted in proximity to the grand centroid for all bats. The glossophagines and carolliines are positioned relatively close to the phyllostomatines and these three subfamilies constitute a core around which the remaining subfamilies are positioned. The stenodermines appear to be morphologically most similar to the glossophagines, carolliines, and phyllostomatines, respectively. The phyllonycterines and desmodontines occupy widely separated positions from each other as well as from the other subfamilies. The phyllonycterines appear to be morphologically nearer phyllostomatines and glossophagines, respectively, than to other subfamilies, whereas desmodontines appear to approach most closely the glossophagines.

Phyllostomatinae

The phyllostomatines are generally the largest bats of the family in terms of absolute size; *Vampyrum spectrum* (40), *Chrotopterus auritus* (39), and *Phyllostomus hastatus* (34) far exceed most New World species in overall size. However, aside from these and several other large-sized species, the phyllostomatines are about average or slightly below average in size. Compared to other phyllostomatids, their wings are relatively long (Table A7) and the relative length of the forearm averages longest of all phyllostomatids (Table A8). The relative length of the third digit is average or slightly above average for the family (Table A9). As a consequence of the interaction between these two lengths, the tip index of phyllostomatines is comparatively low for the family (Table A2). In terms of the overall aspect ratios, the wings of phyllostomatines are in the middle of the range for the family (Tables A3-A5). Wing loading for this subfamily also is near

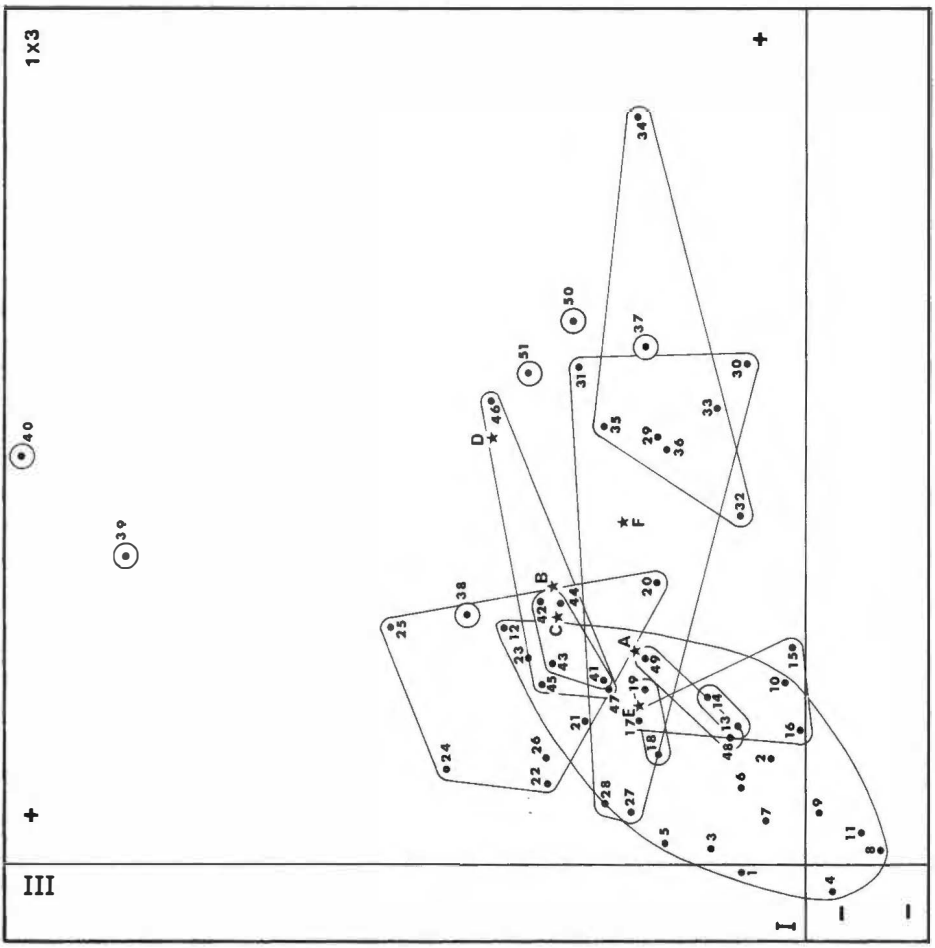


FIG. 11.—Canonical graph of the species of the subfamilies Phyllostomatinae, Carolliinae, and Desmodontinae plotted on the first and third canonical axes. Stars represent the subfamilial group centroids: A, Phyllostomatinae; B, Glossophaginae; C, Carolliinae; D, Stenoderminae; E, Phyllonycterinae; F, Desmodontinae. Genera are encircled as follows: Phyllostomatinae—*Micronycteris* (1-12), *Macrotus* (13-14), *Lonchorhina* (15-17), *Macrophyllum* (18-19), *Tonatia* (20-26), *Mimon* (27-31), *Phyllostomus* (32-36), *Phylloderma* (37), *Trachops* (38), *Chrotopterus* (39), *Vampyrum* (40); Carolliinae—*Carollia* (41-44), *Rhinophylla* (45-47); Desmodontinae—*Desmodus* (48-49), *Diaemus* (50), *Diphylla* (51). Species are identified by corresponding bold-faced numbers in the list of specimens examined.

the median of the family, although the range of variation within the subfamily is large (Table A6).

The centroid for the phyllostomatines is located near the grand centroid for all bats. In the canonical graphs that show positions of individual species (Figs. 11, 12), it will be noted that the genus *Micronycteris* (1-12) encompasses the grand centroid in the first three canonical axes. It is interesting to note here that the five classificatory "misses" from this subfamily to the Vespertilionidae (Fig. 17)

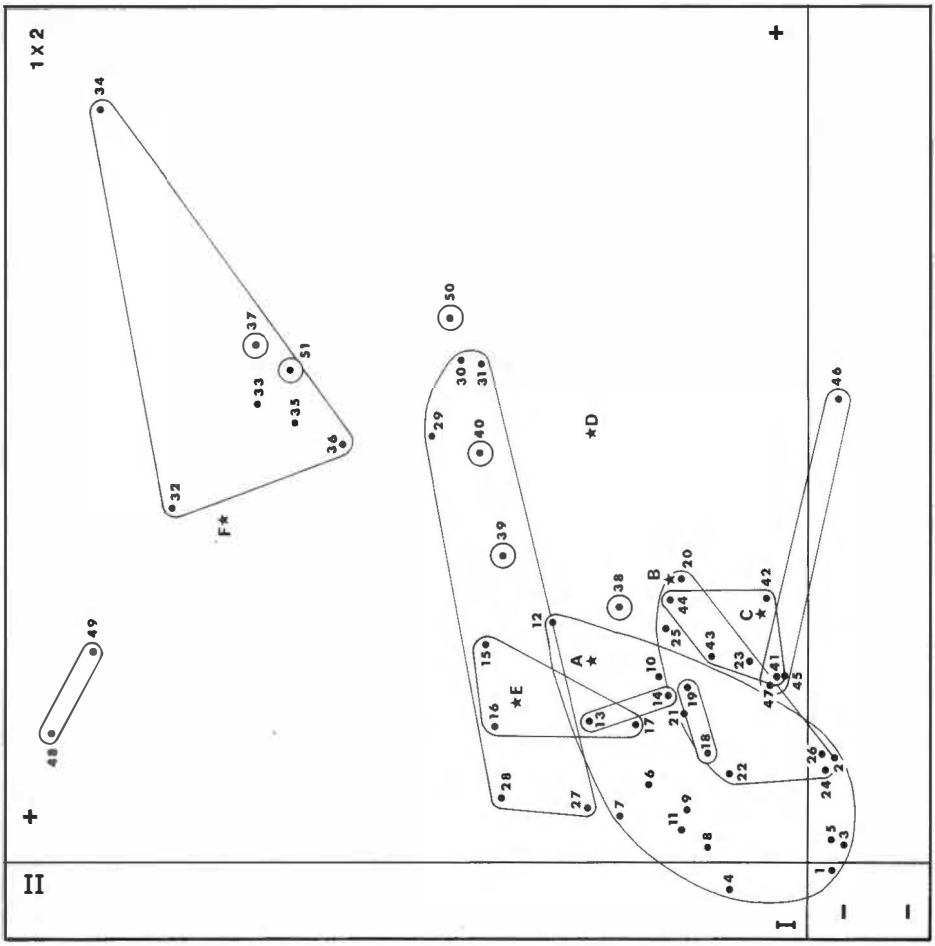


FIG. 12.—Canonical graph of the species of the subfamilies Phyllostomatinae, Carolliinae, and Desmodontinae plotted on the first and second canonical axes. See legend of Fig. 11 for key to group centroids (stars) and genera (encircled dots).

involve *Micronycteris megalotis* (1-2), *M. pusilla* (8), *M. nicefori* (9), and *M. behni* (11). Most of the other species of phyllostomatines cluster together around the centroid for the subfamily. However, there are several notable departures from the group centroid.

Two species, *Vampyrum spectrum* (40) and *Chrotopterus auritus* (39), are most obvious in their departure from the subfamilial centroid, especially along the third canonical axis. Most of this dispersion appears to be caused by the vector for length of the head and body. In addition, vectors associated with comparatively short wings appear to affect these two species. In both, the lengths of forearm and third digit are short as compared to other members of the subfamily (Tables A8, A9). The span of the third digit is most influenced by the vector for the third metacarpal, which implies shortness of this element in these two species (Table

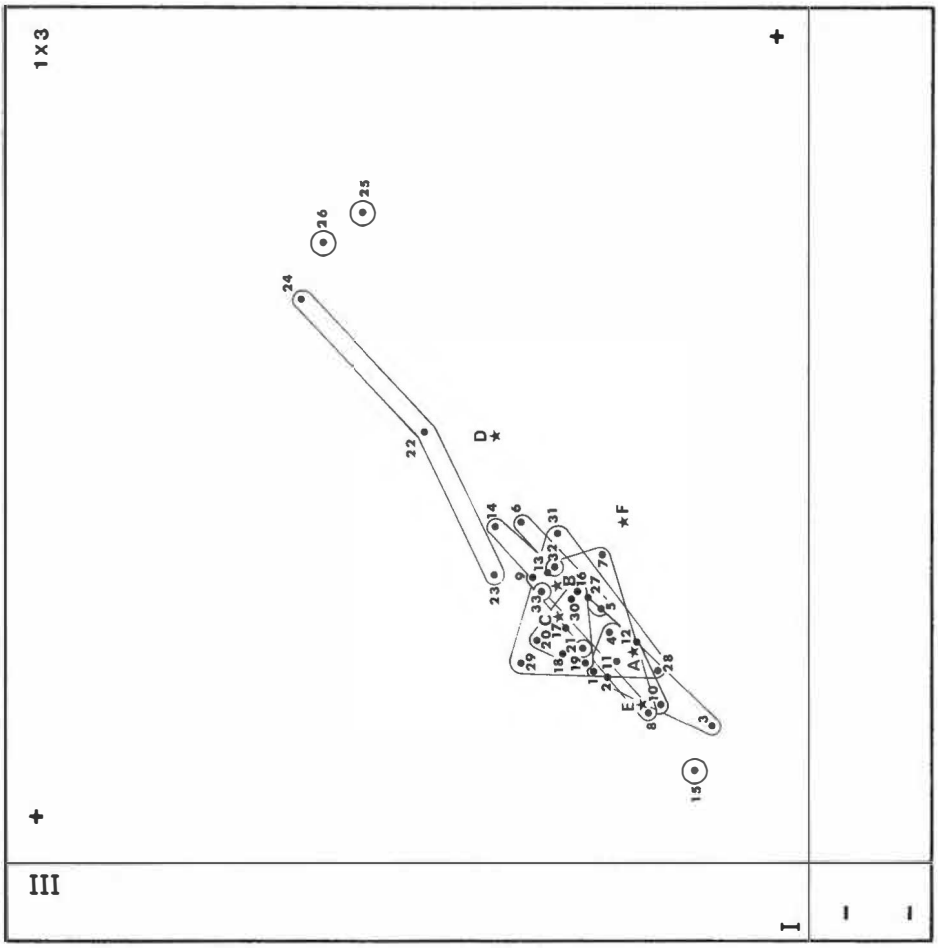


FIG. 13.—Canonical graph of the species of the subfamily Glossophaginae plotted on the first and third canonical axes. Stars represent subfamilial group centroids (see legend of Fig. 11 for key). Genera are encircled as follows: *Glossophaga* (1-4), *Monophyllus* (5-6), *Leptonycteris* (7-9), *Lonchophylla* (10-14), *Lionycteris* (15), *Anoura* (16-20), *Scleronycteris* (21), *Lichonycteris* (22-24), *Hylonycteris* (25), *Platalina* (26), *Choeroniscus* (27-31), *Choeronycteris* (32), *Musonycteris* (33). Species are identified by corresponding bold-faced numbers in the list of specimens examined.

A12). However, the lengths of the first and third phalanges average the largest in percentage contributed to the length of digit III (Tables A13, A15). The metacarpals of the fourth and fifth digit are proportionately short for the subfamily (Table A16, A19), although the phalangeal elements of these two digits are generally long. The terminal phalanx of the fifth digit is comparatively longer than in most other phyllostomatines (Table A21).

For the most part, the genus *Phyllostomus* (32-36) ordinates with the previous two species in the first and second canonical axes (Fig. 12). However, *Phyllostomus* disassociates from this relationship in the third dimension of dis-

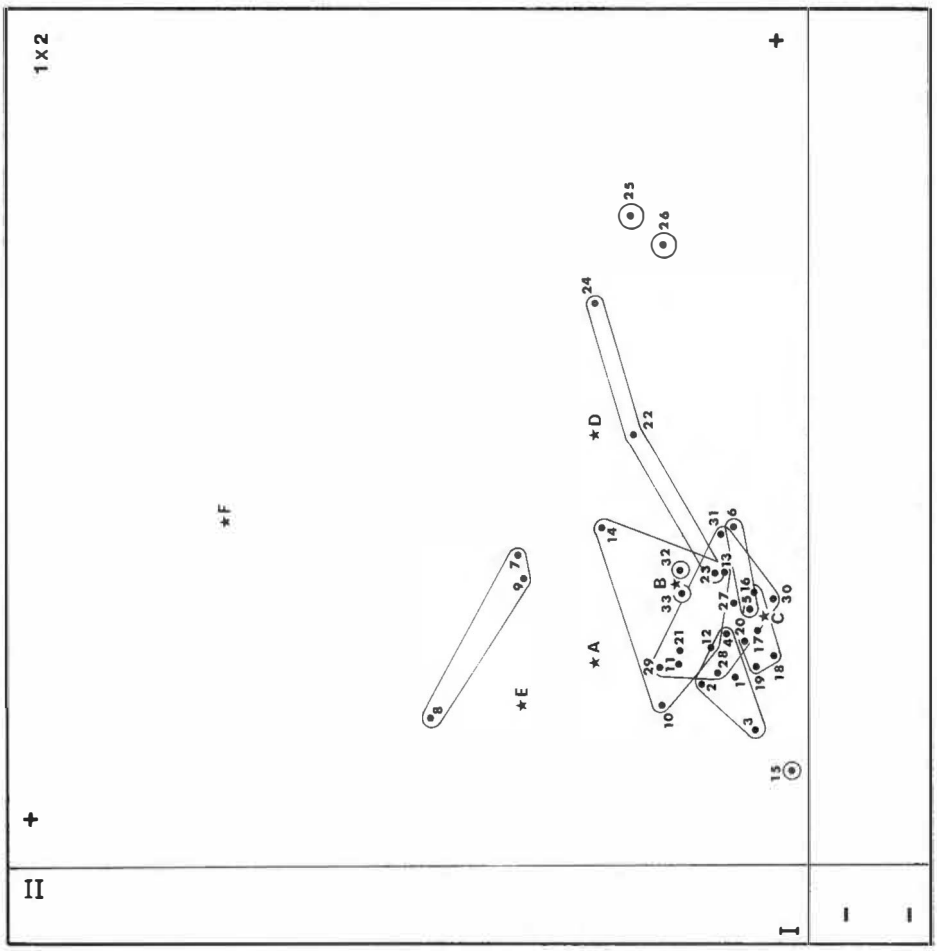


FIG. 14.—Canonical graph of the species of the subfamily Glossophaginae plotted on the first and second canonical axes. See legend of Fig. 11 for key to group centroids (stars) and legend of Fig. 13 for key to genera (encircled dots).

criminant space (Fig. 11). In this axis, *Phyllostomus* tends to deny the influence of length of head and body and is aligned by vectors that imply a long third digit. The vector for the metacarpal (C) is especially important in this regard (Table A12). The first phalanx is the shortest among all members of the subfamily and nearly the family as a whole (Table A13); only the vampire bats have a proportionately shorter first phalanx in the third digit. Other features that distinguish *Phyllostomus* from most other phyllostomatines are long fourth and fifth metacarpals (Table A16, A19), and short distal phalanx in digit V (Table A21). These features also are characteristic of the vampire bats, and it is interesting to note that all species of *Phyllostomus*, except *P. latifolius* (36) and a close associate *Phylloderma stenops* (37), "misclassify" as desmodontines. The species *latifolius* and *stenops* "misclassify" as stenodermines (Fig. 17).

The genera *Mimon* (27-31) and *Tonatia* (20-26) portray an interestingly antagonistic relationship to each other relative to the group centroid. This relationship is exaggerated by *M. crenulatum* (29-30) and *M. koepckeae* (31) on the one hand and *T. silvicola* (25) and *T. venezuelae* (26) on the other. Generally, *Mimon* has the highest aspect ratio as compared to other phyllostomatines, whereas *Tonatia* has the lowest (Tables A3-A5). *Mimon* has the longest wing, in a relative sense, of any phyllostomatid, whereas the wing of *Tonatia* is much shorter (Table A7). This relationship applies to most features examined in this study. Incidently, the two extreme species of *Mimon* "misclassify" as stenodermines (Fig. 17), which generally have longer, narrower wings as compared to the other phyllostomatids. Other phyllostomatines that are "misclassified" (Fig. 17) are *Micronycteris daviesi* (12) and *Macrophyllum macrophyllum* (18-19), which are aligned with the Glossophaginae.

Glossophaginae

The long-tongued bats tend to form a rather tightly packed cluster (Figs. 13, 14), which nestles close to the clusters of the phyllostomatines and carolliines (Table 7). As a group, the glossophagines have relatively short wings as compared to other phyllostomatids (Table A7). The relative length of the forearm averages a little over half (0.63) the length of head and body (Table A8). Comparatively speaking, the third digit is relatively long, which produces a rather large average tip index (2.06) for the subfamily (Table A2). The overall aspect ratio of the wings of glossophagines is highest for the family—notable extremes are *Anoura* (16-20) 6.50, *Musonycteris* (33) 6.30, and *Scleronycteris* (21) 6.23. This also applies to the aspect ratio of the tip region (Tables A3, A4).

In view of the tight packing of the group, a precise interpretation of the variable vectors on the dispersion of glossophagines is difficult. Most of the differences are small, quantitative shifts in the range of variation. The vectors that appear to affect most heavily the ordination of the glossophagines are those for the forearm (B), third metacarpal (C), and second phalanx in the fifth digit (L). The vector for the forearm (B) implies shortness for most species. However, *Leptonycteris* (7-9), *Lionycteris* (15), *Scleronycteris* (21), and *Choeronycteris* (32) generally have longer forearms than other glossophagines (Table A8).

The vector for the metacarpal of digit III (C) suggests large size and *Leptonycteris* and *Lionycteris* represent the large extremes relative to this feature (Table A12). As a group, the glossophagines possess proportionately longer second phalanges of digit V than do any other bats except the pteropodids (Table A21).

Two species, *Hylonycteris underwoodi* (25) and *Platalina genovensium* (26), "misclassify" to the Stenoderminae and are most closely associated with *Sturnira* and *Vampyrops*. Also, *Lichonycteris* (23-24) disperses among these stenodermine genera, although its classification is mostly to the Glossophaginae.

Carolliinae

The group discrimination vectors for this subfamily are relatively weak. In Fig. 17, two species, *Rhinophylla pumilio* (45) and *R. fischerae* (47) are "mis-

classified" as glossophagines and four other species, *Rhinophylla alethina* (46), *Carollia subrufa* (42), *C. brevicauda* (43), and *C. perspicillata* (44) are associated with the Stenoderminae. This leaves only one species, *Carollia castanea* (41), which suggests that, in terms of wing shape, the carolliines are rather indistinct and may bridge the gap between glossophagines and the stenodermines (Figs. 11, 12; Table 7).

As a group, the carolliines have relatively long wings (Table A7). This results from the combination of a moderately long forearm and an exceptionally long digit III. These features also characterize the stenodermines. Carolliines further resemble stenodermines in possessing a comparatively short digit IV; primarily the result of a proportionately short fourth metacarpal (Table A16).

Stenoderminae

Stenodermines represent the most diverse of the phyllostomatid subfamilies. The dispersion of the various species of this subfamily in discriminant space is comparable to that seen in the Phyllostomatinae, although the group generally occupies space unfilled by other taxa (Figs. 15, 16). The group, as a whole, is generally displaced away from the congested area nearer the grand centroid. However, two small-sized species, *Vampyressa pusilla* (24) and *Sphaeronycteris toxophyllum* (56), approach the grand centroid close enough to be confused with the Vespertilionidae (Fig. 17). In addition, *Phyllops haitiensis* (51) and *Centurio senex* (57) are "misclassified" as phyllostomatines, and *Vampyressa nymphaea* (26), *Pygoderma bilabiatum* (54), and *Ametrida centurio* (55) are confused with glossophagines.

Unlike any other subfamily of phyllostomatids, which tend to orient in unimodal directions in discriminant space, the stenodermines appear to ordinate into two slightly different portions of this space (Figs. 15, 16). The extremes of this dichotomy are *Artibeus* (35-47) on one hand and *Vampyrops* (13-22) and *Sturnira* (1-10) on the other. Although the small-sized species of both groups tend to congregate around the group centroid, the large-sized species of each group orient away from each other (Fig. 16).

In the first three canonical axes (Figs. 15 and 16), vectors that imply large size for the forearm (B), fifth metacarpal (J), and second phalanx of digit V (L) ordinate *Artibeus* away from *Vampyrops* and *Sturnira* (Fig. 16). These vectors imply shortness of these variables in both *Sturnira* and *Vampyrops*. The latter two taxa are more directly ordinated by vectors associated with the third metacarpal (C), and second and third phalanges of digit III (E, F). All suggest long length.

The tip index and aspect ratio of the tip are generally higher in *Vampyrops* and *Sturnira* than in *Artibeus*. As might be expected, *Artibeus* has a somewhat higher aspect ratio of the plagiopatagial region, primarily as a result of a proportionately longer forearm (Table A8). The composition of the third digit is similar in both groups, although *Artibeus* tends to have a long metacarpal and generally short phalangeal elements, whereas in *Vampyrops* and, to a lesser extent, *Sturnira*, construction of most of the span of this digit results from long phalangeal elements.

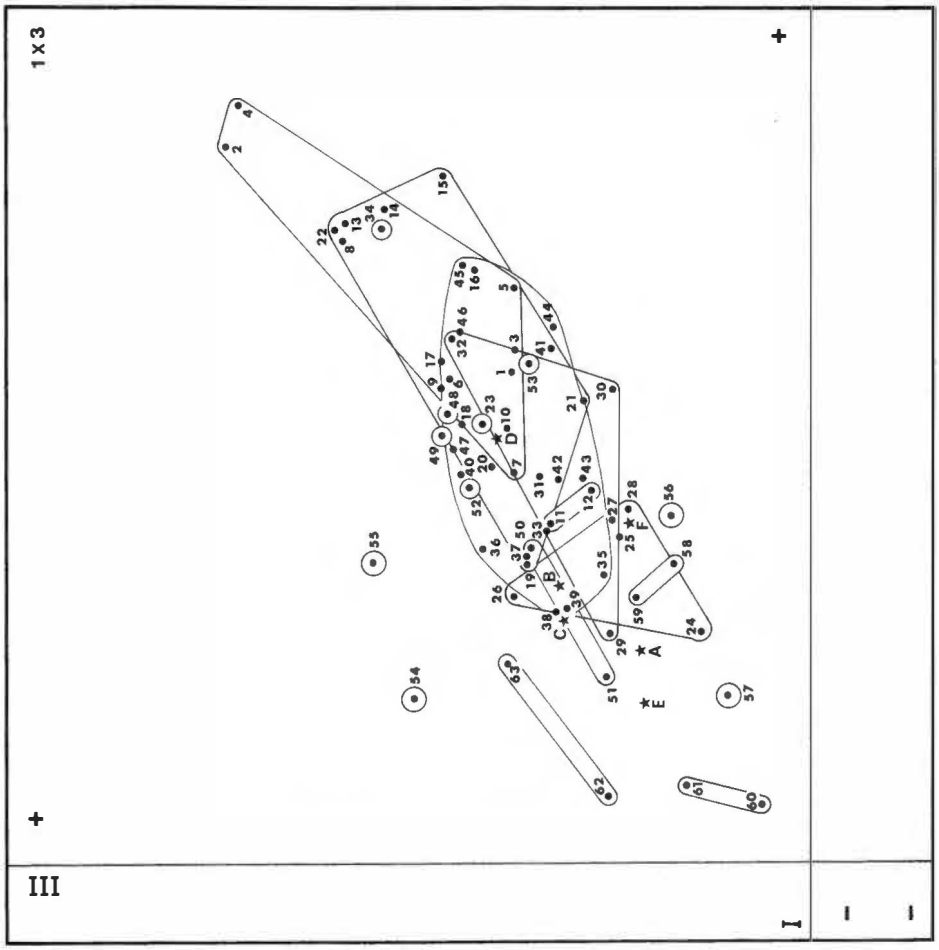


FIG. 15.—Canonical graph of the species of the subfamilies Stenoderminae and Phyllonycterinae plotted on the first and third canonical axes. Stars represent subfamilial group centroids (see legend of Fig. 11 for key). Genera are encircled as follows: Stenoderminae—*Sturnira* (1-10), *Uroderma* (11-12), *Vampyrops* (13-22), *Vampyrodes* (23), *Vampyressa* (24-28), *Chiroderma* (29-33), *Ectophylla* (34), *Artibeus* (35-47), *Enchisthenes* (48), *Ardops* (49), *Phyllops* (50-51), *Ariteus* (52), *Stenoderma* (53), *Pygoderma* (54), *Ametrida* (55), *Sphaeronycteris* (56), *Centurio* (57); Phyllonycterinae—*Brachyphylla* (58-59), *Erophylla* (60-61), *Phyllonycteris* (62-63). Species are identified by corresponding bold-faced numbers in the list of specimens examined.

Sturnira does not quite fit this scheme because the second phalanx is proportionately short (Table A14). However, the proportional length of the distalmost phalanx of the third digit appears to compensate for this (Table A15).

Phyllonycterinae

This subfamily, as well as the desmodontines, is ordinated into a peripheral position of discriminant space relative to the other phyllostomatid subfamilies

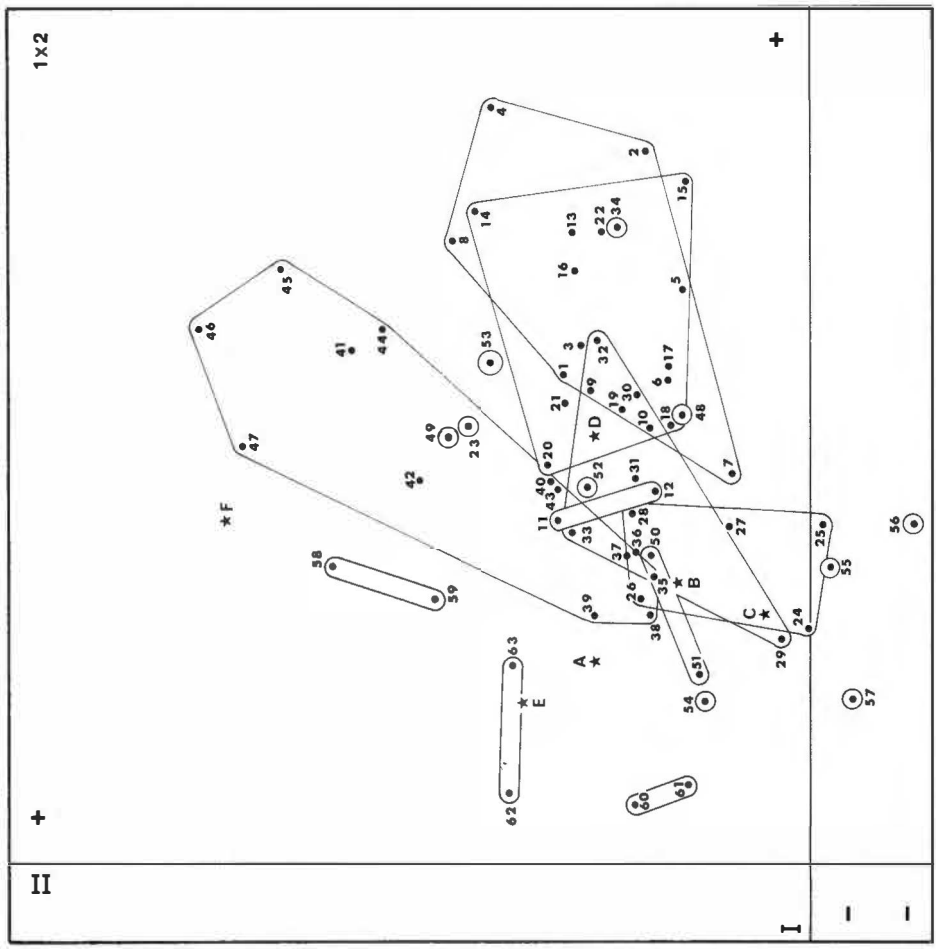


FIG. 16.—Canonical graph of the species of the subfamilies Stenoderminae and Phyllonycterinae plotted on the first and second canonical axes. See legend of Fig. 11 for key to group centroids (stars) and legend of Fig. 15 for key to genera (encircled dots).

(Figs. 11-12, 15-16; Table 7). The flower bats have the shortest wings, in a relative sense, among the Phyllostomatidae (Table A7). They resemble phyllostomatines in possessing relatively long forearms (Table A8). The group has the shortest relative length of digit III as compared to that of other phyllostomatids. This is not particularly surprising inasmuch as the vectors for elements of this digit (C, D, E, F) are oriented away from the group centroid (Figs. 4D-E, 15, 16). The length of the third digit is composed primarily of the phalangeal elements, which are equal or subequal in length (Fig. 8). As might be predicted from their relative position in discriminant space, *Erophylla bombifrons* (60) and *E. sezekorni* (61) "misclassify" as phyllostomatines (Fig. 17).

Desmodontinae

The vampire bats occupy the most peripheral position in discriminant space relative to all other phyllostomatid subfamilies. As there is complete fidelity to their discriminant vectors, there are no instances of "misclassification" of members of this group (Fig. 17), which suggests the distinctive shape of the desmodontine wing (Fig. 8). This distinctness also is reflected in the rather large generalized distance from the other phyllostomatid centroids: Carolliinae, 5.65; Stenoderminae, 4.46; Glossophaginae, 4.43; Phyllostomatinae, 4.28; and Phyllonycterinae, 4.28. The most important vectors in the ordination of the group appear to be those associated with the third metacarpal (C), which imply large size, and those for the first phalanx of digit III (D) and first and second phalanx of digit V (K, L), which emphasize shortness (Tables A12, A13, A20, and A21). Because of the compensating effects of long metacarpal elements in the fourth and fifth digits, the wing of vampire bats tends to be relatively short and broad and of generally low aspect ratio. The vampire wing is the most heavily loaded of all phyllostomatids (Table A6); note that the phyllonycterines follow the desmodontines in this regard.

Natalidae

An interpretation of the alar shape of natalid wings is difficult. Part of this results from the rather small sample size for this family as well as for other families with which the natalids appear to be associated—namely, the Thyropteridae and Craseonycteridae. Also, these three families appear to be associated with the Vespertilionidae, for which there was a disproportionately large sample size. Finally, the centroids of all four families as well as that of the Myzapodidae lie in proximity to the grand centroid for all bats (Figs. 5, 6), tending to obscure the precise relationships of one to another.

In the principal component analysis, the natalids, craseonycterids, and thyropterids dispersed together towards the right-hand portion of Euclidean space (Fig. 3), which, as we have noted above, indicates their general small size for all variables. The vespertilionid centroid, although ordinated towards the small-sized side of the array, occupies a more central position in the overall dispersion. On the other hand, the position of these four group centroids in discriminant space is somewhat different (Figs. 5, 6).

The natalids align most closely with the craseonycterids in the discriminant analysis. The shared absence of the third phalanx of digit III appears overly to bias this association. On the basis of this variable alone, the generalized distances between natalids/craseonycterids, thyropterids, and vespertilionids; craseonycterids/thyropterids and vespertilionids; and thyropterids/vespertilionids are: 0.093, 1.466, and 2.016; 1.466 and 2.016, and 0.550, respectively. The overall generalized distances between these centroids are 4.050, 3.540, and 4.400; 5.580 and 5.457; and 2.489, respectively. However, the generalized distances between these four families, on the basis of each variable, tend to indicate a closer association between natalids, thropterids, and vespertilionids than between craseonycterids and these three families.

Thus, the resemblance of natalids and craseonycterids might be spurious as a result of the absence of the third phalanx of digit III and a concomitant compensation in the length of elements of this digit, especially that of the second phalanx (Fig. 9). In addition, there appears to be a "general" tendency for small-sized bats to have similarly constructed wings (that is, long forearm, long digit III, and generally long digits IV and V). Findley *et al.* (1972) also noted this tendency, but we would caution the reader by noting that some relatively large-sized bats, such as noctilionids, emballonurids, and nycterids (among others), also follow this trend (Tables A2, A7, A8-A11). Hence, we reiterate our earlier statement that the relationships between general body size and wing morphometrics are much more complicated than bivariate comparisons would seem to indicate.

In the first three canonical axes (Figs. 4D-E, 5, 6), the ordination of the natalid centroid appears to be affected by interactions among variables, similar to those noted above for the craseonycterids. In the previous accounts, we have discussed the apparent minor role of the length of the head and body in the discrimination of groups. With regards to the natalids as well as the thyropterids and myzapodids the influence of this variable, albeit weak, is comparatively stronger than noted for other families (Table 6). The relative length of the wing of natalids is 2.61 times the length of the head and body and is among the longest found among all bats (Table A7). This span is composed of a relatively long forearm (Table A8), and digit III has a mean relative length (1.69) that is highest among all bats, Table A9. Similarly, large values for these relative lengths will be noted for craseonycterids, thyropterids, and furipterids.

The composition of the third digit of natalids is more like that of thyropterids and vespertilionids than that of craseonycterids. The vector for the third metacarpal (C) of natalids implies shortness as was the case in the Craseonycteridae. However, the reader will recall that the second phalanx of digit III offset the proportional length of the third metacarpal in the craseonycterids. In the extradimensional fourth and fifth canonical axes, the vector for the third metacarpal more strongly implies longness of this variable for natalids, thyropterids, and vespertilionids. This also is generally the case for the first and second phalanx of digit III for these three families.

The combined effect of variable vectors for elements of the fourth digit (G, H, I) of natalids indicates longness of this digit (Table A10). The most important components of length appear to be the phalangeal elements, although these are generally below the average computed for all bats (Tables A17, A18). The length of the first phalanx of digit IV contributes markedly to the discrimination of the group (Table 6). Again, an interpretation of the vectors for this digit is obscured by the synergistic interaction among all variables. Shortness of the fourth metacarpal (G) is suggested in the first three canonical axes. However, in extradimensional axes this vector implies longness of this variable in natalids, thyropterids, and vespertilionids; shortness is indicated for that of craseonycterids.

The relative length of the fifth digit of natalids averages the longest among all bats (Table A11); the mean relative length of this digit for furipterids and thyropterids also is high. The variable vectors for the lengths of the metacarpal (J)

and second phalanx (L) strongly suggest longness in the first three canonical axes (Figs. 4D-E, 5, 6), whereas that for the length of the first phalanx of digit V implies shortness.

In general appearance (Fig. 9), the wings of natalids are below average in their overall aspect ratio (Table A3). This low aspect also is reflected in the aspects of the tip and plagiopatagial portions of the wing (Fig. 10; Tables A4, A5). Craseonycterids, thyropterids, furipterids, myzapodids, and to a certain extent, vespertilionids resemble natalids in these respects. It is interesting to note that, with regard to wing loading, the craseonycterids possess more heavily loaded wings than do any of the five aforementioned families (Table A6).

Little is known concerning the flight characteristics of natalids. We concur with Findley *et al.* (1972) in their suggestion of slow, maneuverable flight potential for these bats; also, hovering may be well within this potential.

Thyropteridae

The interpretation of wing morphometrics of the disc-winged bats is obscured by the positioning of their group centroid almost exactly on the grand centroid of all bats (Figs. 5, 6). This, in itself, reflects the average character of the shape of their wings. However, the confidence circle for the group centroid is comparatively large, possibly reflecting the rather small sample size utilized in this study.

In the classificatory phase of the discriminant analysis (Fig. 17), both species of thyropterids "misclassify" as vespertilionids. This could reflect a correct assignment or it simply might be an artifact of small sample size. The generalized distance between these two families is comparatively small (2.489) and the generalized distances, based on each variable, likewise support this close association of the two.

Myzapodidae

Little can be said concerning the shape of the wing of *Myzapoda aurita.* The group centroid is in proximity to the grand centroid for all bats (Figs. 5, 6); the confidence circle exceeds the limit of the figures and probably reflects the small sample size of two specimens. In the classificatory phase of the discriminant analysis, these bats as well as the thyropterids (noted above) were "misclassified" as vespertilionids.

Vespertilionidae

The members of this family are extremely diverse in the shapes of their wings and presumably in their flight characteristics. The group centroid is located near the grand centroid for all bats (Figs. 5, 6), but unlike the previous two groups the confidence circle is small, and the group discrimination vector appears to be relatively strong. The one "misclassification" from this family involved *Eudiscopus denticulus,* which was confused with the Phyllostomatinae (Fig. 17). Several other species of vespertilionids were associated with phyllostomatid subfamilies, but

only this one was so classified. In previous accounts, it was noted that several phyllostomatids, as well as thyropterids and myzapodids, were incorrectly assigned to the Vespertilionidae. Aside from possible errors associated with sample size, we suspect that these "misclassifications" reflect general similarities among these species as a result of their proximity to the chiropteran norm (grand centroid).

Generally, the wings of the vespertilionids are moderately long and average about twice (2.07) the length of head and body (Table A7). The range in variation is markedly large and extends from *Mimetillus moloneyi*, with its peculiarly-shaped wing (barely 1.4 times the length of its head and body), to *Otonycteris*, *Kerivoula*, *Miniopterus*, and *Eudiscopus*, wings of which are nearly 2.5 times the head and body length.

The vector for length of the forearm (B) contributes moderately to the group discrimination vector of the family (Table 6). The mean relative length of the forearm is slightly above average for all bats (0.74), but the range within the family includes nearly the total of variation exhibited by the order (Table A8).

The position of the group centroid relative to the vectors associated with the elements of digit III (C, D, E, F) generally reflects the emphasis on the long length of this digit in the composition of the wing (Figs. 4D-E, 5, 6). The mean tip index for the family (1.81) is slightly below the average for all bats (Table A2), but the range in variation includes values that are twice the length of the forearm (for example, *Eudiscopus*, 2.17; *Kerivoula*, 2.12; *Harpiocephalus*, 2.04; and *Lasiurus*, 2.00). In the first three canonical axes, the vector for the metacarpal (C) implies large size. The percentage of variation contributed to the group discrimination vector by this vector is relatively high (18.60, Table 6). Table A12 shows that, on the average, approximately 50 per cent of the length of the third digit is accounted for by this element. As has been the case for the majority of the families discussed to this point, the vector for the first phalanx of digit III (D) implies shortness. On the whole, vespertilionids fall just below the average for all bats with respect to this feature (Table A13). The vector for the length of the second phalanx of digit III (E) nearly equals the metacarpal in its influence in the discrimination of the group centroid (Table 6). The implication of this variable vector is shortness and the mean percentage contributed to the length of the digit III (Table A14) tends to support this. The high extremes in the range of variation of this percentage are noteworthy. The second phalanx constitutes 33.77 per cent of the total length of digit III in *Miniopterus*. Similarly, this phalanx is proportionately long in *Lasionycteris*, *Chalinolobus*, and *Kerivoula* (27.31, 26.77, and 26.42 per cent, respectively). The vector for the length of the third phalanx of digit III (F) is moderately important in the discrimination of the family. However, its precise effect on the dispersion of the group centroid is difficult to assess because this phalanx is indistinguishable or absent in some species and markedly elongate in others. In most vespertilionid species, this phalanx comprises 10 per cent or less of the length of digit III (Table A15); 20.13 per cent is contributed by this element in the wing of *Eudiscopus*.

The interaction among the elements that compose the fourth digit is complex and, as will be noted in Tables A16-A18, the range of variation is wide. The

vector for the metacarpal (G) implies large size. The effect of this vector on the ordination of the vespertilionids appears to be similar to that exerted in the Molossidae (Figs. 4D-E, 5, 6), although, in the latter, all vectors associated with elements of the fourth digit appear to apply a more direct force on the ordination. The first phalangeal element of the fourth digit is about average in its proportional length as compared to that of other bats (Table A17). The vector for the length of the second phalanx of digit IV (I) emphasizes shortness and this is generally supported in Table A18, although, again, the range of variation is wide.

The length of the fifth digit of vespertilionids appears to be controlled mainly by the length of the metacarpal element. The vector for this variable (J) is important in the overall ordination of the vespertilionids as indicated by the relatively high percentage (16.53) contributed to the discrimination vector of the group (Table 6). The vespertilionids rank second highest with regard to the mean per cent contributed by the fifth metacarpal to the total length of digit V (Table A19). Whereas noctilionids average larger than vespertilionids with regard to the proportional length of the fifth metacarpal, the high extremes in the range of variation among vespertilionids far exceed that of any other bats. Notable among these extremes are *Mimetillus* (82.35 per cent), *Philetor* (75.87), *Scotophilus* (73.07), *Tylonycteris* (72.84), and *Nyctalus* (72.56). The vector for length of the first phalanx of digit V (K) implies shortness, but this variable is of minor importance in the discrimination of the group (Table 6). The vector for the length of the distal phalanx of this digit (L) is somewhat stronger in its influence on the group discrimination vector (Table 6) and it suggests shortness.

In a general descriptive sense, the wings of vespertilionids are not particularly striking; they are about average or slightly below average in most respects as compared to those of other members of the order. However, in terms of internal composition, wing variation in vespertilionids is the most complex of any family we have examined. This is particularly true of species that depart from the family norm, that is, those vespertilionids with wings of higher than average aspect ratio.

To illustrate some of this variation, we can examine the construction of the tip region in three species—*Eudiscopus denticulus*, *Lasiurus cinereus*, and *Mimetillus moloneyi*. The aspect ratio for the tip followed by the tip index (in parentheses) for each of these species is 5.98 (2.16), 5.04 (1.99), and 4.41 (1.59), respectively. In *Eudiscopus*, the third metacarpal is proportionately short (41.82 per cent of digital length), the bulk of the length being contributed by the phalangeal elements, especially the third phalanx. The fourth and fifth metacarpals are proportionately longer (61.55 and 64.55 per cent, respectively) than the third, but nearly half the length of each of these digits is accounted for by the phalanges. In *Lasiurus*, the metacarpals are proportionately longer (54.07, 65.01, and 70.63 per cent, respectively) than in *Eudiscopus*, and the first and second phalanx of digit III account for most of the remaining length of this digit; the third phalanx is markedly shortened. The phalanges of digits IV and V are nearly equal in length. The third metacarpal of *Mimetillus* is proportionately longer than that of either of the two aforementioned species (63.40 per cent of the length). The third phalanx of digit III is indistinguishable, and the remaining two are about equal in length. The

majority of the length of the fourth and fifth digits is contributed by the metacarpal elements (73.59 and 82.35 per cent, respectively). The second phalanx of digit IV is much reduced, (comprising less than five per cent of the length of the digit). Both phalanges of digit V are extremely short and equal or subequal in length. Together, they comprise 17.65 per cent of the length of this digit.

These three species are only exemplary of the kinds of variation that exist within the family Vespertilionidae. This would seem to confirm the wide variety of flight behaviors reported for the family, which range from the swift, sustained flight of migratory species to the erratic, highly maneuverable flight of some of the smaller nonmigratory species. Norberg (1972, 1976*a*, 1976*b*) has clearly demonstrated the hovering ability of *Plecotus auritus*, and certainly other species will be shown to possess this flight behavior.

Mystacinidae

The group centroid for this rather unusual, monotypic family ordinates into the upper right-hand quadrant of discriminant space (Figs. 4D-E, 5, 6). As we have noted above, this portion of discriminant space is defined generally by a relatively long and broad chiropatagium and relatively short and broad plagiopatagium. The centroid of *Mystacina tuberculata* is most closely associated with that of the Mormoopidae in the first two canonical axes (Fig. 6). However, interactions among variable vectors in the third canonical axis (Figs. 4E, 5) cause a rather marked dissociation of these two centroids, suggesting basic differences in the composition of the wings of these two families.

The effect of the vector for length of forearm (B), albeit weak as compared to that of other groups of bats, is somewhat stronger in discrimination of *Mystacina* than in mormoopids (Table 6). In both groups and in the first two canonical axes (Figs. 4D, 6), this variable vector generally suggests longness. In the third canonical axis (Figs. 4E, 5), the mystacinid centroid appears to be more strongly influenced by the tail (smallness) end of this vector, whereas the mormoopid centroid is aligned closer to the positive (longness) end. The relative length of the forearm of *Mystacina* ranks slightly below the mean for all bats: mormoopids rank above this mean (Table A8). This indicates a somewhat greater length of head and body for *Mystacina* as compared with that of mormoopids.

Interactions among variable vectors associated with length of digit III (C, D, E, F) of *Mystacina* are similar to those discussed for mormoopids. The vector for the length of the third metacarpal (C) of both these families implies large size (Figs. 4D-E, 5, 6). The proportional length of this wing element is slightly greater in *Mystacina* than in mormoopids and, in both, contributes more than 50 per cent to the length of digit III (Table A12). As appears to be typical of bats arrayed in this portion of discriminant space, the vector for the length of the first phalanx of digit III (D) suggests shortness. This wing element comprises only 14.33 per cent of the length of the third digit in *Mystacina*, which is only slightly higher than that contributed in mormoopids (Table Al 3). These two variable vectors appear to be important in the group discrimination vectors of both *Mystacina* and mormoopids (Table 6). Although the variable vectors for the two distal phalanges

(E, F) of both families suggest long length, the contribution of each of these elements to the wing of these two groups is somewhat different. The proportional lengths of all three phalangeal elements are maintained nearly equal or subequal in the wing of *Mystacina* (Fig. 9; Tables A13-15). On the other hand, there appears to be a definite allometric relationship among these phalangeal elements in the wing of mormoopids. The relative length of the third digit of the mystacinid wing lies below the average for all bats (Table A9). Likewise, the tip index of *Mystacina* is below the average computed for all bats (Table A2). However, as noted above, the long forearm tends to mask the length of digit III in these bats as well as in emballonurids and mormoopids.

The effects of the vectors for elements of the fourth digit (G, H, I) of *Mystacina* are similar to those discussed for mormoopids. The vector for the length of the fourth metacarpal (G) indicates shortness in the first two canonical axes (Figs. 4D, 6), but a slightly positive (longness) influence is suggested in the third axis (Figs. 4E, 5). The proportional length of this element is well above the average for all bats (Table A16). The variable vectors for the phalangeal elements of digit IV (H, I) both imply longness. In terms of the group discrimination vector, the variable vector for the first phalanx of this digit (H) appears to be important (Table 6). The proportional length of the second phalanx of digit IV ranks slightly above the mean for all bats and this element contributes 21.04 per cent of the length of the digit (Table A18).

The greatest differences in composition of the wing of *Mystacina* and that of mormoopids concern features of the fifth digit. In *Mystacina,* variable vector for the length of the fifth metacarpal (J) suggests longness in the first two canonical axes (Figs. 4D, 6). However, the implication shifts toward smallness in the third axis (Figs. 4E, 5). Paradoxically, the proportional length of this wing element (67.42) ranks well above the average for all bats (61.02), whereas that for mormoopids (59.29) falls below the average (Table A19). This variable vector appears to be relatively unimportant in the discrimination of the Mystacinidae (Table 6). The strongest vectors in this regard are those for lengths of the first and second phalanx of digit V (K L). The vector for the first phalanx (K) strongly suggests shortness in all three canonical axes (Figs. 4D-E, 5, 6). The proportional length of this element averages the shortest among all bats (Table A20); mormoopids rank above the overall average with regard to this feature. On the other hand, the vector for the length of the second phalanx of digit V (L) strongly implies longness and this element contributes 21.00 per cent to the length of this digit (Table A21).

The overall aspect ratio of the wing, as well as that of the tip, of *Mystacina* falls slightly below the average of all bats (Tables A3, A4). However, the relatively long forearm and comparatively short fifth digit contribute to the higher than average aspect ratio of the plagiopatagium (Table A5).

Little is known concerning the flight behavior of *Mystacina tuberculata.* The family is endemic to New Zealand where it and *Chalinolobus tuberculatus* (Vespertilionidae) comprise the total chiropteran fauna. The phylogenetic relationships of the family are poorly understood although relationship to the

Molossidae has been suggested by various authors (Dobson, 1875, Miller, 1907). In terms of wing shape, *Mystacina* most closely resembles mormoopids and phyllostomatids. This is particularly interesting in view of Daniel's (1976) recent report on the food habits of *Mystacina* in which he included fruit and possibly nectar along with aerial and terrestrial insects in the feeding regime. If the morphometric resemblance between *Mystacina*, mormoopids, and phyllostomatids is conveyed in functional similarity, the wing of *Mystacina* should be found to be relatively versatile.

Molossidae

The shape of the wing in this family is perhaps the most distinctive among all bats. The molossid wing is extremely narrow and has an unusually long tip region (Fig. 9). As a consequence, the wing is highest in overall aspect ratio among bats. We have already discussed some features of molossid wings in the accounts of emballonurids and noctilionids. Of particular interest is the fact that, even though the bats of these three families possess wings of high aspect, the mode by which their wings are constructed is markedly different.

Whereas the forearm is usually long in most other groups of bats, especially those that possess high aspect wings, the relative length of the forearm of molossids averages the shortest among all bats (Table A8). The vector for this variable (B) is oriented almost directly away from the group centroid in the first three canonical axes and thereby suggests shortness (Figs. 4D-E, 5, 6). The forearm contributes only 30 to 35 per cent to the total span of the wing. Among molossids, *Cheiromeles*, *Otomops*, and *Eumops* possess the largest forearms, whereas *Sauromys* and *Molossus* have the shortest. As the orientation and length of the variable vector indicate, the length of the forearm is an important factor in the group discrimination vector (Table 6).

The great length of the wing is reflected in the generally positive orientation of all vectors associated with elements of the third digit toward the molossid centroid (Figs. 4D-E, 5, and 6). The vectors for the metacarpal, and second and third phalanges (C, E, F) are not as positively associated with the molossid centroid as was noted for the noctilionids, mormoopids, phyllostomatids, and vespertilionids. Nonetheless, these vectors do imply longness of these elements in the Molossidae. The vector for the first phalanx of digit III (D) strongly suggests longness in the first two canonical axes and to a certain extent in the third axis. Proportionately, the length of this phalanx (19 to 26 per cent of the length of digit III) averages among the largest for all bats (Table A13). Although the proportional length of the second phalanx averages below the mean for all bats (Table A14), these two phalangeal elements in consort with the metacarpal produce the major portion of the span of digit III. It is difficult to interpret the vector for the third phalanx of this digit because, by comparison, it is rather short. However, this vector appears to be rather important in the group discrimination vector (Table 6). In this case, the vector seems to imply simple presence of the phalanx rather than length. Shortness or absence of the distal phalanx of digit III seems to be the case in other families

that have proportionately long first and second phalanges (for example, emballonurids, noctilionids, and vespertilionids).

In most of the other groups of bats considered in this study, vectors associated with elements of the fourth digit (G, H, I) are not easily interpreted, mostly because of their tangential orientation to centroids and their synergistic interaction with other variables. All three of these vectors are directed toward the molossid centroid and all imply longness. The most powerful among these are the vectors for length of metacarpal (G) and second phalanx (I). In addition, these two vectors are important in the group discrimination vector (Table 6). The relative length of the fourth digit is not particularly impressive and it averages below the mean for all bats (Table A10). However, this value is greatly masked by the generally long length of head and body of these bats. The fourth digit of molossids constitutes nearly 60 per cent of the span of the wing, and in these terms, is the largest among all bats. The metacarpal alone contributes 55 to 69 per cent of the length of this digit (Table A16). The first phalanx constitutes the bulk of the remaining length (18 to 28 per cent, Table A17). The length of the second phalanx of digit IV is variable and can contribute as much as 18.11 per cent (*Sauromys*) or as little as 2.88 and 3.94 (*Tadarida* and *Promops*, respectively) to the length of this digit. *Eumops* and *Molossus*, on the average, possess a rather short second phalanx on digit IV.

Unusually long third and fourth digits have been discussed in the accounts of several groups, especially the Phyllostomatidae, which have generally long-tipped, low aspect wings. Perhaps the most striking feature of the molossid wing is the markedly short fifth digit, which converts the long tip region into a high aspect surface. The vector for the length of the fifth metacarpal (J) strongly implies shortness in the first three canonical axes (Figs. 4D-E, 5, 6). Similarly, the vectors for the lengths of the two phalangeal elements of this digit (K, L) orient away from the molossid centroid and thereby imply shortness. All three of these variable vectors are important factors in the discrimination of the group (Table 6).

In other high aspect wings such as those of emballonurids and noctilionids, the shortening of the fifth digit is accomplished by shortening the phalangeal elements while maintaining the metacarpal more or less isometric with the third and fourth metacarpals. If the apparent versatility in flight behavior of these bats is any indication, we could assume the formation of a high aspect wing in this fashion to be a less than total commitment to swift flight. On the other hand, by shortening the fifth metacarpal, molossids gain dexterous control of a smaller portion of the camberable surface but at the same time might lose a sizable degree of flight versatility. In this light, it is interesting to note that the genus *Tadarida* (the most diverse, yet least specialized, of the family with some 45 or so species) exhibits a wide range of variation in the composition of the fifth digit and other digital elements.

To illustrate the degree of variation in wing composition within the Molossidae, we have used *Cheiromeles*, *Otomops*, *Sauromys*, and *Tadarida*. *Cheiromeles*

torquatus is the largest molossid, with a head and body length of 115 to 135 millimeters and a weight of 150 to 170 grams. The proportional lengths of the metacarpal elements of digits III to V are shortest among the family (43.21, 54.62, and 49.37 per cent contribution to digital length, respectively). On the other hand, the phalanges of the third and fourth digits are proportionately longer than those of any other molossid. The first phalanx of the fifth digit is proportionately longer than that of any other molossid, comprising nearly 40 per cent of the length of the digit; the second phalanx is about average for the family (11.50 per cent of digital length).

On the average, *Otomops* possesses the proportionately longest third and fourth metacarpals of any molossid (54.42 and 68.78 per cent of the digital length, respectively), although individual species of *Tadarida* and *Eumops* possess longer fourth metacarpal elements (72.52 and 70.18 per cent, respectively). The proportional lengths of phalangeal elements vary in *Otomops*. Generally the major portion of the length of digit III is contributed by the second, first, and third phalanx (21.18, 20.59, and 4.65 per cent, respectively). *Otomops* possesses the shortest first phalangeal element of digit IV of the family (17.82 per cent of the digital length), and the proportional length of the second phalanx (7.21 per cent) is well below the average for the family. Whereas the metacarpal of digit V is extremely short, the proportional length of the phalanges of this digit are nearly the largest for the family (35.27 and 12.57 per cent, respectively).

Whereas the two genera discussed above might be considered as among the more specialized molossids, *Sauromys* appears to be among the least specialized. The metacarpal elements of digits III and IV are proportionately average for the family (50.81 and 59.05 per cent, respectively); the fifth metacarpal is unusually long for the family (63.56 per cent of the digital length). The proportional lengths of the first and second phalangeal elements of digits III to V vary although they are generally isometric and range between 22 and 15 per cent of the digital length. The third phalanx of digit III is proportionately long for the family (7.93 per cent of the digital length).

Finally, *Tadarida* is perhaps the most variable among the molossids in terms of wing composition. The proportional lengths of the metacarpals of digits III to V rank near the family average, but the range is broad (53.97 to 46.02, 72.52 to 57.16, and 67.51 to 53.55 per cent of the digital length, respectively). There is a general trend of isometry among the proportional lengths of the first and second phalanx of digit III (20.59 to 19.81 and 23.34 to 18.02 per cent, respectively). The proportional length of the third phalanx of this digit varies (10.80 to 4.92 per cent). With regard to the phalanges of the fourth digit, patterns of allometry and isometry vary markedly, especially with respect to proportional length of the second phalanx (27.10 to 19.94 and 20.49 to 2.88 per cent of digital length, respectively). Freeman (1977) noted this allometric variation in the composition of digit IV and interpreted it in terms of zoogeographic distribution. Allometry is even more pronounced in the proportional lengths of the phalangeal complement of the fifth digit (36.43 to 21.81 and 15.05 to 7.97 per cent, respectively).

Generally speaking, the wings of molossids are highly specialized, although we remind the reader that within this family a degree of variability exists. Wing loading is normally high (Table A6): *Eumops* averages highest in the family (28.47 Nt/m^2; *Eumops auripendulus* is highest among all bats with 58.00 Nt/m^2); and *Tadarida*, although nearly average in this feature (19.54 Nt/m^2), exhibits loadings down to 8.43 Nt/m^2. The general composition of the molossid wing suggests a reduction in the control of camberable surface. No doubt the "automatic" flexing and extending devices in the elbow and shoulder regions discussed by Vaughan (1959, 1970*a*) relate to this alar composition. We suspect that the more generalized species of the family will be shown to have a greater degree of "manual" control of their flight surfaces.

Classification

As has been discussed above, in the discriminant analysis a discrimination vector is computed for each group (in this case families or subfamilies) based on the synergistic interaction among variables. In the classification phase of the analysis, each case (species in this analysis) is scrutinized and assigned to that group to which it is most closely aligned in discriminant space (Fig. 17). Inasmuch as the discrimination vector for each group is an expression of the complex qualitative and quantitative aspects of wing shape, species are grouped together based on similarity of wing shape.

In the overall classificatory analysis, only 14 of 466 species (three per cent) were incorrectly assigned. The high degree of correct associations appears to indicate a rather large phylogenetic component in the overall shape of bat wings. "Misclassifications" may be attributed to several possible sources of error.

The first of these is insufficient sample size, which could have greatly effected the formulation of an accurate discrimination vector for various groups. We suspect this might be the case with regard to the Thyropteridae and Myzapodidae, in which the sample sizes were extremely small. We would not be particularly surprised if the association of these two families with the Vespertilionidae was found not to be related to the sample size, because the shape of the wing in these two families is in fact similar to that of the vespertilionids. Another source of error involves "leakage" of taxa that ordinate close to the grand centroid for all bats. This we suspect is the explanation for most of the "misclassifications" encountered in the Phyllostomatidae.

Yet another source of error might be that of functional similarity. With regard to the two species assigned to the Megadermatidae, as well as *Hypsignathus monstrosus* (Pteropodidae) and *Rhinolophus luctus* (Rhinolophidae), it is noteworthy to point out that each has a relatively long second phalanx in digit III, which is a major feature of megadermatids. Similarly, the association of *Pteronotus parnellii* with the Phyllonycterinae appears to relate to the overall similarity of alar shape, especially with respect to length of forearm. As noted above, this association also may reflect some phylogenetic similarity between mormoopids and phyllostomatids. One molossid species, *Tadarida loriae*, is classified as a

	PTEROP	RHINOP	CRASEO	EMBALL	RHINOL	NYCTER	MEGAD	NOCTIL	MORMO	PHYLOS	GLOSSO	CAROLL	STENOD	PHYNYC	DESMOD	NATALL	THYROP	MYZAPO	VESPER	MYSTAC	MOLOS
PTEROP	57						1														
RHINOP		3																			
CRASEO			1																		
EMBALL				36																	
RHINOL					62		1														
NYCTER						8															
MEGAD							5														
NOCTIL								2													
MORMO									4					1							
PHYLOS										19	2		5		3				4		
GLOSSO											31		2								
CAROLL											2	1	4								
STENOD										2	3		50						2		
PHYNYC										2				4							
DESMOD															3						
NATALL																3					
THYROP																	0		2		
MYZAPO																		0	1		
VESPER										1									77		
MYSTAC																				1	
MOLOS																			1		59

FIG. 17.—Classification graph from the discriminant analysis. Numbers on the diagonal represent number of species correctly associated by the group discrimination vector for each group, with their respective taxonomic category. Numbers in rows, and off the diagonal, represent number of "misclassifications" to other taxonomic groups. This analysis resulted in 97 per cent correct associations. See text for discussion.

vespertilionid. This is not surprising because other generalized species of *Tadarida* are ordinated toward the vespertilionid dispersion.

The Phyllostomatidae, as a whole, illustrates a rather high affinity to its various group discrimination vectors; only 4.32 per cent of its species are assigned outside the limits of the family. However, within the family there is a relatively high percentage of "misclassification" (22.30 per cent); this could reflect phylogenetic infidelity or, again, it simply might be attributable to functional similarities in wing shape.

The Desmodontinae is the only phyllostomatid subfamily that does not exhibit a "misclassification." However, three species of *Phyllostomus* are confused as

desmodontines. Of these, two different samples of *P. discolor* follow this trend with 91 to 50 per cent affinity, respectively, to the discrimination vector of vampires. *Phyllostomus latifolius* exhibits 44 per cent affinity and *P. hastatus*, in two separate analyses, showed 100 per cent affinity with this subfamily. A tentative explanation of this might be that these large-sized phyllostomatines have flight requirements similar to those of vampires (high weight-bearing capacity) and hence wings of similar shape.

The glossophagines illustrate the tightest packing of taxa among the phyllostomatids. Only two species, *Hylonycteris underwoodi* and *Platalina genovensium*, are associated outside of the group. It is difficult to assess their relationship with the stenodermines other than to say that these two species appear to be similar to *Vampyrops* and *Sturnira*.

The stenodermines, although not so tightly packed, occupy a fairly discrete portion of discriminant space. The seven "misclassified" species are located in the congested region near the grand centroid for all bats. The Carolliinae is practically engulfed in this congestion, and they show little fidelity to their group discrimination vector. The fact that this congested area exists and that it is composed primarily of phyllostomatines would suggest the generalized nature of the wings of this subfamily. Also this seems generally to support the basal assignment of this group in terms of phylogenetic relationships within the family.

Conclusions

As stated in our introductory comments, the wide range of variation and complicated nature of the interactions among the intrinsic wing elements of chiropteran species makes impossible a precise and definitive explanation of wing shape. However, the essence of wing shape and the variables that affect it can be perceived in multidimensional space using such multivariate procedures as discriminant analysis. This study has been as much an analysis of chiropteran wings as it has been an example of this morphometric procedure.

The interactions among the variables utilized in this study are summarized below.

1. Length of head and body appears to have little effect on the shape of chiropteran wings. Generally speaking, bats tend to possess wings that range between one and one half and two and one-half times the length of the head and body. Extremes in excess of three times the length of head and body were noted among the Emballonuridae. Whereas small-sized bats tend to have longer wings with lighter loading than do larger bats, there is a great deal of variation and the picture appears to be more complex than simple bivariate analysis indicates. We do not believe that the questions of mass, area, and wing shape have been adequately dealt with, and certainly these considerations were beyond the focus of our analysis. We suggest that these questions will require further analysis under free-flight conditions.

2. Lengths of forearm and digit III certainly constitute the majority of the wing span. However, derived variables that describe their relative proportions

(such as tip index) do not adequately represent their influence on wing shape. We have shown that the forearm can be relatively short or relatively long and in conjunction with the span of digit III produce a wing of similar or different shape. Pteropodids, emballonuroids, and rhinolophoids tend to emphasize the long length of forearm in wing construction. The remaining chiropteran families generally possess shorter forearms.

3. The composite length of digit III can be relatively short (Rhinopomatidae) or long (Phyllostomatidae and Molossidae). The interactions among the bony elements that comprise the length of the third digit are extremely complex. Chiropteran families are ordinated, rather markedly, into two general groups in discriminant space by the presence or absence of the third phalanx of this digit. However, wing tips of nearly equal proportional length are achieved by members of both groups. Those that possess long wing tips, the phyllostomatoids and vespertilionoids (except molossids) tend to have a lengthened second phalangeal element of digit III. The phyllostomatoids generally have a lengthened third phalanx as well and a shortened first phalanx. Vespertilionoids (except molossids) tend to possess a lengthened first and second phalanx, in an isometric fashion, and have a shortened terminal phalanx of digit III. Molossids follow the general pattern of vespertilionoids, but also have a lengthened metacarpal of this digit. Those bats with generally short wing tips illustrate an allometric mixture in the composition of digit III. Most, with the notable exceptions of the Pteropodidae and Craseonycteridae, possess a moderately long metacarpal. However, most of the span of digit III is contributed by a relatively long second phalanx or, in some cases, moderately long first and second phalanges of nearly equal length.

4. The effect of the fourth digit on the shape of the wing is complex and, in most cases, the influence of its elements are involved in an overall synergism among variables. In those bats with low aspect tip regions, the length of this digit is intermediate between digits III and V. The fourth digit is relatively long in the high aspect wing tips of noctilionids and molossids; in those of emballonurids this digit is shortened. The composition of the fourth digit also varies. In the phyllostomatoids, the metacarpal is moderately long and has proportionately lengthened first and second phalanges. The terminal phalanx is especially long in noctilionids. The metacarpal element is lengthened in emballonuroids and rhinolophoids, and the first phalanx also tends to be proportionately long. In the Pteropodidae, the metacarpal is markedly shortened, and the length of the digit is produced by proportionately long first and second phalangeal elements. The long fourth digit of molossids is comprised of the long metacarpal and first phalanx.

5. Whereas digit III is important in determining the span of the wing, digit V determines the chord. The interactions between this digit and other wing components in determining shape are somewhat dualistic in nature. The aspect ratio of the plagiopatagium can be affected either by a lengthening or shortening of digit V or the forearm. Thus, in the Rhinopomatidae and Emballonuridae, a relatively long forearm in combination with a moderately long fifth digit produces

a high aspect plagiopatagium. On the other hand, in the Molossidae, shortening of both elements produces an aspect ratio of similar or higher magnitude. The interaction of digit III with the fifth digit yields a tip region of high aspect in the Emballonuridae and Molossidae; by comparison, that of rhinopomatids is low in aspect. In the Phyllostomatidae, a long fifth digit tends to offset the effects of the long span of digit III and, in combination with a relatively short forearm, produces an overall low aspect wing. The composition of the fifth digit, like that of digits III and IV, varies from group to group. Most bats lengthen or shorten the fifth digit by differentially lengthening or shortening phalangeal elements; most taxa, especially molossids, retain a moderately long metacarpal. The pteropodids, as we have noted, have markedly short metacarpal elements in all three digits. Of the Microchiroptera, the molossids illustrate the most drastic proportional shortening of the fifth metacarpal.

6. Finally, we reemphasize that although the overall shape of the wing (silhouette) may be important from the standpoint of such aerodynamic features as wetted surface area and wing loading, it is the internal composition of the wing that determines the camberability and ultimately the dynamics of lifting potential. Far too little is known concerning the comparative aspects of actual free-flight behavior of bats to permit meaningful functional interpretation of wing shape. It is to this end that we suggest future morphometric analyses be directed, for without this, functional speculations can only be misleading and may further confound an understanding of mammalian flight.

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APPENDIX

Tables A1-A21 follow and consist of ranked means and statistics for selected derived variables. Statistics include mean for taxa (range in parentheses), plus or minus one standard error of the mean, and the coefficient of variation. Variable means are based on genera within families or subfamilies, or species within genera. Familial means are ranked from largest to smallest. Within the Phyllostomatidae, subfamilial means are similarly ranked as are genera within subfamilies. The grand mean for all bats is ranked with the familial ranking. These tables were generated aside from the primary principal component and discriminant analyses, and are discussed in the text to illuminate the interpretation of these multivariate procedures.

TABLE A1.—*Ranked means and statistics for the alpha angle.*

Taxon	*N*	Mean	Max-min	± 1 SE	CV
Rhinopomatidae	1	40.25			
Rhinolophidae	7	39.10	(42.55-37.09)	0.663	4.488
Nycteridae	1	37.75			
Furipteridae	1	37.74			
Megadermatidae	5	37.52	(38.63-37.10)	0.281	1.672
Natalidae	1	36.74			
Pteropodidae	30	36.45	(39.23-33.61)	0.206	3.094
Craseonycteridae	1	35.83			
Thyropteridae	1	35.73			
Myzapodidae	1	35.37			
Phyllostomatidae	49	35.32	(39.29-31.73)	0.239	4.740
Phyllonycterinae	3	37.71	(38.08-37.24)	0.249	1.145
Phyllonycteris	2	38.08	(38.49-37.68)	0.403	1.498
Erophylla	2	37.80	(38.16-37.45)	0.352	1.316
Brachyphylla	2	37.24	(37.37-37.11)	0.131	0.497
Phyllostomatinae	11	36.70	(39.29-34.69)	0.470	4.247
Tonatia	7	39.29	(40.74-36.98)	0.517	3.481
Vampyrum	1	38.49			
Chrotopterus	1	38.44			
Micronycteris	12	37.31	(39.21-35.40)	0.395	3.670
Macrotus	2	36.83	(37.74-35.93)	0.904	3.469
Trachops	1	36.72			
Macrophyllum	2	36.37	(36.68-36.07)	0.308	1.199
Phylloderma	1	35.32			
Mimon	5	35.15	(37.91-33.04)	1.066	6.782
Lonchorhina	3	35.12	(36.29-34.37)	0.592	2.918
Phyllostomus	5	34.69	(35.85-33.31)	0.435	2.802
Desmodontinae	3	36.27	(39.05-33.86)	1.509	7.204
Desmodus	2	39.05	(39.37-38.72)	0.329	1.190
Diphylla	1	35.91			
Diaemus	1	33.86			
Carolliinae	2	35.41	(35.91-34.90)	0.505	2.018
Carollia	4	35.91	(36.31-35.66)	0.143	0.796
Rhinophylla	3	34.90	(35.95-33.95)	0.578	2.870
Stenoderminae	17	35.04	(36.58-34.07)	0.165	1.943
Ametrida	2	36.58	(37.16-36.01)	0.578	2.234
Phyllops	2	35.94	(36.18-35.70)	0.241	0.950
Ariteus	1	35.75			
Centurio	1	35.42			
Ardops	1	35.41			
Pygoderma	1	35.37			
Artibeus	13	35.12	(35.71-33.99)	0.141	1.444
Sphaeronycteris	1	35.08			
Vampyrodes	1	35.03			
Ectophylla	2	35.02	(35.66-34.38)	0.641	2.589
Enchisthenes	1	34.89			
Sturnira	10	34.77	(35.22-33.97)	0.129	1.177
Stenoderma	1	34.42			
Uroderma	2	34.29	(34.53-34.06)	0.231	0.954
Vampyressa	5	34.29	(35.39-33.81)	0.279	1.822
Vampyrops	10	34.16	(34.70-33.46)	0.145	1.346
Chiroderma	5	34.07	(34.66-33.49)	0.234	1.538
Glossophaginae	13	33.73	(35.41-31.73)	0.290	3.101
Glossophaga	4	35.41	(35.63-35.20)	0.089	0.504
Platalina	1	35.34			
Leptonycteris	3	34.93	(35.43-34.22)	0.365	1.811
Lonchophylla	5	34.47	(35.18-33.74)	0.246	1.598
Choeronycteris	1	33.62			
Lionycteris	1	33.48			
Choeroniscus	5	33.46	(34.25-32.43)	0.331	2.209
Lichonycteris	3	33.45	(33.85-33.00)	0.246	1.273
Hylonycteris	1	33.39			
Musonycteris	1	33.22			
Scleronycteris	1	33.00			
Monophyllus	2	32.97	(33.38-32.57)	0.407	1.747
Anoura	5	31.73	(32.57-30.79)	0.320	2.255
Mormoopidae	2	35.17	(37.13-33.21)	1.963	7.894
All bats	153	35.08	(42.55-24.09)	0.237	8.373
Vespertilionidae	31	35.02	(38.84-31.41)	0.391	6.220
Mystacinidae	1	34.78			
Emballonuridae	12	32.95	(35.66-29.07)	0.507	5.330
Noctilionidae	1	30.38			
Molossidae	9	26.93	(29.82-24.09)	0.516	5.754

TABLE A2.—*Ranked means and statistics for the tip index.*

Taxon	*N*	Mean	Max-min	± 1 SE	CV
Phyllostomatidae	49	2.04	(2.35-1.59)	0.025	8.546
Carolliinae	2	2.24	(2.30-2.18)	0.061	3.831
Rhinophylla	3	2.30	(2.50-2.20)	0.102	7.674
Carollia	4	2.18	(2.22-2.15)	0.016	1.457
Stenoderminae	17	2.15	(2.35-2.04)	0.020	3.902
Pygoderma	1	2.35			
Ametrida	2	2.27	(2.28-2.25)	0.018	1.114
Vampyrops	10	2.22	(2.34-2.07)	0.024	3.464
Sphaeronycteris	1	2.22			
Ariteus	1	2.21			
Vampyressa	5	2.20	(2.33-2.08)	0.046	4.699
Chiroderma	5	2.19	(2.24-2.10)	0.026	2.657
Sturnira	10	2.17	(2.29-2.10)	0.020	2.898
Stenoderma	1	2.15			
Vampyrodes	1	2.14			
Ardops	1	2.11			
Ectophylla	2	2.10	(2.14-2.07)	0.036	2.446
Uroderma	2	2.09	(2.09-2.08)	0.004	0.286
Phyllops	2	2.08	(2.11-2.05)	0.030	2.015
Centurio	1	2.05			
Enchisthenes	1	2.05			
Artibeus	13	2.04	(2.13-1.91)	0.020	3.550
Glossophaginae	13	2.06	(2.20-1.81)	0.033	5.776
Scleronycteris	1	2.20			
Anoura	5	2.20	(2.29-2.12)	0.035	3.574
Lichonycteris	3	2.19	(2.28-2.09)	0.055	4.329
Hylonycteris	1	2.19			
Choeroniscus	5	2.11	(2.21-2.03)	0.035	3.740
Lonchophylla	5	2.07	(2.19-1.92)	0.044	4.799
Choeronycteris	1	2.05			
Lionycteris	1	2.02			
Glossophaga	4	2.00	(2.03-1.95)	0.020	2.021
Monophyllus	2	1.99	(2.00-1.99)	0.004	0.252
Musonycteris	1	1.96			
Platalina	1	1.96			
Leptonycteris	3	1.81	(1.85-1.76)	0.024	2.328
Phyllostomatinae	11	1.92	(2.11-1.68)	0.033	5.696
Macrophyllum	2	2.11	(2.13-2.10)	0.017	1.158
Phylloderma	1	2.03			
Mimon	5	1.98	(2.10-1.84)	0.045	5.076
Trachops	1	1.96			
Lonchorhina	3	1.95	(2.02-1.89)	0.036	3.190
Vampyrum	1	1.94			
Chrotopterus	1	1.90			
Micronycteris	12	1.89	(2.16-1.68)	0.038	7.029
Tonatia	7	1.87	(1.95-1.80)	0.018	2.495
Phyllostomus	5	1.85	(1.97-1.75)	0.038	4.548
Macrotus	2	1.68	(1.70-1.66)	0.020	1.643
Desmodontinae	3	1.86	(2.03-1.59)	0.141	13.083
Diphylla	1	2.03			
Diaemus	1	1.98			
Desmodus	2	1.59	(1.60-1.57)	0.015	1.348
Phyllonycterinae	3	1.69	(1.74-1.66)	0.025	2.613
Brachyphylla	2	1.74	(1.74-1.74)	0.000	0.025
Erophylla	2	1.66	(1.69-1.64)	0.023	1.955
Phyllonycteris	2	1.66	(1.68-1.65)	0.016	1.321
Molossidae	9	1.98	(2.30-1.81)	0.044	6.669
Noctilionidae	1	1.95			
Craseonycteridae	1	1.86			
Natalidae	1	1.85			
All bats	153	1.85	(2.35-1.09)	0.018	12.280
Vespertilionidae	31	1.81	(2.17-1.60)	0.027	8.396
Thyropteridae	1	1.81			
Myzapodidae	1	1.79			
Pteropodidae	30	1.78	(2.06-1.57)	0.021	6.596
Nycteridae	1	1.78			
Megadermatidae	5	1.76	(1.83-1.74)	0.017	2.101
Mystacinidae	1	1.75			
Mormoopidae	2	1.70	(1.82-1.58)	0.123	10.221
Emballonuridae	12	1.62	(1.92-1.48)	0.032	6.950
Furipteridae	1	1.58			
Rhinolophidae	7	1.40	(1.52-1.29)	0.036	6.764
Rhinopomatidae	1	1.09			

TABLE A3.—*Ranked means and statistics for the overall aspect ratio.*

Taxon	*N*	Mean	Max-min	± 1 SE	CV
Molossidae	9	7.54	(8.05-6.46)	0.174	6.935
Emballonuridae	12	6.71	(7.93-6.05)	0.147	7.620
Noctilionidae	1	6.69			
Mormoopidae	2	6.04	(6.39-5.68)	0.356	8.346
All bats	153	5.86	(8.05-4.71)	0.051	10.866
Phyllostomatidae	49	5.74	(6.50-5.05)	0.046	5.615
Glossophaginae	13	6.09	(6.50-5.71)	0.061	3.623
Anoura	5	6.50	(6.74-6.23)	0.087	2.991
Musonycteris	1	6.30			
Scleronycteris	1	6.23			
Lionycteris	1	6.19			
Monophyllus	2	6.18	(6.29-6.07)	0.109	2.482
Choeroniscus	5	6.17	(6.40-6.01)	0.073	2.653
Lichonycteris	3	6.13	(6.30-5.98)	0.091	2.563
Hylonycteris	1	6.09			
Choeronycteris	1	6.09			
Lonchophylla	5	5.94	(6.10-5.81)	0.056	2.102
Leptonycteris	3	5.92	(6.09-5.82)	0.083	2.425
Platalina	1	5.72			
Glossophaga	4	5.71	(5.80-5.64)	0.033	1.149
Stenoderminae	17	5.71	(5.96-5.26)	0.050	3.632
Chiroderma	5	5.96	(6.14-5.78)	0.060	2.240
Uroderma	2	5.94	(5.97-5.91)	0.027	0.648
Vampyrops	10	5.93	(6.11-5.78)	0.030	1.606
Stenoderma	1	5.88			
Vampyressa	5	5.88	(5.96-5.69)	0.049	1.869
Centurio	1	5.88			
Ectophylla	2	5.76	(5.92-5.61)	0.151	3.713
Sturnira	10	5.76	(5.88-5.62)	0.026	1.404
Artibeus	13	5.75	(6.04-5.57)	0.036	2.231
Vampyrodes	1	5.71			
Ardops	1	5.66			
Pygoderma	1	5.63			
Enchisthenes	1	5.62			
Phyllops	2	5.58	(5.64-5.53)	0.054	1.365
Ariteus	1	5.49			
Sphaeronycteris	1	5.32			
Ametrida	2	5.26	(5.33-5.19)	0.070	1.874
Carolliinae	2	5.69	(5.74-5.64)	0.049	1.205
Rhinophylla	3	5.74	(5.95-5.52)	0.124	3.748
Carollia	4	5.64	(5.74-5.54)	0.041	1.442
Phyllostomatinae	11	5.55	(5.92-5.05)	0.094	5.620
Mimon	5	5.92	(6.36-5.41)	0.209	7.892
Phyllostomus	5	5.91	(6.18-5.54)	0.109	4.107
Lonchorhina	3	5.89	(6.04-5.60)	0.140	4.135
Phylloderma	1	5.78			
Macrotus	2	5.77	(6.06-5.49)	0.284	6.945
Macrophyllum	2	5.45	(5.48-5.43)	0.029	0.747
Trachops	1	5.42			
Micronycteris	12	5.41	(5.84-5.02)	0.076	4.867
Chrotopterus	1	5.25			
Vampyrum	1	5.23			
Tonatia	7	5.05	(5.57-4.74)	0.113	5.913
Desmodontinae	3	5.50	(5.81-5.17)	0.186	5.874
Diaemus	1	5.81			
Diphylla	1	5.51			
Desmodus	2	5.17	(5.23-5.11)	0.057	1.572
Phyllonycterinae	3	5.40	(5.44-5.35)	0.027	0.872
Brachyphylla	2	5.44	(5.46-5.42)	0.016	0.428
Erophylla	2	5.42	(5.52-5.32)	0.098	2.559
Phyllonycteris	2	5.35	(5.43-5.27)	0.082	2.169
Vespertilionidae	31	5.73	(6.90-4.92)	0.085	8.229
Mystacinidae	1	5.71			
Thyropteridae	1	5.70			
Myzapodidae	1	5.65			
Craseonycteridae	1	5.64			
Natalidae	1	5.60			
Rhinopomatidae	1	5.58			
Megadermatidae	5	5.55	(5.74-5.29)	0.073	2.938
Furipteridae	1	5.52			
Pteropodidae	30	5.49	(5.97-5.01)	0.035	3.533
Nycteridae	1	5.48			
Rhinolophidae	7	5.42	(5.99-4.71)	0.157	7.645

TABLE A4.—*Ranked means and statistics for the aspect ratio of the wing tip.*

Taxon	*N*	Mean	Max-min	± 1 SE	CV
Molossidae	9	5.79	(6.31-4.79)	0.163	8.465
Embalonuridae	12	5.22	(6.35-4.77)	0.133	8.790
Noctilionidae	1	5.21			
Mormoopidae	2	4.73	(5.12-4.34)	0.390	11.655
Phyllostomatidae	49	4.67	(5.41-3.86)	0.048	7.155
Glossophaginae	13	4.98	(5.41-4.60)	0.066	4.804
Anoura	5	5.41	(5.68-5.10)	0.105	4.328
Scleronycteris	1	5.21			
Musonycteris	1	5.13			
Lichanycteris	3	5.13	(5.32-5.03)	0.096	3.252
Choeroniscus	5	5.11	(5.29-4.91)	0.076	3.320
Lionycteris	1	5.06			
Hylonycteris	1	5.06			
Choeronycteris	1	4.97			
Monophyllus	2	4.95	(5.04-4.85)	0.097	2.779
Lonchophylla	5	4.89	(5.11-4.67)	0.088	4.006
Leptonycteris	3	4.67	(4.81-4.59)	0.072	2.673
Glossophaga	4	4.62	(4.67-4.58)	0.025	1.094
Platalina	1	4.60			
Carolliinae	2	4.78	(4.83-4.74)	0.043	1.279
Rhinophylla	3	4.83	(5.13-4.58)	0.163	5.865
Carollia	4	4.74	(4.85-4.62)	0.052	2.215
Stenoderminae	17	4.70	(4.96-4.22)	0.053	4.628
Vampyrops	10	4.96	(5.15-4.84)	0.034	2.146
Chiroderma	5	4.96	(5.16-4.71)	0.073	3.313
Centurio	1	4.93			
Uroderma	2	4.88	(4.89-4.87)	0.009	0.269
Vampyressa	5	4.88	(4.99-4.70)	0.057	2.615
Stenoderma	1	4.87			
Pygoderma	1	4.76			
Sturnira	10	4.74	(4.88-4.66)	0.020	1.301
Ectophylla	2	4.73	(4.84-4.63)	0.104	3.107
Vampyrodes	1	4.70			
Artibeus	13	4.67	(4.87-4.48)	0.037	2.883
Ardops	1	4.65			
Phyllops	2	4.57	(4.65-4.50)	0.071	2.194
Ariteus	1	4.52			
Enchisthenes	1	4.47			
Ametrida	2	4.33	(4.37-4.28)	0.045	1.484
Sphaeronycteris	1	4.22			
Phyllostomatinae	11	4.48	(4.86-4.04)	0.079	5.878
Mimon	5	4.86	(5.26-4.38)	0.193	8.892
Lonchorhina	3	4.79	(4.90-4.60)	0.094	3.413
Phylloderma	1	4.74			
Phyllostomus	5	4.66	(4.83-4.32)	0.098	4.710
Macrotus	2	4.59	(4.87-4.32)	0.275	8.475
Macrophyllum	2	4.47	(4.49-4.45)	0.017	0.535
Trachops	1	4.33			
Micronycteris	12	4.32	(4.73-3.90)	0.076	6.058
Vampyrum	1	4.27			
Chrotopterus	1	4.25			
Tonatia	7	4.04	(4.60-3.69)	0.120	7.839
Desmodontinae	3	4.28	(4.54-3.86)	0.209	8.457
Diaemus	1	4.54			
Diphylla	1	4.42			
Desmodus	2	3.86	(3.88-3.84)	0.019	0.692
Phyllonycterinae	3	4.16	(4.21-4.10)	0.032	1.320
Brachyphylla	2	4.21	(4.22-4.20)	0.008	0.254
Erophylla	2	4.17	(4.24-4.10)	0.069	2.356
Phyllonycteris	2	4.10	(4.19-4.01)	0.087	2.999
All bats	153	4.58	(6.35-3.44)	0.044	12.004
Natalidae	1	4.51			
Thyropteridae	1	4.46			
Craseonycteridae	1	4.45			
Megadermatidae	5	4.45	(4.72-4.19)	0.089	4.463
Nycteridae	1	4.39			
Vespertilionidae	31	4.38	(5.99-3.72)	0.083	10.512
Myzapodidae	1	4.33			
Mystacinidae	1	4.27			
Pteropodidae	30	4.22	(4.48-3.65)	0.029	3.782
Furipteridae	1	4.19			
Rhinolophidae	7	3.93	(4.27-3.44)	0.099	6.667
Rhinopomatidae	1	3.69			

TABLE A5.—*Ranked means and statistics for the aspect ratio of the plagiopatagium.*

Taxon	*N*	Mean	Max-min	± 1 SE	CV
Rhinopomatidae	1	2.17			
Molossidae	9	2.00	(2.21-1.82)	0.038	5.762
Emballonuridae	12	1.93	(2.20-1.66)	0.054	9.630
Rhinolophidae	7	1.78	(2.06-1.51)	0.077	11.440
Noctilionidae	1	1.75			
Mormoopidae	2	1.68	(1.68-1.68)	0.002	0.158
Mystacinidae	1	1.65			
Furipteridae	1	1.64			
Vespertilionidae	31	1.59	(1.99-1.32)	0.028	9.742
All bats	153	1.58	(2.21-1.20)	0.018	14.364
Myzapodidae	1	1.57			
Thyropteridae	1	1.54			
Pteropodidae	30	1.52	(1.74-1.34)	0.018	6.619
Craseonycteridae	1	1.49			
Megadermatidae	5	1.48	(1.52-1.43)	0.018	2.688
Nycteridae	1	1.46			
Natalidae	1	1.45			
Phyllostomatidae	49	1.40	(1.59-1.19)	0.015	7.265
Phyllonycterinae	3	1.53	(1.55-1.51)	0.011	1.215
Erophylla	2	1.55	(1.59-1.51)	0.040	3.670
Phyllonycteris	2	1.54	(1.54-1.53)	0.007	0.673
Brachyphylla	2	1.51	(1.52-1.51)	0.006	0.583
Desmodontinae	3	1.47	(1.56-1.36)	0.060	7.004
Desmodus	2	1.56	(1.59-1.52)	0.034	3.082
Diaemus	1	1.51			
Diphylla	1	1.36			
Glossophaginae	13	1.46	(1.58-1.38)	0.019	4.670
Leptonycteris	3	1.58	(1.62-1.54)	0.023	2.530
Musonycteris	1	1.55			
Monophyllus	2	1.55	(1.57-1.53)	0.022	2.013
Lionycteris	1	1.50			
Anoura	5	1.47	(1.51-1.44)	0.010	1.538
Choeronycteris	1	1.46			
Platalina	1	1.44			
Choeroniscus	5	1.44	(1.50-1.37)	0.021	3.253
Lonchophylla	5	1.41	(1.52-1.36)	0.028	4.507
Glossophaga	4	1.41	(1.46-1.37)	0.019	2.700
Scleronycteris	1	1.40			
Hylonycteris	1	1.38			
Lichonycteris	3	1.38	(1.45-1.31)	0.040	4.986
Phyllostomatinae	11	1.40	(1.59-1.29)	0.031	7.392
Macrotus	2	1.59	(1.66-1.52)	0.071	6.292
Phyllostomus	5	1.57	(1.67-1.44)	0.048	6.789
Lonchorhina	3	1.46	(1.53-1.35)	0.055	6.526
Mimon	5	1.44	(1.51-1.35)	0.032	5.007
Micronycteris	12	1.39	(1.51-1.24)	0.025	6.144
Phylloderma	1	1.39			
Trachops	1	1.37			
Chrotopterus	1	1.33			
Tonatia	7	1.31	(1.36-1.26)	0.015	2.985
Vampyrum	1	1.30			
Macrophyllum	2	1.29	(1.29-1.28)	0.003	0.380
Stenoderminae	17	1.33	(1.41-1.19)	0.015	4.689
Uroderma	2	1.41	(1.42-1.40)	0.009	0.949
Enchisthenes	1	1.40			
Artibeus	13	1.40	(1.50-1.32)	0.016	4.023
Centurio	1	1.37			
Ectophylla	2	1.36	(1.41-1.30)	0.056	5.803
Stenoderma	1	1.36			
Chiroderma	5	1.35	(1.38-1.33)	0.009	1.414
Vampyressa	5	1.34	(1.42-1.27)	0.026	4.300
Vampyrodes	1	1.33			
Sturnira	10	1.33	(1.38-1.25)	0.013	2.999
Ardops	1	1.33			
Phyllops	2	1.33	(1.34-1.32)	0.007	0.762
Vampyrops	10	1.33	(1.40-1.26)	0.012	2.823
Sphaeronycteris	1	1.28			
Ariteus	1	1.26			
Pygoderma	1	1.20			
Ametrida	2	1.19	(1.21-1.17)	0.015	1.818
Carolliinae	2	1.26	(1.27-1.25)	0.009	1.006
Carollia	4	1.27	(1.28-1.25)	0.006	0.870
Rhinophylla	3	1.25	(1.31-1.19)	0.036	4.936

TABLE A6.—*Ranked means and statistics for wing loading in newtons per square meter.*

Taxon	*N*	Mean	Max-min	±1 SE	CV
Molossidae	9	21.41	(28.47-15.56)	1.239	17.358
Pteropodidae	30	19.18	(36.24-11.48)	1.084	30.959
Noctilionidae	1	17.65			
Craseonycteridae	1	16.70			
All bats	153	14.62	(36.08- 3.69)	0.507	42.905
Phyllostomatidae	49	14.50	(28.89- 3.92)	0.686	33.119
Desmodontinae	3	20.87	(29.23-14.99)	4.293	35.639
Diaemus	1	32.71			
Diphylla	1	20.34			
Desmodus	2	15.72	(17.26-14.17)	1.548	13.931
Phyllonycterinae	3	18.40	(21.04-13.75)	2.331	21.940
Phyllonycteris	2	21.04	(24.56-17.52)	3.522	23.675
Brachyphylla	2	20.41	(22.74-18.08)	2.329	16.134
Erophylla	2	13.75	(15.46-12.05)	1.708	17.557
Stenoderminae	17	15.01	(22.66-10.96)	0.776	21.319
Enchisthenes	1	22.66			
Sturnira	10	17.85	(28.58-10.68)	2.071	36.690
Ariteus	1	17.42			
Vampyrodes	1	17.10			
Chiroderma	5	17.09	(21.86-13.15)	1.424	18.632
Sphaeronycteris	1	16.96			
Centurio	1	16.76			
Vampyrops	10	16.09	(21.13-10.38)	0.895	17.576
Artibeus	13	15.94	(23.23-10.56)	1.084	24.515
Uroderma	2	14.04	(16.59-11.49)	2.549	25.675
Stenoderma	1	13.39			
Ametrida	2	12.77	(13.85-11.69)	1.079	11.954
Ardops	1	11.98			
Vampyressa	5	11.50	(13.01- 8.90)	0.840	16.327
Ectophylla	2	11.47	(12.73-10.22)	1.256	15.485
Phyllops	2	11.16	(13.29- 9.03)	2.128	26.968
Pygoderma	1	10.96			
Phyllostomatinae	11	14.04	(19.94- 7.88)	1.205	28.473
Phyllostomus	5	19.94	(24.11-16.47)	1.242	13.927
Chrotopterus	1	18.81			
Trachops	1	17.36			
Phylloderma	1	16.30			
Vampyrum	1	15.48			
Tonatia	7	14.64	(19.35-10.86)	1.206	21.797
Macrotus	2	12.96	(14.68-11.25)	1.715	18.708
Mimon	5	11.23	(13.94- 6.81)	1.295	25.786
Lonchorhina	3	11.05	(13.22- 9.56)	1.110	17.392
Micronycteris	12	8.77	(15.43- 5.47)	0.809	31.949
Macrophyllum	2	7.88	(10.24- 5.52)	2.361	42.356
Glossophaginae	13	12.51	(15.58-10.01)	0.421	12.128
Musonycteris	1	15.58			
Leptonycteris	3	14.17	(15.97-11.77)	1.249	15.270
Choeronycteris	1	13.75			
Hylonycteris	1	13.50			
Lonchophylla	5	13.21	(17.03-11.46)	1.005	17.015
Glossophaga	4	12.54	(14.81-11.32)	0.774	12.343
Anoura	5	12.31	(17.35- 9.36)	1.415	25.706
Choeroniscus	5	12.16	(14.01-11.25)	0.510	9.390
Menophyllus	2	11.93	(12.45-11.41)	0.519	6.151
Lichonycteris	3	11.63	(12.03-11.27)	0.220	3.276
Lionycteris	1	10.94			
Platalina	1	10.94			
Scleronycteris	1	10.01			
Carolliinae	2	10.98	(11.14-10.81)	0.168	2.168
Rhinophylla	3	11.14	(12.46- 9.70)	0.800	12.428
Carollia	4	10.81	(12.87- 9.10)	0.857	15.863
Rhinopomatidae	1	11.82			
Megadermatidae	5	11.33	(15.16- 8.32)	1.428	25.220
Mystacinidae	1	11.15			
Mormoopidae	2	10.57	(12.40- 8.75)	1.825	24.406
Vespertilionidae	31	10.54	(19.71- 6.92)	0.544	28.713
Nycteridae	1	9.82			
Emballonuridae	12	9.67	(21.16- 4.73)	1.364	48.847
Rhinolophidae	7	8.05	(14.48- 1.84)	1.769	58.147
Myzapodidae	1	7.41			
Thyropteridae	1	5.91			
Natalidae	1	5.43			
Furipteridae	1	4.20			

TABLE A7.—*Ranked means and statistics for the relative length of the wing.*

Taxon	*N*	Mean	Max-min	± 1 SE	CV
Furipteridae	1	2.62			
Natalidae	1	2.61			
Noctilionidae	1	2.53			
Emballonuridae	12	2.44	(3.34-2.06)	0.110	15.553
Myzapodidae	1	2.43			
Thyropteridae	1	2.42			
Craseonycteridae	1	2.35			
Nycteridae	1	2.31			
Mormoopidae	2	2.21	(2.33-2.09)	0.118	7.531
Rhinolophidae	7	2.20	(2.51-2.03)	0.064	7.644
Megadermatidae	5	2.18	(2.43-1.95)	0.084	8.643
Vespertilionidae	31	2.07	(2.49-1.44)	0.048	12.907
Phyllostomatidae	49	2.07	(2.40-1.69)	0.024	8.174
Carolliinae	2	2.22	(2.24-2.20)	0.018	1.162
Carollia	4	2.24	(2.46-2.04)	0.090	8.029
Rhinophylla	3	2.20	(2.39-2.03)	0.105	8.251
Phyllostomatinae	11	2.18	(2.40-2.00)	0.034	5.103
Mimon	5	2.40	(2.75-2.22)	0.096	8.969
Lonchorhina	3	2.31	(2.49-2.18)	0.094	7.087
Macrophyllum	2	2.25	(2.36-2.14)	0.106	6.656
Micronycteris	12	2.22	(2.56-1.82)	0.058	9.078
Phylloderma	1	2.19			
Macrotus	2	2.18	(2.29-2.07)	0.111	7.204
Trachops	1	2.13			
Vampyrum	1	2.12			
Chrotopterus	1	2.11			
Phyllostomus	5	2.08	(2.18-1.99)	0.036	3.845
Tonatia	7	2.00	(2.22-1.60)	0.081	10.764
Stenoderminae	17	2.14	(2.36-1.89)	0.035	6.840
Ardops	1	2.36			
Stenoderma	1	2.34			
Phyllops	2	2.27	(2.49-2.06)	0.212	13.188
Centurio	1	2.24			
Vampyrodes	1	2.22			
Pygoderma	1	2.21			
Vampyrops	10	2.20	(2.46-1.99)	0.042	5.999
Artibeus	13	2.19	(2.44-2.00)	0.039	6.343
Ectophylla	2	2.19	(2.34-2.03)	0.150	9.731
Chiroderma	5	2.16	(2.23-2.10)	0.024	2.528
Vampyressa	5	2.15	(2.41-2.03)	0.074	7.713
Sturnira	10	2.05	(2.22-1.83)	0.043	6.606
Uroderma	2	2.03	(2.06-2.00)	0.029	2.034
Ariteus	1	1.96			
Ametrida	2	1.96	(2.04-1.87)	0.083	5.968
Enchisthenes	1	1.90			
Sphaeronycteris	1	1.89			
Glossophaginae	13	1.93	(2.16-1.75)	0.033	6.112
Scleronycteris	1	2.16			
Lionycteris	1	2.10			
Choeronycteris	1	2.01			
Anoura	5	1.98	(2.26-1.75)	0.102	11.532
Lichonycteris	3	1.98	(2.03-1.93)	0.029	2.571
Monophyllus	2	1.96	(2.04-1.87)	0.085	6.174
Choeroniscus	5	1.92	(2.00-1.83)	0.029	3.312
Platalina	1	1.91			
Glossophaga	4	1.87	(1.91-1.84)	0.016	1.683
Leptonycteris	3	1.84	(1.97-1.75)	0.068	6.354
Lonchophylla	5	1.84	(1.90-1.79)	0.021	2.516
Hylonycteris	1	1.79			
Musonycteris	1	1.75			
Desmodontinae	3	1.93	(2.05-1.69)	0.118	10.617
Desmodus	2	2.05	(2.06-2.05)	0.005	0.314
Diphylla	1	2.05			
Diaemus	1	1.69			
Phyllonycterinae	3	1.92	(2.05-1.78)	0.077	6.951
Erophylla	2	2.05	(2.14-1.96)	0.093	6.384
Brachyphylla	2	1.94	(2.00-1.87)	0.068	4.933
Phyllonycteris	2	1.78	(1.89-1.68)	0.106	8.400
All bats	153	2.06	(3.34-1.44)	0.023	13.586
Mystacinidae	1	1.97			
Rhinopomatidae	1	1.97			
Molossidae	9	1.86	(2.10-1.63)	0.053	8.476
Pteropodidae	30	1.80	(2.13-1.59)	0.027	8.108

TABLE A8.—*Ranked means and statistics for the relative length of the forearm.*

Taxon	*N*	Mean	Max-min	± 1 SE	CV
Furipteridae	1	1.02			
Rhinopomatidae	1	0.94			
Emballonuridae	12	0.93	(1.14-0.76)	0.034	12.771
Rhinolophidae	7	0.92	(1.01-0.86)	0.022	6.479
Natalidae	1	0.92			
Myzapodidae	1	0.87			
Thyropteridae	1	0.86			
Noctilionidae	1	0.86			
Nycteridae	1	0.83			
Craseonyctridae	1	0.82			
Mormoopidae	2	0.82	(0.82-0.81)	0.007	1.130
Megadermatidae	5	0.79	(0.88-0.71)	0.028	7.967
Vespertilionidae	31	0.74	(0.92-0.56)	0.014	10.850
All bats	153	0.73	(1.14-0.52)	0.010	16.238
Mystacinidae	1	0.72			
Phyllostomatidae	49	0.68	(0.81-0.56)	0.009	9.145
Phyllostomatinae	11	0.75	(0.81-0.69)	0.012	5.232
Macrotus	2	0.81	(0.85-0.78)	0.035	6.162
Mimon	5	0.80	(0.91-0.71)	0.034	9.502
Lonchorhina	3	0.78	(0.85-0.74)	0.032	7.171
Micronycteris	12	0.77	(0.90-0.64)	0.021	9.585
Phyllostomus	5	0.73	(0.77-0.70)	0.013	3.857
Chrotopterus	1	0.73			
Macrophyllum	2	0.72	(0.75-0.69)	0.030	5.940
Phylloderma	1	0.72			
Vampyrum	1	0.72			
Trachops	1	0.72			
Tonatia	7	0.69	(0.77-0.57)	0.026	9.746
Phyllonycterinae	3	0.72	(0.77-0.67)	0.029	6.996
Erophylla	2	0.77	(0.81-0.73)	0.042	7.640
Brachyphylla	2	0.71	(0.73-0.68)	0.025	4.913
Phyllonycteris	2	0.67	(0.71-0.63)	0.044	9.255
Carolliinae	2	0.69	(0.70-0.67)	0.018	3.807
Carollia	4	0.70	(0.77-0.65)	0.026	7.338
Rhinophylla	3	0.67	(0.69-0.63)	0.018	4.555
Desmodontinae	3	0.68	(0.79-0.57)	0.065	16.603
Desmodus	2	0.79	(0.80-0.79)	0.003	0.523
Diphylla	1	0.67			
Diaemus	1	0.57			
Stenoderminae	17	0.68	(0.76-0.59)	0.013	7.756
Ardops	1	0.76			
Stenoderma	1	0.74			
Phyllops	2	0.74	(0.80-0.68)	0.062	11.844
Centurio	1	0.73			
Artibeus	13	0.72	(0.80-0.66)	0.011	5.679
Vampyrodes	1	0.71			
Ectophylla	2	0.70	(0.76-0.65)	0.057	11.414
Vampyrops	10	0.68	(0.76-0.61)	0.013	5.890
Chiroderma	5	0.68	(0.69-0.66)	0.006	2.041
Vampyressa	5	0.67	(0.74-0.64)	0.017	5.645
Pygoderma	1	0.66			
Uroderma	2	0.66	(0.67-0.65)	0.010	2.229
Sturnira	10	0.65	(0.70-0.56)	0.014	6.773
Enchisthenes	1	0.62			
Ariteus	1	0.61			
Ametrida	2	0.60	(0.63-0.57)	0.028	6.712
Sphaeronycteris	1	0.59			
Glossophaginae	13	0.63	(0.70-0.56)	0.010	5.819
Lionycteris	1	0.70			
Scleronycteris	1	0.68			
Choeronycteris	1	0.66			
Leptonycteris	3	0.66	(0.71-0.62)	0.030	7.848
Monophyllus	2	0.65	(0.68-0.63)	0.028	6.059
Platalina	1	0.65			
Glossophaga	4	0.62	(0.65-0.61)	0.008	2.675
Lichonycteris	3	0.62	(0.64-0.59)	0.016	4.520
Choeroniscus	5	0.62	(0.65-0.59)	0.010	3.751
Anoura	5	0.62	(0.69-0.55)	0.027	9.645
Lonchophylla	5	0.60	(0.63-0.56)	0.013	4.816
Musonycteris	1	0.59			
Hylonycteris	1	0.56			
Pteropodidae	30	0.65	(0.80-0.52)	0.012	9.730
Molossidae	9	0.63	(0.72-0.56)	0.018	8.610

TABLE A9.—*Ranked means and statistics for the relative length of digit III.*

Taxon	*N*	Mean	Max-min	± 1 SE	CV
Natalidae	1	1.69			
Noctilionidae	1	1.67			
Furipteridae	1	1.61			
Myzapodidae	1	1.56			
Thyropteridae	1	1.56			
Craseonycteridae	1	1.53			
Emballonuridae	12	1.51	(2.19-1.28)	0.077	17.721
Nycteridae	1	1.48			
Mormoopidae	2	1.39	(1.50-1.28)	0.111	11.291
Megadermatidae	5	1.39	(1.55-1.24)	0.057	9.091
Phyllostomatidae	49	1.39	(1.60-1.11)	0.018	9.206
Carolliinae	2	1.54	(1.54-1.54)	0.000	0.018
Rhinophylla	3	1.54	(1.71-1.39)	0.092	10.325
Carollia	4	1.54	(1.69-1.40)	0.064	8.370
Stenoderminae	17	1.46	(1.60-1.28)	0.024	6.728
Ardops	1	1.60			
Stenoderma	1	1.59			
Pygoderma	1	1.55			
Phyllops	2	1.54	(1.69-1.39)	0.150	13.834
Vampyrops	10	1.51	(1.70-1.36)	0.030	6.345
Vampyrodes	1	1.51			
Centurio	1	1.51			
Chiroderma	5	1.48	(1.54-1.42)	0.021	3.098
Ectophylla	2	1.48	(1.57-1.39)	0.094	8.931
Vampyressa	5	1.48	(1.68-1.38)	0.059	8.884
Artibeus	13	1.47	(1.66-1.31)	0.028	6.936
Sturnira	10	1.40	(1.54-1.27)	0.030	6.720
Uroderma	2	1.37	(1.39-1.35)	0.019	1.941
Ametrida	2	1.36	(1.41-1.30)	0.054	5.639
Ariteus	1	1.35			
Sphaeronycteris	1	1.30			
Enchisthenes	1	1.28			
Phyllostomatinae	11	1.43	(1.59-1.30)	0.026	6.095
Mimon	5	1.59	(1.84-1.48)	0.065	9.137
Macrophyllum	2	1.53	(1.60-1.45)	0.076	6.995
Lonchorhina	3	1.52	(1.65-1.43)	0.064	7.265
Phylloderma	1	1.47			
Micronycteris	12	1.45	(1.66-1.18)	0.040	9.658
Trachops	1	1.41			
Vampyrum	1	1.40			
Chrotopterus	1	1.38			
Macrotus	2	1.37	(1.44-1.29)	0.076	7.823
Phyllostomus	5	1.35	(1.41-1.27)	0.028	4.658
Tonatia	7	1.30	(1.46-1.03)	0.056	11.356
Glossophaginae	13	1.30	(1.49-1.16)	0.026	7.090
Scleronycteris	1	1.49			
Lionycteris	1	1.41			
Anoura	5	1.36	(1.57-1.20)	0.076	12.464
Lichonycteris	3	1.36	(1.40-1.34)	0.020	2.487
Choeronycteris	1	1.35			
Choeroniscus	5	1.30	(1.38-1.24)	0.022	3.759
Monophyllus	2	1.30	(1.36-1.25)	0.057	6.231
Platalina	1	1.27			
Glossophaga	4	1.25	(1.27-1.23)	0.009	1.423
Lonchophylla	5	1.24	(1.28-1.21)	0.013	2.432
Hylonycteris	1	1.23			
Leptonycteris	3	1.19	(1.26-1.14)	0.038	5.529
Musonycteris	1	1.16			
Desmodontinae	3	1.25	(1.37-1.13)	0.071	9.809
Diphylla	1	1.37			
Desmodus	2	1.26	(1.27-1.25)	0.007	0.841
Diaemus	1	1.13			
Phyllonycterinae	3	1.21	(1.28-1.11)	0.050	7.107
Erophylla	2	1.28	(1.33-1.23	0.051	5.629
Brachyphylla	2	1.23	(1.27-1.19)	0.043	4.945
Phyllonycteris	2	1.11	(1.17-1.05)	0.062	7.885
Vespertilionidae	31	1.34	(1.69-0.89)	0.035	14.739
All bats	153	1.33	(2.19-0.89)	0.015	14.209
Rhinolophidae	7	1.28	(1.52-1.15)	0.046	9.478
Mystacinidae	1	1.26			
Molossidae	9	1.24	(1.41-1.07)	0.038	9.294
Pteropodidae	30	1.15	(1.33-0.99)	0.017	8.043
Rhinopomatidae	1	1.03			

TABLE A10.—*Ranked means and statistics for the relative length of digit IV.*

Taxon	*N*	Mean	Max-min	± 1 SE	CV
Noctilionidae	1	1.27			
Natalidae	1	1.25			
Furipteridae	1	1.25			
Myzapodidae	1	1.25			
Thyropteridae	1	1.20			
Craseonycteridae	1	1.18			
Nycteridae	1	1.10			
Emballonuridae	12	1.07	(1.43-0.85)	0.049	15.900
Vespertilionidae	31	1.07	(1.27-0.74)	0.022	11.381
Rhinolophidae	7	1.04	(1.20-0.89)	0.038	9.718
Mystacinidae	1	1.03			
Mormoopidae	2	1.03	(1.07-0.99)	0.044	5.998
Phyllostomatidae	49	1.03	(1.19-0.82)	0.012	8.208
Carolliinae	2	1.11	(1.11-1.10)	0.004	0.516
Rhinophylla	3	1.11	(1.19-1.04)	0.045	6.930
Carollia	4	1.10	(1.19-1.01)	0.038	6.933
Stenoderminae	17	1.08	(1.19-1.00)	0.013	4.954
Ardops	1	1.19			
Stenoderma	1	1.16			
Phyllops	2	1.14	(1.24-1.04)	0.101	12.438
Pygoderma	1	1.13			
Vampyrodes	1	1.12			
Artibeus	13	1.10	(1.22-1.00)	0.016	5.277
Ectophylla	2	1.09	(1.15-1.03)	0.062	8.082
Vampyrops	10	1.09	(1.19-0.98)	0.019	5.659
Vampyressa	5	1.08	(1.21-1.02)	0.037	7.644
Sphaeronycteris	1	1.07			
Chiroderma	5	1.07	(1.09-1.05)	0.008	1.605
Centurio	1	1.06			
Ametrida	2	1.05	(1.09-1.01)	0.039	5.234
Sturnira	10	1.04	(1.16-0.93)	0.023	6.938
Ariteus	1	1.02			
Uroderma	2	1.00	(1.01-0.99)	0.010	1.403
Enchisthenes	1	1.00			
Phyllostomatinae	11	1.07	(1.15-1.00)	0.015	4.726
Macrophyllum	2	1.15	(1.21-1.09)	0.061	7.502
Mimon	5	1.14	(1.30-1.05)	0.046	9.065
Lonchorhina	3	1.11	(1.20-1.02)	0.050	7.846
Micronycteris	12	1.11	(1.23-0.92)	0.026	8.110
Trachops	1	1.09			
Phylloderma	1	1.07			
Vampyrum	1	1.05			
Chrotopterus	1	1.05			
Tonatia	7	1.02	(1.16-0.86)	0.035	9.170
Phyllostomus	5	1.02	(1.10-0.97)	0.028	6.068
Macrotus	2	1.00	(1.09-0.90)	0.094	13.335
Desmodontinae	3	0.99	(1.06-0.89)	0.052	9.075
Diphylla	1	1.06			
Desmodus	2	1.04	(1.04-1.03)	0.004	0.520
Diaemus	1	0.89			
Phyllonycterinae	3	0.95	(1.00-0.88)	0.036	6.533
Erophylla	2	1.00	(1.03-0.97)	0.031	4.418
Brachyphylla	2	0.97	(1.00-0.93)	0.035	5.093
Phyllonycteris	2	0.88	(0.94-0.82)	0.060	9.631
Glossophaginae	13	0.94	(1.05-0.82)	0.016	6.247
Scleronycteris	1	1.05			
Lionycteris	1	1.01			
Choeronycteris	1	0.98			
Monophyllus	2	0.97	(1.00-0.93)	0.034	5.003
Lichonycteris	3	0.96	(0.97-0.96)	0.003	0.515
Anoura	5	0.96	(1.08-0.83)	0.047	10.987
Platalina	1	0.95			
Glossophaga	4	0.93	(0.94-0.92)	0.007	1.420
Choeroniscus	5	0.93	(0.98-0.88)	0.017	4.156
Lonchophylla	5	0.90	(0.93-0.86)	0.014	3.618
Leptonycteris	3	0.89	(0.94-0.86)	0.028	5.496
Hylonycteris	1	0.88			
Musonycteris	1	0.82			
Megadermatidae	5	1.03	(1.09-0.95)	0.029	6.294
All bats	153	1.02	(1.43-0.74)	0.010	11.544
Molossidae	9	0.95	(1.10-0.85)	0.026	8.256
Pteropodidae	30	0.92	(1.04'0.80)	0.013	7.458
Rhinopomatidae	1	0.86			

TABLE A11.—*Ranked means and statistics for the relative length of digit V.*

Taxon	N	Mean	Max-min	± 1 SE	CV
Natalidae	1	1.26			
Furipteridae	1	1.24			
Nycteridae	1	1.14			
Thyropteridae	1	1.12			
Myzapodidae	1	1.11			
Craseonycteridae	1	1.10			
Megadermatidae	5	1.07	(1.18-0.99)	0.038	7.920
Rhinolophidae	7	1.04	(1.21-0.86)	0.046	11.774
Phyllostomatidae	49	0.98	(1.14-0.76)	0.015	10.554
Carolliinae	2	1.09	(1.11-1.07)	0.021	2.713
Carollia	4	1.11	(1.21-1.01)	0.043	7.690
Rhinophylla	3	1.07	(1.15-1.01)	0.041	6.683
Phyllostomatinae	11	1.07	(1.12-0.93)	0.017	5.211
Macrophyllum	2	1.12	(1.17-1.08)	0.044	5.498
Mimon	5	1.12	(1.24-1.00)	0.052	10.289
Vampyrum	1	1.11			
Micronycteris	12	1.10	(1.19-0.96)	0.021	6.469
Chrotopterus	1	1.10			
Lonchorhina	3	1.07	(1.13-0.99)	0.042	6.774
Tonatia	7	1.06	(1.21-0.89)	0.040	10.035
Trachops	1	1.05			
Phylloderma	1	1.04			
Macrotus	2	1.03	(1.12-0.94)	0.090	12.441
Phyllostomus	5	0.93	(1.01-0.88)	0.025	5.971
Stenoderminae	17	1.02	(1.14-0.89)	0.017	6.888
Ardops	1	1.14			
Phyllops	2	1.11	(1.21-1.01)	0.099	12.597
Pygoderma	1	1.10			
Stenoderma	1	1.09			
Centurio	1	1.07			
Vampyrodes	1	1.06			
Ectophylla	2	1.04	(1.08-0.99)	0.042	5.669
Artibeus	13	1.04	(1.17-0.93)	0.019	6.750
Vampyrops	10	1.03	(1.13-0.94)	0.016	4.962
Ametrida	2	1.01	(1.07-0.95)	0.061	8.608
Vampyressa	5	1.01	(1.12-0.93)	0.035	7.779
Chiroderma	5	1.00	(1.02-0.98)	0.007	1.554
Sturnira	10	0.98	(1.08-0.85)	0.024	7.917
Ariteus	1	0.97			
Uroderma	2	0.94	(0.96-0.92)	0.021	3.186
Sphaeronycteris	1	0.91			
Enchisthenes	1	0.89			
Phyllonycterinae	3	0.93	(0.99-0.87)	0.034	6.389
Erophylla	2	0.99	(1.02-0.96)	0.027	3.915
Brachyphylla	2	0.93	(0.96-0.91)	0.028	4.249
Phyllonycteris	2	0.87	(0.93-0.81)	0.061	9.876
Desmodontinae	3	0.92	(1.02-0.76)	0.085	15.868
Desmodus	2	1.02	(1.04-1.00)	0.018	2.472
Diphylla	1	0.99			
Diaemus	1	0.76			
Glossophaginae	13	0.87	(0.97-0.76)	0.015	6.188
Scleronycteris	1	0.97			
Lionycteris	1	0.93			
Lichonycteris	3	0.90	(0.91-0.89)	0.006	1.213
Platalina	1	0.90			
Choeronycteris	1	0.90			
Glossophaga	4	0.89	(0.90-0.87)	0.007	1.554
Choeroniscus	5	0.86	(0.91-0.79)	0.021	5.493
Lonchophylla	5	0.85	(0.90-0.82)	0.016	4.147
Monophyllus	2	0.84	(0.87-0.82)	0.024	4.045
Anoura	5	0.84	(0.93-0.75)	0.037	9.846
Leptonycteris	3	0.83	(0.90-0.79)	0.034	7.116
Hylonycteris	1	0.81			
Musonycteris	1	0.76			
Noctilionidae	1	0.98			
Emballonuridae	12	0.98	(1.38-0.72)	0.052	18.283
Mormoopidae	2	0.98	(0.98-0.97)	0.009	1.250
All bats	153	0.94	(1.38-0.57)	0.012	16.083
Vespertilionidae	31	0.94	(1.22-0.57)	0.025	15.026
Mystacinidae	1	0.87			
Rhinopomatidae	1	0.87			
Pteropodidae	30	0.85	(1.01-0.72)	0.014	8.678
Molossidae	9	0.63	(0.72-0.57)	0.015	7.133

TABLE A12.—*Ranked means and statistics for the percentage contributed to length of digit III by the metacarpal.*

Taxon	*N*	Mean	Max-min	± 1 SE	CV
Rhinopomatidae	1	61.70			
Emballonuridae	12	57.67	(63.21-53.06)	0.920	5.524
Furipteridae	1	54.80			
Thyropteridae	1	53.85			
Mystacinidae	1	53.37			
Mormoopidae	2	52.87	(56.37-49.36)	3.505	9.375
Vespertilionidae	31	51.74	(63.40-41.82)	0.708	7.621
Rhinolophidae	7	51.57	(56.03-46.57)	1.246	6.391
Molossidae	9	50.70	(54.42-43.21)	1.015	6.004
Natalidae	1	49.92			
All bats	153	47.04	(63.40-35.39)	0.533	14.017
Phyllostomatidae	49	45.12	(54.67-36.15)	0.456	7.081
Desmodontinae	3	50.53	(54.67-48.44)	2.068	7.088
Desmodus	2	54.67	(55.89-53.44)	1.227	3.175
Diaemus	1	48.48			
Diphylla	1	48.44			
Phyllonycterinae	3	48.71	(49.70-47.69)	0.581	2.065
Phyllonycteris	2	49.70	(50.43-48.98)	0.727	2.069
Brachyphylla	2	48.73	(49.53-47.92)	0.805	2.336
Erophylla	2	47.69	(47.85-47.54)	0.156	0.462
Glossophaginae	13	46.99	(49.43-44.66)	0.413	3.167
Leptonycteris	3	49.43	(50.21-48.95)	0.393	1.377
Lionycteris	1	48.71			
Platalina	1	48.37			
Glossophaga	4	48.02	(48.33-47.18)	0.283	1.177
Lonchophylla	5	47.72	(49.55-46.75)	0.534	2.503
Monophyllus	2	47.13	(47.47-46.79)	0.342	1.026
Musonycteris	1	47.12			
Hylonycteris	1	46.98			
Choeroniscus	5	46.80	(47.75-45.32)	0.435	2.077
Choeronycteris	1	45.84			
Lichonycteris	3	45.13	(45.65-44.22)	0.460	1.765
Scleronycteris	1	45.02			
Anoura	5	44.66	(46.46-43.17)	0.542	2.714
Phyllostomatinae	11	43.61	(48.03-36.15)	1.178	8.960
Phyllostomus	5	48.03	(49.21-46.62)	0.500	2.330
Lonchorhina	3	47.34	(48.55-45.80)	0.810	2.963
Macrophyllum	2	46.66	(46.82-46.50)	0.158	0.480
Phylloderma	1	46.23			
Micronycteris	12	46.17	(48.80-43.72)	0.588	4.415
Macrotus	2	44.35	(44.39-44.32)	0.035	0.111
Mimon	5	43.70	(45.18-42.78)	0.473	2.419
Tonatia	7	42.21	(43.08-41.27)	0.276	1.729
Trachops	1	40.82			
Chrotopterus	1	38.08			
Vampyrum	1	36.15			
Stenoderminae	17	43.41	(45.49-40.92)	0.273	2.594
Uroderma	2	45.49	(45.52-45.46)	0.028	0.088
Artibeus	13	44.76	(46.66-43.21)	0.279	2.251
Enchisthenes	1	44.75			
Ariteus	1	44.34			
Vampyrodes	1	43.97			
Ectophylla	2	43.68	(43.69-43.68)	0.005	0.015
Sphaeronycteris	1	43.67			
Ardops	1	43.58			
Chiroderma	5	43.57	(45.49-42.29)	0.676	3.467
Stenoderma	1	43.42			
Sturnira	10	43.11	(44.51-41.67)	0.323	2.370
Vampyressa	5	43.11	(44.34-40.57)	0.659	3.416
Phyllops	2	42.97	(44.08-41.86)	1.115	3.669
Centurio	1	42.37			
Vampyrops	10	42.25	(44.06-40.46)	0.426	3.187
Ametrida	2	42.00	(42.35-41.66)	0.345	1.161
Pygoderma	1	40.92			
Carolliinae	2	42.34	(42.83-41.85)	0.489	1.634
Carollia	4	42.83	(43.39-42.37)	0.241	1.126
Rhinophylla	3	41.85	(42.81-40.06)	0.896	3.708
Myzapodidae	1	44.82			
Noctilionidae	1	44.77			
Craseonycteridae	1	43.44			
Nycteridae	1	41.44			
Megadermatidae	5	39.43	(40.53-37.48)	0.566	3.210
Pteropodidae	30	38.71	(42.49-35.39)	0.311	4.396

TABLE A13.—*Ranked means and statistics for the percentage contributed to length of digit III by the first phalanx.*

Taxon	*N*	Mean	Max-min	± 1 SE	CV
Nycteridae	1	28.50			
Pteropodidae	30	27.16	(29.52-25.32)	0.186	3.743
Thyropteridae	1	23.32			
Megadermatidae	5	22.65	(25.68-21.22)	0.788	7.776
Molossidae	9	22.30	(26.36-19.15)	0.701	9.425
Natalidae	1	21.38			
Rhinolophidae	7	20.39	(23.54-12.46)	1.390	18.039
Myzapodidae	1	20.26			
All bats	153	20.14	(29.52- 9.96)	0.379	23.292
Vespertilionidae	31	19.94	(24.70-11.77)	0.373	10.417
Emballonuridae	12	17.33	(21.77-10.76)	1.086	21.711
Phyllostomatidae	49	16.89	(21.00-10.21)	0.329	13.638
Carolliinae	2	18.93	(19.00-18.87)	0.065	0.488
Carollia	4	19.00	(19.23-18.55)	0.154	1.619
Rhinophylla	3	18.87	(19.34-18.37)	0.279	2.560
Phyllonycterinae	3	17.77	(20.14-15.60)	1.312	12.791
Erophylla	2	20.14	(20.45-19.83)	0.309	2.170
Phyllonycteris	2	17.57	(18.13-17.01)	0.562	4.525
Brachyphylla	2	15.60	(16.06-15.15)	0.453	4.108
Phyllostomatinae	11	17.73	(21.00-13.03)	0.667	12.472
Vampyrum	1	21.00			
Chrotopterus	1	19.99			
Macrotus	2	18.84	(19.15-18.54)	0.305	2.292
Micronycteris	12	18.80	(21.17-16.87)	0.437	8.047
Tonatia	7	18.77	(20.16-17.72)	0.320	4.511
Macrophyllum	2	18.46	(18.90-18.02)	0.439	3.366
Trachops	1	17.55			
Mimon	5	16.29	(19.37-14.51)	1.053	14.445
Lonchorhina	3	16.28	(17.61-15.50)	0.668	7.105
Phylloderma	1	16.04			
Phyllostomus	5	13.03	(14.25-12.07)	0.426	7.304
Glossophaginae	13	17.08	(18.76-14.98)	0.365	7.706
Platalina	1	18.76			
Choeronycteris	1	18.53			
Scleronycteris	1	18.11			
Lichonycteris	3	18.09	(18.61-17.48)	0.329	3.150
Hylonycteris	1	17.95			
Glossophaga	4	17.67	(18.09-16.89)	0.267	3.021
Musonycteris	1	17.47			
Choeroniscus	5	17.15	(17.81-16.41)	0.225	2.937
Lonchophylla	5	16.90	(19.41-16.05)	0.632	8.354
Monophyllus	2	15.99	(16.30-15.68)	0.308	2.721
Anoura	5	15.23	(16.09-14.65)	0.265	3.886
Lionycteris	1	15.22			
Leptonycteris	3	14.98	(15.48-14.40)	0.312	3.609
Stenoderminae	17	16.94	(19.58-14.97)	0.350	8.513
Centurio	1	19.58			
Pygoderma	1	19.44			
Phyllops	2	19.13	(19.48-18.77)	0.356	2.632
Vampyressa	5	17.75	(19.57-16.58)	0.664	8.365
Chiroderma	5	17.25	(18.45-15.81)	0.488	6.329
Sphaeronycteris	1	17.25			
Ectophylla	2	17.20	(19.08-15.33)	1.876	15.423
Sturnira	10	17.19	(18.55-16.55)	0.182	3.344
Enchisthenes	1	17.01			
Vampyrops	10	16.78	(17.69-15.31)	0.237	4.465
Uroderma	2	16.52	(16.72-16.32)	0.200	1.716
Vampyrodes	1	16.37			
Artibeus	13	15.80	(17.66-14.11)	0.316	7.220
Ametrida	2	15.44	(15.57-15.31)	0.131	1.204
Stenoderma	1	15.25			
Ardops	1	15.08			
Ariteus	1	14.97			
Desmodontinae	3	10.51	(10.99-10.21)	0.244	4.015
Desmodus	2	10.99	(11.03-10.95)	0.041	0.525
Diphylla	1	10.33			
Diaemus	1	10.21			
Mystacinidae	1	14.33			
Craseonycteridae	1	14.32			
Rhinopomatidae	1	13.42			
Noctilionidae	1	12.30			
Mormoopidae	2	11.18	(11.36-11.00)	0.182	2.302
Furipteridae	1	9.96			

TABLE A14.—*Ranked means and statistics for the percentage contributed to length of digit III by the second phalanx.*

Taxon	*N*	Mean	Max-min	± 1 SE	CV
Craseonycteridae	1	42.23			
Megadermatidae	5	37.92	(40.32-35.44)	0.782	4.612
Furipteridae	1	35.23			
Pteropodidae	30	34.13	(37.82-29.33)	0.347	5.566
Noctilionidae	1	30.95			
Nycteridae	1	30.05			
Natalidae	1	28.70			
Rhinolophidae	7	28.03	(39.31-23.55)	2.245	21.185
All bats	153	25.47	(42.23-14.21)	0.528	25.647
Emballonuridae	12	24.99	(28.71-21.06)	0.691	9.574
Rhinopomatidae	1	24.88			
Phyllostomatidae	49	23.62	(28.68-18.04)	0.297	8.810
Carolliinae	2	24.68	(25.03-24.33)	0.354	2.030
Rhinophylla	3	25.03	(25.93-24.17)	0.507	3.508
Carollia	4	24.33	(25.30-23.44)	0.396	3.257
Stenoderminae	17	24.39	(28.68-21.11)	0.405	6.840
Pygoderma	1	28.68			
Vampyrodes	1	25.84			
Ariteus	1	25.37			
Stenoderma	1	25.18			
Centurio	1	25.00			
Ardops	1	24.89			
Sphaeronycteris	1	24.57			
Vampyrops	10	24.51	(26.17-23.57)	0.280	3.610
Chiroderma	5	24.49	(25.47-23.68)	0.340	3.105
Vampyressa	5	24.43	(25.66-22.83)	0.469	4.294
Artibeus	13	24.28	(25.43-23.52)	0.164	2.440
Ametrida	2	24.17	(24.50-23.84)	0.330	1.930
Uroderma	2	23.77	(24.14-23.41)	0.362	2.153
Ectophylla	2	23.67	(24.51-22.84)	0.835	4.989
Phyllops	2	23.23	(23.27-23.19)	0.039	0.236
Sturnira	10	21.44	(22.84-20.41)	0.237	3.494
Enchisthenes	1	21.11			
Glossophaginae	13	23.73	(26.05-21.92)	0.296	4.504
Lionycteris	1	26.05			
Anoura	5	24.79	(25.53-24.30)	0.248	2.234
Lichonycteris	3	24.60	(25.07-23.91)	0.350	2.467
Scleronycteris	1	24.06			
Hylonycteris	1	23.98			
Choeroniscus	5	23.93	(24.54-23.18)	0.233	2.178
Leptonycteris	3	23.87	(24.54-23.14)	0.404	2.934
Lonchophylla	5	23.44	(24.38-22.69)	0.272	2.593
Monophyllus	2	23.27	(24.09-22.45)	0.820	4.982
Musonycteris	1	23.11			
Choeronycteris	1	23.03			
Glossophaga	4	22.41	(23.25-21.54)	0.358	3.198
Platalina	1	21.92			
Desmodontinae	3	23.54	(26.32-18.80)	2.385	17.547
Diaemus	1	26.32			
Diphylla	1	25.52			
Desmodus	2	18.80	(18.99-18.60)	0.192	1.445
Phyllostomatinae	11	23.45	(26.41-20.27)	0.529	7.484
Trachops	1	26.41			
Lonchorhina	3	25.77	(26.26-24.97)	0.402	2.704
Mimon	5	24.42	(25.29-23.17)	0.346	3.168
Vampyrum	1	23.84			
Phyllostomus	5	23.75	(24.31-22.50)	0.323	3.041
Macrophyllum	2	23.42	(23.43-23.42)	0.003	0.019
Chrotopterus	1	23.34			
Micronycteris	12	22.69	(27.07-20.16)	0.630	9.612
Phylloderma	1	22.55			
Tonatia	7	21.45	(22.41-20.36)	0.302	3.724
Macrotus	2	20.27	(20.28-20.27)	0.005	0.036
Phyllonycterinae	3	18.87	(20.47-18.04)	0.803	7.371
Brachyphylla	2	20.47	(20.50-20.44)	0.031	0.213
Erophylla	2	18.08	(18.72-17.45)	0.636	4.976
Phyllonycteris	2	18.04	(18.57-17.52)	0.523	4.103
Myzapodidae	1	21.59			
Molossidae	9	20.31	(21.51-18.76)	0.272	4.023
Mormoopidae	2	19.31	(23.16-15.46)	3.850	28.203
Vespertilionidae	31	19.30	(33.77-14.21)	0.790	22.797
Mystacinidae	1	17.60			
Thyropteridae	1	14.86			

TABLE A15.—*Ranked means and statistics for the percentage contributed to length of digit III by the third phalanx.*

Taxon	*N*	Mean	Max-min	± 1 SE	CV
Mormoopidae	2	16.64	(16.81-16.48)	0.163	1.386
Mystacinidae	1	14.70			
Phyllostomatidae	49	14.36	(19.01-10.02)	0.318	15.510
Desmodontinae	3	15.42	(15.71-14.99)	0.218	2.449
Diphylla	1	15.71			
Desmodus	2	15.55	(16.62-14.47)	1.076	9.789
Diaemus	1	14.99			
Stenoderminae	17	15.26	(18.39-10.96)	0.446	12.044
Ametrida	2	18.39	(19.19-17.58)	0.806	6.200
Sturnira	10	18.26	(20.31-16.48)	0.359	6.222
Enchisthenes	1	17.13			
Vampyrops	10	16.46	(18.17-14.15)	0.384	7.374
Ardops	1	16.45			
Stenoderma	1	16.15			
Ectophylla	2	15.44	(16.49-14.40)	1.045	9.574
Ariteus	1	15.32			
Artibeus	13	15.16	(16.79-13.92)	0.240	5.708
Vampyressa	5	14.71	(15.72-14.08)	0.326	4.953
Chiroderma	5	14.69	(15.40-13.98)	0.241	3.674
Phyllops	2	14.67	(16.18-13.16)	1.510	14.551
Sphaeronycteris	1	14.52			
Uroderma	2	14.22	(14.41-14.03)	0.190	1.887
Vampyrodes	1	13.82			
Centurio	1	13.05			
Pygoderma	1	10.96			
Phyllostomatinae	11	15.21	(19.01-10.62)	0.835	18.209
Vampyrum	1	19.01			
Chrotopterus	1	18.59			
Tonatia	7	17.57	(19.17-15.18)	0.467	7.037
Macrotus	2	16.53	(16.80-16.27)	0.265	2.270
Mimon	5	15.59	(17.89-12.56)	0.988	14.167
Trachops	1	15.23			
Phyllostomus	5	15.20	(16.03-14.18)	0.335	4.925
Phylloderma	1	15.18			
Micronycteris	12	12.35	(15.57- 7.56)	0.671	18.828
Macrophyllum	2	11.46	(11.74-11.18)	0.278	3.429
Lonchorhina	3	10.62	(11.62- 9.69)	0.560	9.130
Phyllonycterinae	3	14.66	(15.20-14.09)	0.321	3.791
Brachyphylla	2	15.20	(15.52-14.88)	0.321	2.984
Phyllonycteris	2	14.68	(16.50-12.87)	1.813	17.458
Erophylla	2	14.09	(14.26-13.92)	0.172	1.722
Carolliinae	2	14.05	(14.25-13.85)	0.200	2.013
Rhinophylla	3	14.25	(17.40-12.37)	1.584	19.259
Carollia	4	13.85	(14.98-13.10)	0.430	6.217
Glossophaginae	13	12.20	(15.32-10.02)	0.360	10.640
Anoura	5	15.32	(17.46-11.92)	1.011	14.753
Monophyllus	2	13.61	(14.47-12.76)	0.854	8.868
Scleronycteris	1	12.81			
Choeronycteris	1	12.60			
Musonycteris	1	12.31			
Lichonycteris	3	12.18	(12.36-11.92)	0.133	1.885
Choeroniscus	5	12.13	(13.02-11.55)	0.250	4.601
Lonchophylla	5	11.94	(14.28- 9.91)	0.808	15.128
Glossophaga	4	11.90	(12.71-10.99)	0.382	6.415
Leptonycteris	3	11.73	(12.72-10.21)	0.773	11.415
Hylonycteris	1	11.08			
Platalina	1	10.96			
Lionycteris	1	10.02			
Myzapodidae	1	13.33			
All bats	93	12.14	(20.13- 4.64)	0.378	30.027
Noctilionidae	1	11.98			
Vespertilionidae	31	9.02	(20.13- 0.00)	0.672	41.474
Thyropteridae	1	7.97			
Molossidae	9	6.68	(8.92- 4.64)	0.506	22.711

TABLE A16.—*Ranked means and statistics for the percentage contributed to length of digit IV by the metacarpal.*

Taxon	*N*	Mean	Max-min	± 1 SE	CV
Thyropteridae	1	68.56			
Emballonuridae	12	66.37	(70.34-63.19)	0.690	3.600
Mormoopidae	2	65.88	(66.33-65.44)	0.442	0.949
Natalidae	1	64.78			
Furipteridae	1	64.38			
Molossidae	9	63.63	(68.78-54.62)	1.557	7.342
Mystacinidae	1	62.95			
Rhinolophidae	7	62.92	(65.78-59.65)	0.864	3.633
Vespertilionidae	31	62.67	(73.59-58.48)	0.577	5.128
Craseonycteridae	1	61.46			
Noctilionidae	1	60.13			
Nycteridae	1	59.88			
Rhinopomatidae	1	59.77			
Phyllostomatidae	49	58.95	(67.11-47.84)	0.425	5.045
Desmodontinae	3	63.63	(67.11-61.36)	1.765	4.805
Desmodus	2	67.11	(68.09-66.13)	0.980	2.066
Diphylla	1	62.43			
Diaemus	1	61.36			
Glossophaginae	13	60.72	(63.09-59.66)	0.263	1.562
Hylonycteris	1	63.09			
Lionycteris	1	61.70			
Scleronycteris	1	61.28			
Anoura	5	61.17	(62.12-58.96)	0.574	2.100
Lichonycteris	3	60.85	(62.43-59.77)	0.808	2.299
Monophyllus	2	60.83	(61.49-60.18)	0.656	1.525
Choeroniscus	5	60.46	(61.05-59.61)	0.277	1.024
Musonycteris	1	60.43			
Glossophaga	4	60.12	(61.07-58.97)	0.483	1.606
Lonchophylla	5	60.06	(61.59-58.75)	0.499	1.857
Choeronycteris	1	59.84			
Leptonycteris	3	59.79	(60.33-58.78)	0.507	1.470
Platalina	1	59.66			
Phyllonycterinae	3	59.16	(59.54-58.72)	0.237	0.695
Phyllonycteris	2	59.54	(60.32-58.77)	0.775	1.841
Brachyphylla	2	59.21	(59.77-58.64)	0.568	1.357
Erophylla	2	58.72	(58.88-58.57)	0.152	0.366
Phyllostomatinae	11	58.48	(63.24-52.65)	1.060	6.013
Phylloderma	1	63.24			
Phyllostomus	5	63.01	(64.30-61.83)	0.485	1.723
Lonchorhina	3	61.41	(63.66-59.56)	1.201	3.388
Mimon	5	60.75	(64.94-56.94)	1.495	5.502
Micronycteris	12	59.79	(63.15-56.99)	0.578	3.347
Macrophyllum	2	59.14	(60.04-58.24)	0.898	2.147
Macrotus	2	56.79	(57.44-56-13)	0.659	1.641
Trachops	1	55.96			
Tonatia	7	55.93	(60.05-53.09)	1.048	4.957
Chrotopterus	1	54.63			
Vampyrum	1	52.65			
Stenoderminae	17	57.29	(59.08-47.84)	0.628	4.519
Uroderma	2	59.08	(59.11-59.05)	0.034	0.081
Stenoderma	1	58.75			
Chiroderma	5	58.67	(60.47-57.08)	0.735	2.802
Artibeus	13	58.56	(59.93-56.96)	0.229	1.410
Phyllops	2	58.53	(59.46-57.60)	0.929	2.244
Ardops	1	58.38			
Ectophylla	2	58.16	(58.33-57.99)	0.173	0.422
Vampyressa	5	58.12	(58.83-56.63)	0.395	1.521
Ariteus	1	58.04			
Vampyrodes	1	57.98			
Sturnira	10	57.65	(59.91-55.77)	0.368	2.020
Enchisthenes	1	57.63			
Vampyrops	10	57.60	(60.27-56.03)	0.426	2.339
Sphaeronycteris	1	56.84			
Centurio	1	56.08			
Pygoderma	1	55.92			
Ametrida	2	47.84	(48.26-47.42)	0.420	1.241
Carolliinae	2	56.97	(57.16-56.77)	0.195	0.484
Carollia	4	57.16	(58.11-56.20)	0.459	1.607
Rhinophylla	3	56.77	(58.04-55.50)	0.734	2.239
Megadermatidae	5	58.66	(60.84-56.58)	0.712	2.715
All bats	153	58.59	(73.59-41.96)	0.567	11.978
Myzapodidae	1	57.18			
Pteropodidae	30	46.52	(53.21-41.96)	0.451	5.306

TABLE A17.—*Ranked means and statistics for the percentage contributed to length of digit IV by the first phalanx.*

Taxon	*N*	Mean	Max-min	± 1 SE	CV
Pteropodidae	30	26.23	(28.69-22.90)	0.291	6.069
Molossidae	9	23.62	(27.95-17.82)	1.128	14.327
Rhinopomatidae	1	22.57			
Nycteridae	1	21.62			
Myzapodidae	1	20.88			
All bats	153	20.49	(28.69-10.23)	0.327	19.719
Vespertilionidae	31	20.25	(25.71-13.30)	0.448	12.318
Rhinolophidae	7	19.41	(21.07-15.88)	0.687	9.358
Thyropteridae	1	18.93			
Emballonuridae	12	18.88	(22.35-14.01)	0.684	12.559
Phyllostomatidae	49	18.10	(22.93-11.92)	0.362	14.008
Carolliinae	2	20.60	(20.99-20.20)	0.394	2.708
Carollia	4	20.99	(21.21-20.63)	0.136	1.295
Rhinophylla	3	20.20	(21.15-19.38)	0.514	4.407
Phyllostomatinae	11	19.23	(22.93-14.33)	0.818	14.113
Macrotus	2	22.93	(22.98-22.88)	0.048	0.298
Vampyrum	1	22.00			
Tonatia	7	21.84	(23.10-20.50)	0.429	5.197
Chrotopterus	1	21.04			
Micronycteris	12	19.48	(22.83-17.35)	0.556	9.888
Trachops	1	19.15			
Macrophyllum	2	18.95	(19.44-18.46)	0.488	3.640
Lonchorhina	3	18.49	(19.91-17.42)	0.738	6.914
Mimon	5	18.21	(20.75-15.92)	0.886	10.877
Phylloderma	1	15.17			
Phyllostomus	5	14.33	(16.93-12.10)	0.910	14.207
Stenoderminae	17	19.08	(22.12-16.84)	0.353	7.619
Centurio	1	22.12			
Ametrida	2	21.31	(21.35-21.27)	0.039	0.260
Phyllops	2	20.42	(20.47-20.38)	0.044	0.306
Ectophylla	2	20.07	(21.53-18.60)	1.465	10.328
Chiroderma	5	19.91	(21.13-18.80)	0.416	4.673
Vampyressa	5	19.55	(21.48-17.70)	0.751	8.592
Vampyrops	10	19.45	(20.51-18.04)	0.256	4.161
Enchisthenes	1	19.26			
Sturnira	10	19.03	(19.89-18.37)	0.156	2.590
Uroderma	2	18.90	(18.93-18.87)	0.029	0.217
Vampyrodes	1	18.76			
Pygoderma	1	18.34			
Stenoderma	1	18.34			
Artibeus	13	17.99	(19.85-16.12)	0.349	6.992
Ardops	1	17.09			
Ariteus	1	16.99			
Sphaeronycteris	1	16.84			
Phyllonycterinae	3	18.64	(20.44-17.25)	0.944	8.770
Erophylla	2	20.44	(20.56-20.32)	0.121	0.834
Phyllonycteris	2	18.22	(18.67-17.77)	0.453	3.517
Brachyphylla	2	17.25	(17.47-17.03)	0.222	1.824
Glossophaginae	13	16.75	(18.58-14.31)	0.340	7.314
Glossophaga	4	18.58	(19.15-18.03)	0.260	2.794
Platalina	1	18.35			
Choeronycteris	1	17.62			
Scleronycteris	1	17.25			
Lonchophylla	5	17.22	(17.99-16.08)	0.316	4.102
Lichonycteris	3	17.11	(17.89-16.51)	0.408	4.136
Choeroniscus	5	16.99	(17.71-15.70)	0.365	4.807
Musonycteris	1	16.88			
Leptonycteris	3	16.45	(16.75-16.06)	0.202	2.123
Anoura	5	16.17	(17.15-15.34)	0.320	4.420
Hylonycteris	1	16.02			
Monophyllus	2	14.81	(14.92-14.70)	0.112	1.074
Lionycteris	1	14.31			
Desmodontinae	3	12.05	(12.14-11.92)	0.065	0.931
Diphylla	1	12.14			
Desmodus	2	12.09	(12.63-11.54)	0.548	6.412
Diaemus	1	11.92			
Megadermatidae	5	17.86	(19.85-16.18)	0.746	9.338
Natalidae	1	17.28			
Mormoopidae	2	16.64	(18.28-15.01)	1.634	13.885
Mystacinidae	1	16.01			
Furipteridae	1	15.98			
Noctilionidae	1	10.61			
Craseonycteridae	1	10.23			

TABLE A18.—*Ranked means and statistics for the percentage contributed to length of digit IV by the second phalanx.*

Taxon	*N*	Mean	Max-min	± 1 SE	CV
Noctilionidae	1	29.27			
Craseonycteridae	1	28.31			
Pteropodidae	30	27.25	(29.77-22.67)	0.335	6.742
Megadermatidae	5	23.48	(24.93-19.30)	1.054	10.039
Phyllostomatidae	49	22.95	(30.84-20.10)	0.280	8.528
Desmodontinae	3	24.32	(26.71-20.80)	0.795	12.788
Diaemus	1	26.71			
Diphylla	1	25.44			
Desmodus	2	20.80	(21.24-20.37)	0.432	2.940
Stenoderminae	17	23.63	(30.84-21.05)	0.577	10.061
Ametrida	2	30.84	(31.22-30.46)	0.380	1.745
Sphaeronycteris	1	26.32			
Pygoderma	1	25.74			
Ariteus	1	24.97			
Ardops	1	24.53			
Artibeus	13	23.45	(25.33-21.41)	0.257	3.949
Sturnira	10	23.32	(25.59-21.69)	0.349	4.730
Vampyrodes	1	23.26			
Enchisthenes	1	23.11			
Vampyrops	10	22.95	(23.94-20.97)	0.285	3.923
Stenoderma	1	22.91			
Vampyressa	5	22.33	(23.71-20.43)	0.557	5.579
Uroderma	2	22.02	(22.08-21.95)	0.063	0.405
Centurio	1	21.80			
Ectophylla	2	21.77	(23.06-20.48)	1.292	8.393
Chiroderma	5	21.42	(23.08-19.05)	0.712	7.430
Phyllops	2	21.05	(21.93-20.16)	0.885	5.944
Glossophaginae	13	22.53	(24.35-20.90)	0.287	4.599
Monophyllus	2	24.35	(24.90-23.81)	0.544	3.157
Lionycteris	1	23.99			
Leptonycteris	3	23.76	(24.47-23.14)	0.387	2.822
Lonchophylla	5	22.72	(25.17-21.29)	0.658	6.474
Musonycteris	1	22.70			
Anoura	5	22.66	(23.89-22.09)	0.321	3.169
Choeroniscus	5	22.55	(23.25-22.13)	0.212	2.106
Choeronycteris	1	22.54			
Lichonycteris	3	22.04	(23.30-21.06)	0.662	5.199
Platalina	1	21.99			
Scleronycteris	1	21.47			
Glossophaga	4	21.29	(22.03-20.05)	0.451	4.239
Hylonycteris	1	20.90			
Carolliinae	2	22.43	(23.02-21.85)	0.589	3.716
Rhinophylla	3	23.02	(25.11-21.88)	1.046	7.872
Carollia	4	21.85	(22.60-21.25)	0.334	3.061
Phyllostomatinae	11	22.28	(25.35-20.10)	0.555	8.257
Vampyrum	1	25.35			
Trachops	1	24.89			
Chrotopterus	1	24.33			
Phyllostomus	5	22.66	(24.06-20.15)	0.692	6.824
Tonatia	7	22.23	(23.96-18.74)	0.773	9.204
Macrophyllum	2	21.91	(23.30-20.52)	1.386	8.945
Phylloderma	1	21.58			
Mimon	5	21.05	(22.44-19.13)	0.632	6.713
Micronycteris	12	20.73	(22.77-18.64)	0.359	6.005
Macrotus	2	20.29	(20.99-19.58)	0.707	4.931
Lonchorhina	3	20.10	(20.84-18.92)	0.596	5.135
Phyllonycterinae	3	22.21	(23.54-20.84)	0.781	6.091
Brachyphylla	2	23.54	(23.89-23.20)	0.346	2.077
Phyllonycteris	2	22.24	(22.56-21.92)	0.322	2.048
Erophylla	2	20.84	(21.11-20.57)	0.272	1.849
Myzapodidae	1	21.94			
Mystacinidae	1	21.04			
All bats	153	20.92	(31.22- 5.27)	0.441	26.054
Furipteridae	1	19.63			
Nycteridae	1	18.51			
Natalidae	1	17.94			
Rhinolophidae	7	17.67	(24.48-14.13)	1.458	21.842
Rhinopomatidae	1	17.66			
Mormoopidae	2	17.47	(18.67-16.28)	1.192	9.646
Vespertilionidae	31	17.08	(26.56- 5.31)	0.771	25.135
Emballonuridae	12	14.75	(19.47-10.33)	0.851	19.977
Molossidae	9	12.75	(18.11- 5.27)	1.683	39.616
Thyropteridae	1	12.51			

TABLE A19.—*Ranked means and statistics for the percentage contributed to length of digit V by the metacarpal.*

Taxon	*N*	Mean	Max-Min	± 1 SE	CV
Noctilionidae	1	74.69			
Vespertilionidae	31	68.57	(82.35-59.25)	0.808	6.557
Rhinopomatidae	1	68.18			
Mystacinidae	1	67.42			
Thyropteridae	1	65.80			
Craseonycteridae	1	65.57			
Furipteridae	1	63.91			
Natalidae	1	63.86			
Myzapodidae	1	63.85			
Emballonuridae	12	63.57	(67.72-57.70)	0.811	4.417
Phyllostomatidae	49	62.12	(67.99-52.13)	0.429	4.838
Desmodontinae	3	66.34	(67.76-64.29)	1.049	2.740
Diaemus	1	67.76			
Desmodus	2	66.96	(67.54-66.38)	0.578	1.221
Diphylla	1	64.29			
Phyllonycterinae	3	62.93	(65.09-61.36)	1.113	3.063
Brachyphylla	2	65.09	(65.97-64.20)	0.889	1.932
Phyllonycteris	2	62.36	(62.76-61.96)	0.401	0.910
Erophylla	2	61.36	(62.06-60.66)	0.697	1.606
Stenoderminae	17	62.53	(64.80-52.13)	0.785	5.178
Uroderma	2	64.80	(65.16-64.44)	0.362	0.789
Stenoderma	1	64.67			
Artibeus	13	64.58	(67.64-62.21)	0.522	2.916
Sturnira	10	64.52	(66.05-62.75)	0.439	2.153
Vampyrodes	1	64.48			
Chiroderma	5	63.89	(65.51-62.95)	0.432	1.514
Vampyressa	5	63.69	(66.00-61.89)	0.707	2.482
Enchisthenes	1	63.67			
Sphaeronycteris	1	63.60			
Vampyrops	10	63.50	(65.47-61.98)	0.372	1.854
Ariteus	1	63.48			
Ectophylla	2	63.42	(64.68-62.16)	1.258	2.806
Ardops	1	63.00			
Phyllops	2	62.14	(62.72-61.56)	0.581	1.323
Pygoderma	1	59.15			
Centurio	1	58.32			
Ametrida	2	52.13	(52.49-51.76)	0.366	0.993
Phyllostomatinae	11	61.51	(67.99-55.66)	1.213	6.542
Phyllostomus	5	67.99	(70.39-66.08)	0.880	2.894
Phylloderma	1	67.07			
Mimon	5	64.20	(69.16-59.32)	1.886	6.570
Lonchorhina	3	63.38	(65.11-60.19)	1.600	4.372
Macrophyllum	2	62.22	(62.30-62.15)	0.074	0.169
Micronycteris	12	61.67	(65.46-58.16)	0.718	4.030
Macrotus	2	60.48	(61.61-59.35)	1.130	2.643
Trachops	1	59.89			
Chrotopterus	1	57.18			
Tonatia	7	56.91	(60.78-54.38)	0.928	4.316
Vampyrum	1	55.66			
Glossophaginae	13	61.22	(62.70-59.21)	0.254	1.495
Choeronycteris	1	62.70			
Leptonycteris	3	62.40	(62.96-61.91)	0.306	0.848
Lonchophylla	5	62.01	(63.12-61.52)	0.290	1.046
Musonycteris	1	61.87			
Glossophaga	4	61.35	(61.96-60.62)	0.291	0.950
Choeroniscus	5	61.32	(62.51-59.84)	0.488	1.780
Hylonycteris	1	61.28			
Lionycteris	1	60.99			
Lichonycteris	3	60.83	(61.27-60.22)	0.315	0.896
Platalina	1	60.77			
Scleronycteris	1	60.76			
Anoura	5	60.36	(61.06-59.07)	0.379	1.404
Monophyllus	2	59.21	(59.65-58.78)	0.435	1.040
Carolliinae	2	60.26	(60.48-60.04)	0.222	0.522
Rhinophylla	3	60.48	(61.79-59.66)	0.660	1.890
Carollia	4	60.04	(60.28-59.59)	0.154	0.515
All bats	153	61.02	(82.35-46.71)	0.551	11.164
Megadermatidae	5	59.85	(61.13-58.53)	0.542	2.027
Nycteridae	1	59.39			
Mormoopidae	2	59.29	(64.15-54.43)	4.861	11.593
Molossidae	9	58.88	(63.56-49.37)	1.679	8.557
Rhinolophidae	7	57.13	(60.70-52.96)	1.091	5.052
Pteropodidae	30	50.78	(53.41-46.71)	0.295	3.184

TABLE A20.—*Ranked means and statistics for the percentage contributed to length of digit V by the first phalanx.*

Taxon	*N*	Mean	Max-min	±1 SE	CV
Molossidae	9	29.46	(39.13-20.66)	1.837	18.703
Pteropodidae	30	24.16	(26.06-22.91)	0.160	3.636
Emballonuridae	12	23.42	(29.75-18.26)	1.038	15.348
Furipteridae	1	23.22			
Rhinolophidae	7	23.12	(27.43-17.74)	1.464	16.759
Mormoopidae	2	22.22	(26.70-17.74)	4.480	28.512
Nycteridae	1	20.58			
All bats	153	20.13	(39.13- 8.83)	0.374	22.977
Megadermatidae	5	20.05	(25.43-17.91)	1.395	15.555
Myzapodidae	1	18.92			
Thyropteridae	1	17.75			
Natalidae	1	17.61			
Vespertilionidae	31	17.44	(20.61- 8.83)	0.395	12.610
Rhinopomatidae	1	17.20			
Noctilionidae	1	17.15			
Phyllostomatidae	49	16.88	(22.86-12.74)	0.303	12.565
Carolliinae	2	18.61	(19.00-18.23)	0.389	2.952
Carollia	4	19.00	(19.62-18.63)	0.224	2.359
Rhinophylla	3	18.23	(19.52-17.06)	0.715	6.799
Phyllostomatinae	11	18.25	(21.50-13.93)	0.708	12.858
Tonatia	7	21.50	(23.11-20.52)	0.337	4.143
Macrotus	2	20.67	(21.28-20.06)	0.613	4.196
Vampyrum	1	19.99			
Chrotopterus	1	19.66			
Micronycteris	12	19.60	(21.83-17.53)	0.478	8.448
Trachops	1	18.66			
Lonchorhina	3	17.47	(18.81-16.80)	0.668	6.617
Macrophyllum	2	17.39	(17.60-17.18)	0.211	1.715
Mimon	5	16.74	(20.05-14.74)	1.106	14.780
Phylloderma	1	15.19			
Phyllostomus	5	13.93	(15.96-12.05)	0.701	11.264
Phyllonycterinae	3	16.89	(19.00-15.58)	1.067	10.940
Erophylla	2	19.00	(19.19-18.81)	0.190	1.413
Brachyphylla	2	16.09	(16.33-15.84)	0.247	2.170
Phyllonycteris	2	15.58	(16.35-14.81)	0.769	6.986
Stenoderminae	17	16.71	(22.86-14.88)	0.547	13.491
Centurio	1	22.86			
Ametrida	2	21.07	(21.35-20.79)	0.279	1.872
Sphaeronycteris	1	18.90			
Phyllops	2	17.26	(17.42-17.10)	0.161	1.317
Ectophylla	2	16.98	(17.89-16.08)	0.904	7.524
Pygoderma	1	16.64			
Vampyressa	5	16.32	(17.70-14.64)	0.515	7.063
Chiroderma	5	16.14	(16.84-15.08)	0.320	4.426
Vampyrops	10	16.09	(17.30-15.05)	0.241	4.744
Stenoderma	1	15.71			
Vampyrodes	1	15.36			
Uroderma	2	15.27	(16.09-14.45)	0.818	7.576
Sturnira	10	15.24	(16.57-14.08)	0.259	5.366
Ariteus	1	15.21			
Ardops	1	15.10			
Artibeus	13	14.94	(16.89-13.48)	0.317	7.652
Enchisthenes	1	14.88			
Glossophaginae	13	16.38	(17.83-14.89)	0.246	5.422
Platalina	1	17.83			
Glossophaga	4	17.69	(18.31-16.83)	0.327	3.697
Monophyllus	2	17.15	(17.31-16.99)	0.162	1.338
Scleronycteris	1	16.93			
Lonchophylla	5	16.66	(18.16-15.52)	0.437	5.862
Choeroniscus	5	16.38	(17.21-15.19)	0.332	4.537
Lionycteris	1	16.34			
Leptonycteris	3	16.24	(16.25-16.23)	0.006	0.059
Lichonycteris	3	16.21	(16.57-15.73)	0.250	2.670
Musonycteris	1	15.77			
Choeronycteris	1	15.76			
Hylonycteris	1	15.11			
Anoura	5	14.89	(15.58-14.18)	0.279	4.196
Desmodontinae	3	13.75	(15.13-12.74)	0.712	8.970
Diphylla	1	15.13			
Diaemus	1	13.39			
Desmodus	2	12.74	(12.85-12.64)	0.102	1.129
Craseonycteridae	1	15.79			
Mystacinidae	1	11.59			

TABLE A21.—*Ranked means and statistics for the percentage contributed to length of digit V by the second phalanx.*

Taxon	*N*	Mean	Max-min	±1 SE	CV
Pteropodidae	30	25.06	(28.54-22.08)	0.291	6.357
Phyllostomatidae	49	21.00	(26.80-17.49)	0.275	9.161
Glossophaginae	13	22.40	(24.75-20.95)	0.310	4.990
Anoura	5	24.75	(25.35-24.47)	0.163	1.473
Monophyllus	2	23.64	(23.91-23.36)	0.273	1.634
Hylonycteris	1	23.62			
Lichonycteris	3	22.96	(23.44-22.42)	0.295	2.229
Lionycteris	1	22.67			
Musonycteris	1	22.36			
Scleronycteris	1	22.31			
Choeroniscus	5	22.30	(24.97-20.80)	0.711	7.129
Choeronycteris	1	21.54			
Platalina	1	21.40			
Leptonycteris	3	21.36	(21.84-20.80)	0.302	2.448
Lonchophylla	5	21.33	(22.51-19.98)	0.464	4.860
Glossophaga	4	20.95	(21.82-19.73)	0.465	4.442
Carolliinae	2	21.13	(21.29-20.96)	0.166	1.112
Rhinophylla	3	21.29	(21.90-20.81)	0.322	2.620
Carollia	4	20.96	(21.17-20.78)	0.102	0.970
Stenoderminae	17	20.76	(26.80-17.49)	0.509	10.101
Ametrida	2	26.80	(26.89-26.72)	0.087	0.459
Pygoderma	1	24.21			
Ardops	1	21.89			
Enchisthenes	1	21.45			
Artiteus	1	21.31			
Phyllops	2	20.60	(21.02-20.18)	0.421	2.889
Artibeus	13	20.47	(22.13-18.87)	0.282	4.964
Vampyrops	10	20.40	(21.39-19.16)	0.277	4.288
Sturnira	10	20.24	(22.43-18.28)	0.367	5.730
Vampyrodes	1	20.16			
Vampyressa	5	19.99	(22.58-17.42)	1.073	11.997
Chiroderma	5	19.97	(21.06-17.72)	0.578	6.476
Uroderma	2	19.93	(20.38-19.47)	0.456	3.238
Stenoderma	1	19.61			
Ectophylla	2	19.60	(19.95-19.24)	0.355	2.559
Centurio	1	18.82			
Sphaeronycteris	1	17.49			
Phyllostomatinae	11	20.23	(24.35-17.75)	0.649	10.646
Vampyrum	1	24.35			
Chrotopterus	1	23.16			
Tonatia	7	21.60	(23.92-18.62)	0.680	8.334
Trachops	1	21.45			
Macrophyllum	2	20.39	(20.52-20.25)	0.137	0.948
Lonchorhina	3	19.14	(21.00-18.07	0.934	8.451
Mimon	5	19.06	(20.93-16.02)	0.880	10.327
Macrotus	2	18.85	(19.37-18.33)	0.517	3.878
Micronycteris	12	18.73	(21.43-16.26)	0.441	8.151
Phyllostomus	5	18.08	(18.90-17.51)	0.269	3.323
Phylloderma	1	17.75			
Phyllonycterinae	3	20.18	(22.07-18.83)	0.973	8.351
Phyllonycteris	2	22.07	(22.43-21.70)	0.368	2.358
Erophylla	2	19.64	(20.15-19.13)	0.507	3.650
Brachyphylla	2	18.83	(19.47-18.19)	0.642	4.826
Desmodontinae	3	19.91	(20.58-18.85)	0.536	4.663
Diphylla	1	20.58			
Desmodus	2	20.30	(20.78-19.82)	0.476	3.319
Diaemus	1	18.85			
Mystacinidae	1	21.00			
Megadermatidae	5	20.09	(21.41-16.04)	1.017	11.315
Nycteridae	1	20.03			
Rhinolophidae	7	19.75	(22.56-18.18)	0.637	8.532
All bats	153	18.84	(28.54- 8.16)	0.406	26.629
Craseonycteridae	1	18.64			
Natalidae	1	18.54			
Mormoopidae	2	18.48	(18.87-18.10)	0.380	2.910
Myzapodidae	1	17.23			
Thyropteridae	1	16.46			
Rhinopomatidae	1	14.62			
Vespertilionidae	31	13.98	(21.09- 8.83)	0.559	22.239
Emballonuridae	12	13.01	(16.23- 9.55)	0.580	15.451
Furipteridae	1	12.87			
Molossidae	9	11.66	(15.78-10.16)	0.570	14.663
Noctilionidae	1	8.16			

REPRODUCTIVE PATTERNS

DON E. WILSON

"It follows, then, that an ecologist setting out to learn the workings of some part of the natural world must study the strategies of individual species. The question he must ask himself is: What are the tricks used to turn resources into babies?" This quotation from Colinvaux (1973) may be appropriate to describe the following approach to the problem of reproductive strategies in phyllostomatid bats.

One function of a review paper is to provide the reader with a summary of available data and pertinent references with which to pursue the subject. I have attempted to do this at the species level, although nothing is known concerning reproduction in some species of leaf-nosed bats.

Knowledge of bat reproductive patterns has undergone a spurt in growth in recent years, as has been the case in many other fields. Enough information is now available to make speculation tantalizing, but not enough to make generalization rewarding. Nevertheless, some general patterns seem to be widespread within the primarily tropical phyllostomatids.

Early knowledge of bat reproduction was based mainly on temperate-zone species. Reproductive cycles in temperate regions usually are forced into a tightly controlled and relatively short time-span owing to rigors of the climate. Thus, most temperate-zone bats produce only one young per year, and populations are highly synchronized.

Some members of the family Phyllostomatidae, such as *Macrotus* and *Leptonycteris*, extend northward into subtropical and temperate zones. *Macrotus californicus* probably has the most distinctive reproductive pattern in the family. Not only is this species monestrous and monotocous, but it has a rather unique system of delayed development that allows the embryo to stay dormant during unfavorable times of the year (Bradshaw, 1961).

A variation of this pattern is seen in *Artibeus jamaicensis* in Panamá (Fleming, 1971). These animals have young in March or April, followed by a postpartum estrus and a second pregnancy. This results in the second young being born in July or August; another postpartum estrus follows. The embryos from the second postpartum estrus implant in the uterus, but undergo delayed development until November, when they resume the normal pace of development and finish the cycle with parturition in March or April.

A far more common pattern is one of bimodal or seasonal polyestry similar to that of *Artibeus jamaicensis*, but without delayed development. Fleming (1973) and Wilson (1973) have discussed this pattern for Panamanian and Costa Rican bats. Members of the genera *Glossophaga*, *Carollia*, *Uroderma*, and *Artibeus* commonly have this bimodal pattern. In Panamá, this pattern involves birth peaks in March-April and July-August. In Costa Rica, the peaks may be shifted to February-March and June-July (Fleming *et al.*, 1972). In Colombia,

the pattern seems to have shifted still more with birth peaks occurring in January-February and May-June for some species. A recent paper by Taddei (1976) has confirmed this pattern for many species in Brazil as well.

In many of the polyestrous species there is so much asynchrony within a given population that it is difficult to determine if the individual animals are producing more than one young per year or if they simply are out of phase with each other. The presence of females that are both pregnant and lactating is one simple indication of polyestry.

It may be possible for some polyestrous individuals to produce three young per year, as is the case with *Myotis nigricans*, a neotropical vespertilionid (Wilson and Findley, 1970). Variation in age of first reproductive activity, copulation time, fertilization, gestation period, and timing of postpartum estrus all tend to cause asynchrony in a population. If an individual bat became pregnant at the onset of copulatory activity and proceeded through the first two pregnancies with little or no delay, there would be sufficient time for a third pregnancy in many cases. I suspect that two per year is a more common occurrence.

At the other extreme from synchronized monestrous cycles are year-round continuous reproductive cycles as exemplified by the vampire *Desmodus rotundus*. Even here, it is likely that individual bats produce only two young per year on the average, and asynchrony within populations gives the appearance of continuous activity. In Colombia, for example, pregnant, lactating, and inactive *Artibeus lituratus* can be taken in any month of the year. Nevertheless, there are peak periods of pregnancies in the months of December and May.

All of these patterns may be viewed as variations on a single theme. Given a year's time, what is the most efficient way to produce offspring? For animals limited by the rigorous climates of the temperate zones, this results in a single, population-wide effort at the time of maximum food availability. For tropical species, it often might be possible to produce two litters during the favorable period of food abundance, which is usually extended in tropical areas. Most reproductive patterns in tropical areas seem to be correlated with seasonal rainfall patterns. The dry season is probably the most stressful time of year for many species, and reproductive strategies seem geared to avoid the weaning of young during this season. In polyestrous species, the weaning of young from the first birth peak is usually timed to coincide with the beginning of the rainy season, a period of maximum food abundance. *Desmodus rotundus* has probably been allowed by natural selection to adopt a year-round, asynchronous cycle due to the year-round availability of its food source, blood from domestic cattle.

Species Accounts

The following accounts are arranged in the same order as the list of species given by Jones and Carter (1976). Each account consists of a short summary or discussion, to be used in conjunction with the listing of available data from the literature presented in tabular form. Within the tables, localities, listed by state or

country, are arranged from North to South, insofar as possible. Dates, listed by month, are arranged chronologically from January to December, although varying dates in a single reference necessitate some departure from the chronological scheme. Numbers under the columns labeled "Pregnant", "Lactating", and "Inactive," refer to number of specimens. An "X" in these columns means the number was not given. In the references column, "USNM" refers to records from the National Museum of Natural History that have not been published previously.

The following list includes those species for which no data are available. I emphasize these species here and in the species accounts in hopes that it will spur efforts to gather such data: *Micronycteris pusilla, Micronycteris behni, Lonchorhina orinocensis, Tonatia brasiliense, Tonatia carrikeri, Tonatia venezuelae, Mimon bennettii, Mimon koepckeae, Phyllostomus latifolius, Lonchophylla hesperia, Lonchophylla thomasi, Anoura werckleae, Scleronycteris ega, Lichonycteris degener, Platalina genovensium, Sturnira nana, Vampyrops aurarius, Vampyrops nigellus, Vampyrops recifinus, Chiroderma doriae, Phyllops falcatus, Phyllops haitiensis, Ariteus flavescens, Ametrida centurio, Sphaeronycteris toxophyllum, Brachyphylla nana, Phyllonycteris major.*

Micronycteris megalotis

Data are insufficient from any one locality to speculate effectively on the seasonal reproductive pattern of *M. megalotis*. The data are not inconsistent with a pattern of seasonal breeding in harmony with the rainfall pattern. In the northern part of the range, females are pregnant during the beginning of the rainy season. In the southern part of the range, however, they become pregnant earlier in the year and the rainy or breeding season may last longer, possibly including two breeding cycles per female per year. This may be due to an earlier and longer lasting rainy season in the southern portions of the range. See Table 1.

Micronycteris schmidtorum

The only reference to this species appears to be that of Mares and Wilson (1971), who reported a male with nonscrotal testes taken in February in Costa Rica.

Micronycteris minuta

Data available (Table 1) fit a pattern of breeding initiated at the beginning of the rainy season. Confirmation of this pattern must await information relating to other seasons. See Table 1.

Micronycteris hirsuta

Trinidad dates (Table 1) are from the appropriate times of year suggesting at least a bimodal reproductive pattern. Lack of data from later in the year precludes further speculation.

TABLE 1.—*Reproductive data for the genus* Micronycteris.

Place	Date	Pregnant	Lactating	Inactive	Reference
		Micronycteris megalotis			
Veracruz	Feb			1	Hall and Dalquest, 1963
	Dec			1	"
	Jun			1	Lackey, 1970
Yucatán	Apr	1			Jones *et al.*, 1973
	May			1	Birney *et al.*, 1974
Michoacán	May	1			Villa-R., 1966
Oaxaca	May	1			"
El Salvador	Mar	1			Burt and Stirton, 1961
Nicaragua	Mar	2		1	Jones *et al.*, 1971*a*
	Apr			2	"
	Jun	1	2	1	"
	Aug			2	"
Costa Rica	Feb			1	Gardner *et al.*, 1970
Panamá	May		1		Enders, 1935
Trinidad	Feb	1			Goodwin and Greenhall, 1961
	Mar	1			"
	Jun		1		"
Colombia	Jun		1		Thomas, 1972
Venezuela	Jul	1			USNM
	Aug		3		"
Perú	Aug	2		18	Tuttle, 1970
Brazil	Jun			3	Peracchi and Albuquerque, 1971
		Micronycteris minuta			
Costa Rica	Mar	1			Gardner *et al.*, 1970
Trinidad	Mar			1	Goodwin and Greenhall, 1961
	May	1	4	2	"
Perú	Jul			2	Tuttle, 1970
		Micronycteris hirsuta			
Trinidad	Mar	1			Goodwin and Greenhall, 1961
	May	2			"
Perú	Jul	1		1	Tuttle, 1970
		Micronycteris sylvestris			
Nayarit	Mar			1	Jones, 1964*b*
Veracruz	Dec			1	Hall and Dalquest, 1963
French Guiana	Feb	X			Brosset and Dubost, 1967
	Mar	X			"

Micronycteris brachyotis

Goodwin and Greenhall (1961) reported a "breeding male" in May and three others in June from Trinidad. Rick (1968) found one pregnant and six lactating females in July in Guatemala.

Micronycteris pusilla

Nothing is known about reproduction in *M. pusilla.*

Micronycteris nicefori

The only records are those of Goodwin and Greenhall (1961), reporting two "breeding males" from Trinidad in October, and Baker and Jones (1975), reporting a lactating female from Nicaragua in July.

Micronycteris sylvestris

In the northern part of the range, known records are from late in the rainy season, whereas from the southern portion they are from early in the rainy season. Data from other times of the year are necessary before speculating further. See Table 1.

Micronycteris behni

Nothing is known about the reproductive pattern of *M. behni.*

Micronycteris daviesi

Tuttle (1970) collected a pregnant female in August in Perú. This is apparently the only record of reproductive activity for this species.

Macrotus waterhousii

In Mexico, *M. waterhousii* probably has a single young per year (Table 2). The available evidence suggests May as the most likely period for parturition. Additional study may reveal a delayed development system such as that described for the congeneric *M. californicus* in the following account. Data from the Caribbean populations are insufficient for any meaningful analysis.

Macrotus californicus

In addition to the information in Table 2, Bradshaw (1961, 1962) has described the reproductive strategy of *M. californicus* in southern Arizona. A good summary of the reproductive pattern also may be found in Anderson (1969). Males undergo spermatogenesis in summer and autumn and inseminate females in autumn; ovulation and fertilization occur immediately following copulation. The single embryo undergoes slow growth during winter until March, when development proceeds at a more rapid rate resulting in a gestation period of about eight months. Bradshaw (1961) coined the term "delayed development" to describe the reproductive pattern. Parturition occurs in June and young are foraging by August. Young-of-the-year females apparently breed during the first autumn, but males are not reproductively mature until the following year.

Lonchorhina aurita

The little evidence available points to a breeding season that is correlated with the beginning of the rainy season (Table 2). Panamanian pregnancies are during the dry season and should result in the young being born at the beginning of the rainy season.

TABLE 2.—*Reproductive data for the genera* Macrotus, Lonchorhina, Macrophyllum, Tonatia, *and* Mimon.

Place	Date	Pregnant	Lactating	Inactive	Reference
		Macrotus waterhousii			
Sinaloa	Jul		X		Jones *et al.*, 1972
Jalisco	Feb	3		X	Watkins *et al.*, 1972
	Mar	2		X	"
	May		X	X	"
	Jul			X	"
	Sep			X	"
	Oct			X	"
Tres Marias Is.	May	X			Merriam, 1898
Durango	Jun		2	1	Jones, 1964*c*
Jamaica	Dec		7	2	Osburn, 1865
	Dec		4		Goodwin, 1970
Crooked Is.	Apr	1			Buden, 1975
Cuba	Mar	4			Anderson, 1969
Caicos Is.	Feb	2			Buden, 1975
	Apr	1			Miller, 1904
		Macrotus californicus			
California	Mar	1			Cockrum, 1955
	Apr	2*			"
	Apr	9			USNM
	Apr	60			Grinnell, 1918
	May	1			Huey, 1925
Baja Calif.	Jul	5	X		Jones *et al.*, 1965
Sonora	Apr		X		Burt, 1938
	May	4			"
	Jul		X		"
	Aug**				"
	Mar	1		3	Cockrum and Bradshaw, 1963
	Apr	6			"
		Lonchorina aurita			
Quintana Roo	Aug			1	Jones *et al.*, 1973
Oaxaca	Feb	X			Walker, 1975
	Mar	8		15	Schaldach, 1965
Guatemala	Jan			1	Jones, 1966
Panamá	Feb	2			Bloedel, 1955
	Mar	2			"
	Feb	2			Fleming *et al.*, 1972
	Mar	2			"
	Nov			1	"
Trinidad	Apr	1			Goodwin and Greenhall, 1961
Perú	Jul		1		Tuttle, 1970
	Aug			1	"

TABLE 2.—*Continued.*

		Macrophyllum macrophyllum			
El Salvador	Oct	2			Harrison, 1975
Costa Rica	Mar	X			LaVal, 1977
	May	X			"
	Aug**				"
French Guiana	Oct	X			Brosset and Dubost, 1967
	Nov	X			"
		Tonatia bidens			
Guatemala	Feb	1			Carter *et al.*, 1966
Honduras	Aug**	2		2	Valdez and LaVal, 1971
Costa Rica	Jan	1			Gardner *et al.*, 1970
	Aug**				LaVal, 1977
Trinidad	May	2			Goodwin and Greenhall, 1961
Perú	Apr			2	Gardner, 1976
	Jul	2		1	"
		Tonatia minuta			
Honduras	Aug		1		Valdez and LaVal, 1971
Nicaragua	Jul	1			"
Costa Rica	Feb	1			LaVal, 1977
	Apr	1			"
Panamá	Feb	1			Davis *et al.*, 1964
		Tonatia silvicola			
Panamá	Mar	2			Fleming *et al.*, 1972
	Oct			1	"
	Nov			1	"
	Dec			1	"
Colombia	Jan	1			Thomas, 1972
Perú	Jul	2			Tuttle, 1970
	Aug	2			"
		Mimon cozumelae			
Veracruz	Apr	2		2	Hall and Dalquest, 1963
Yucatán	Apr	19			Jones *et al.*, 1973
	Jul		1		"
Campeche	May		X		"
Guatemala	Mar	1			Rick, 1968
	Aug		1	1	"
Honduras	Jul		1		Valdez and LaVal, 1971
Costa Rica	Apr	X			LaVal, 1977
	Aug	1			"
		Mimon crenulatum			
Campeche	Feb	1			Jones, 1964*b*
Costa Rica	Apr	1			LaVal, 1977
Venezuela	Mar	2			Goodwin and Greenhall, 1961
Perú	Jul	2			Tuttle, 1970

*One with twins.
**Young taken.

Lonchorhina orinocensis

Nothing is known about reproduction in *L. orinocensis.*

Macrophyllum macrophyllum

Felten (1956*a*) postulated that this species breeds in the dry season. The finding of pregnant animals during the late rainy season in French Guiana is unusual when compared with the cycles in other members of the subfamily. See Table 2.

Tonatia bidens

Although the records are scattered, I suspect that this species breeds more than once a year (Table 2). Records from Honduras suggest a bimodal pattern with subadult animals representing the earlier breeding cycle.

Tonatia brasiliense

Nothing is known about the reproductive pattern of this species.

Tonatia carrikeri

Nothing is known about the reproductive pattern of *T. carrikeri,* although Gardner (1976) reported two reproductively inactive females from Perú in July.

Tonatia minuta

This species also appears to fit the bimodal pattern, although additional data are obviously necessary to confirm this hypothesis. See Table 2.

Tonatia silvicola

Females appear to give birth during the early half of the rainy season; there is thus far no evidence of more than one young per year. See Table 2.

Tonatia venezuelae

No information is available on reproduction in this species.

Mimon bennettii

Nothing is known about the reproductive pattern of this bat.

Mimon cozumelae

This species (Table 2) apparently produces young at the beginning of the rainy season and the available data suggest only a single young per year.

Mimon crenulatum

Records from Campeche and Venezuela are from the dry season, whereas Peruvian records are from the rainy season. The single record from Costa Rica was taken in the period of transition between dry and rainy seasons. See Table 2.

Mimon koepckeae

No data are available on the reproductive pattern of this species.

Phyllostomus discolor

In addition to records listed in Table 3, Mares and Wilson (1971) found 80 per cent of 43 animals in 1968 and 51 per cent of 69 animals in 1970 to be reproductively active during February and March in Costa Rica. Tamsitt (1966) stated that in Colombia this species is acyclic or continuous in its breeding habits. Most of the above data suggest this pattern for other areas as well; however, the lack of reproductive activity as noted by Fleming *et al.* (1972) for Costa Rica seems unusual. Heithaus *et al.* (1975) suggested that *P. discolor* may be monestrous in Costa Rica.

Phyllostomus hastatus

Starrett and de la Torre (1964) reported that one of two July-taken males from Costa Rica had small, inguinal testes, and the other had large, scrotal testes; both were in an early stage of spermatogenesis with no mature sperm in the testes.

The available data could support either a monestrous (in Nicaragua, Panamá, and Trinidad) or polyestrous (in Colombia) pattern. In fact, this may be a species in which the reproductive strategy varies geographically. See Table 3.

Phyllostomus elongatus

Additional data from times of the year other than those listed in Table 3 are needed to elucidate the pattern of this species. The above data show that these animals breed during the middle part of the rainy season.

Phyllostomus latifolius

Nothing is known about the reproductive pattern of this species.

Phylloderma stenops

The only report of reproductive activity for this rare species is that of LaVal (1977), who reported a pregnant female in February (embryo length, 33 mm.) from Costa Rica. Gardner (1976) reported a reproductively inactive female from Perú that was collected in May.

TABLE 3.—*Reproductive data for the genera* Phyllostomus, Trachops, Chrotopterus, *and* Vampyrum.

Place	Date	Pregnant	Lactating	Inactive	Reference
		Phyllostomus discolor			
Guatemala	Mar			1	Jones, 1966
El Salvador	Feb	2		4	Felten, 1956*b*
	Jun	14		29	"
	Aug	11		7	"
	Sep	22		43	"
	Nov	14	X	70	"
	Dec	13			Burt and Stirton, 1961
Nicaragua	Mar	2			Jones, 1964*a*
Costa Rica	Jan			1	Fleming *et al.*, 1972
	Mar	1		11	"
	Apr			3	"
	May			6	"
	Jul			3	"
	Dec		11		"
	Jul		1		Tamsitt and Valdivieso, 1961
Trinidad	Feb	X			Goodwin and Greenhall, 1961
	Mar	X			"
	Jun	X			"
	Aug	X	X		"
	Sep		X		"
	Oct		X		"
Colombia	Feb*	2	2	1	Tamsitt and Valdivieso, 1964
	Mar		3		"
	May		1	1	"
	Sep		1		"
	Oct*	3			"
Venezuela	Jul	1	2	2	Smith and Genoways, 1974
Brazil	Jul		1		Walker, 1975
		Phyllostomus hastatus			
Nicaragua	Mar	2			Jones *et al.*, 1971*a*
	Jun		X		"
	Jul		X		"
	Aug		X		"
Panamá	Apr		1		Fleming *et al.*, 1972
	May		1		"
	Jun			2	"
	Oct			1	"
Trinidad	Mar	X			Goodwin and Greenhall, 1961
	Apr	X	X		"
	Jun		X		"
	Sep		X		"
	Nov			X	"
Venezuela	Aug		X		USNM
Colombia	Mar	1		1	Thomas, 1972
	May			1	"
	Aug			1	"

TABLE 3.—*Continued.*

Colombia	Sep	1	2	1	Thomas, 1972
	Oct	2		2	"
	Nov			1	"
	Dec		1	5	"
	Jul	1		7	Arata and Vaughn, 1970
Perú	Jun			1	Tuttle, 1970
	Aug	12		8	"
Brazil	Aug	1			Peracchi and Albuquerque, 1971
			Phyllostomus elongatus		
Colombia	Jun	1		1	Thomas, 1972
Perú	Jul	6		3	Tuttle, 1970
	Aug	1			"
			Trachops cirrhosus		
Veracruz	Apr			1	Hall and Dalquest, 1963
Campeche	Feb			1	Jones *et al.*, 1973
Oaxaca	Mar	1			Villa-R, 1966
Chiapas	Dec	1			"
	Mar	1			Carter *et al.*, 1966
Guatemala	Mar	4		3	Jones, 1966
	Apr	6		1	"
El Salvador	Feb	3			Burt and Stirton, 1961
Honduras	Aug		1		Valdez and LaVal, 1971
Nicaragua	May	4			Carter *et al.*, 1966
Costa Rica	Mar		1		"
	Aug		1	6	Armstrong, 1969
Panamá	Aug	1			Fleming *et al.*, 1972
	Oct			1	"
	Nov			1	"
Trinidad	Mar	2			Goodwin and Greenhall, 1961
Perú	Jul	1			Tuttle, 1970
			Chrotopterus auritus		
Veracruz	Apr	1			Hall and Dalquest, 1963
Yucatán	Apr	1		1	Jones *et al.*, 1973
	Jul		1	1	"
Argentina	Jul	1			Villa-R. and Villa-C., 1969
			Vampyrum spectrum		
Costa Rica	Aug			1	Gardner *et al.*, 1970
Trinidad	May		1		Goodwin and Greenhall, 1961

*Pregnant and lactating.

Trachops cirrhosus

Felten (1956*a*) stated that *T. cirrhosus* breeds in the dry season in El Salvador, and the data of Burt and Stirton (1961) support this. This species may have an extended season, or may be geographically variable with regard to the reproductive cycle. Additional data on other seasons from any of the above localities would be useful. See Table 3.

Chrotopterus auritus

Data are insufficient (Table 3) to allow speculation on the possible reproductive pattern of *C. auritus* except to note that this species produces young during the early part of the rainy season.

Vampyrum spectrum

The only information available other than that in Table 3 seems to be Greenhall's (1968) report on a birth in captivity. Again, other than the fact that *V. spectrum* produces young during the rainy season, little can be said about its reproductive cycle.

Glossophaga soricina

Cockrum (1955) believed *G. soricina* to be polyestrous, with the young born at any time of the year in México. Fleming (1973) felt that this species is seasonally polyestrous in Panamá, with bimodal birth peaks occurring in March-April and July-August. Tamsitt (1966) indicated that *G. soricina* is acyclic or continuously breeding in Colombia. Felten (1956*a*) noted that this species breeds throughout the year in El Salvador. Heithaus *et al.* (1975) suggested bimodal polyestry for Costa Rican animals.

This is one of the few species of phyllostomatid bats for which a fair amount of reproductive data are available from a variety of localities (Table 4). The data suggest *G. soricina* is polyestrous in most areas. Reproduction may be somewhat geographically variable inasmuch as data from Panamá indicate no pregnancies during the period August-December. Also, in some of the areas where these bats appear to breed continuously, there may well be a bimodal pattern for individuals but enough asynchrony within the population to allow for individuals in all stages of the reproductive cycle to be collected at any given time.

Rasweiler (1972) demonstrated this species to be polyestrous with approximately a 24-day cycle in captivity. He described the preimplantation development and histology of the oviduct in some detail.

Glossophaga alticola

I can find no reproductive information for *G. alticola* in the literature. The National Museum of Natural History has two specimens taken in Oaxaca in April, one of which was pregnant and the other inactive.

Glossophaga commissarisi

The data available (Table 4) are not inconsistent with a pattern of bimodal polyestry. Although the data are scanty, the information from Jalisco supports this hypothesis.

Glossophaga longirostris

This species appears to breed during the rainy season, but the data are inconclusive (Table 4).

TABLE 4.—*Reproductive data for the genus* Glossophaga.

Place	Date	Pregnant	Lactating	Inactive	Reference
		Glossophaga soricina			
Sonora	May	3			Cockrum, 1955
	Dec		1	2	Cockrum and Bradshaw, 1963
Chihuahua	Jul		2		Anderson, 1972
Durango	Jun			3	Jones, 1964*c*
San L. Potosí	Jun		X		Dalquest, 1953
Sinaloa	Jan	X			Jones *et al.*, 1972
	Mar	X			"
	May	X			"
	Aug	X			"
	Sep	X			"
	Oct	X			"
	Nov	X			"
	Dec	X			"
Nayarit	Jan	1			Cockrum, 1955
	Feb	5			"
	Aug	1			"
Jalisco	Feb	X			Watkins *et al.*, 1972
	Mar	X			"
	Apr	X			"
	Sep	X			"
	Oct	X			"
Tres Marias Is.	May	X			Merriam, 1898
Colima	Nov	1		2	Villa-R., 1966
	Dec	X			"
Querétaro	Jan			5	Schmidly and Martin, 1973
	Dec			6	"
Puebla	Jan	1		1	LaVal, 1972
Veracruz	Mar	X			Hall and Dalquest, 1963
	Apr	1		7	"
	Sep	4		5	"
	Nov		X		"
	Jun			2	Lackey, 1970
	Jul			1	"
Tabasco	May	X			Villa-R., 1966
	Jun	X*	X		"
	Jul	X	X		"
Yucatán	Feb	X**	X**		Jones *et al.*, 1973
	Apr	X**	X**		"
	Jul	X**	X**		"
	Apr		1	4	Birney *et al.*, 1974
	Aug		X		Pearse and Kellogg, 1938
Oaxaca	Mar	3		3	USNM
	Apr	4		6	"
	Sep	1			Cockrum, 1955
Chiapas	Feb	X			Villa-R., 1966
	Aug	X***			Barlow and Tamsitt, 1968
Guatemala	Mar	1			Jones, 1966
	Aug	2		5	"

TABLE 4.—*Continued.*

El Salvador	Jan	22	1	28	Felten, 1956*b*
	Feb	2		22	"
	Mar	2	4	5	"
	Apr		1	7	"
	Jun			17	"
	Jul	9		12	"
	Aug	17	3	5	"
	Sep	5		3	"
	Oct		3	3	"
	Nov	1	1	21	"
	Dec	3		3	"
	Sep	1			Burt and Stirton, 1961
	Nov		1		"
	Jul	7			Starrett and de la Torre, 1964
Honduras	Aug	1			"
Costa Rica	Jul	1			"
	Aug	1		1	"
	Jul			X	Tamsitt and Valdivieso, 1961
	Aug			X	"
Panamá	Jan	8		6	Fleming *et al.*, 1972
	Feb	22			"
	Mar	1	2		"
	Apr	1			"
	May	3			"
	Jun	3		1	"
	Jul	2		5	"
	Aug		3	5	"
	Sep			4	"
	Oct			4	"
	Nov			4	"
	Dec			4	"
	Feb	1			Bloedel, 1955
Jamaica	Jan	1		4	Goodwin, 1970
Trinidad	Jan	X	X		Goodwin and Greenhall, 1961
	Feb		X		"
	Mar		X		"
	Apr	X			"
	May	X			"
	Jun	X	X		"
	Dec	X			"
Venezuela	Aug	1			USNM
Colombia	Jan	2			Thomas, 1972
	Feb	8		2	"
	Mar		5	3	"
	Apr		4	5	"
	May			7	"
	Jun	1		2	"
	Jul	1		1	"
	Aug			1	"
	Sep		2	2	"
	Oct	1	6	5	"
	Nov			6	"

TABLE 4.—*Continued.*

Colombia	Dec	5	1	11	Thomas, 1972
	Jan	1		1	Tamsitt and Valdivieso, 1964
	Mar	1			"
	Apr	8		1	"
	Jun		1		"
	Jul		2		"
	Aug	1			"
	Sep		1	1	"
	Oct	2			"
	Nov	7		13	"
	Dec	3	1	1	"
	Jul	32		23	Arata and Vaughn, 1970
	Aug	8		13	"
French Guiana	Feb	X			Brosset and Dubost, 1967
	Mar	X			"
	Oct		X		"
Perú	Jun			2	Tuttle, 1970
	Jul	1		1	"
	Aug			1	"
Brazil	Nov	X			Hamlett, 1935
	Dec	X			"
	Jan	X	X		Peracchi and Albuquerque, 1971
Paraguay	Oct		1		USNM
		Glossophaga commissarisi			
Durango	Jul			1	Baker and Greer, 1962
Sinaloa	Jan	4			Jones *et al.*, 1972
	Jul	1		4	"
Jalisco	Feb	1			Watkins *et al.*, 1972
	Apr	2		1	"
	May			2	"
	Jul			3	"
	Sep	1		1	"
	Nov			2	"
	Dec			1	"
Guatemala	Feb	1			Jones, 1966
Nicaragua	Feb	1		3	Jones, 1964*a*
		Glossophaga longirostris			
Trinidad	Feb	X			Goodwin and Greenhall, 1961
	Mar	X			"
	Apr	X			"
	Aug	X			"
	Sep		X		"
	Jun		X		Goodwin, 1958
Venezuela	Jul		2		USNM
	Jul	8		6	Smith and Genoways, 1974

*Parturition.
**Pregnant or lactating.
***Twins.

Monophyllus redmani

Goodwin (1970) felt that the high percentage of pregnancies in his sample suggested a discrete breeding season for this species. Additional data from other times of the year are needed in order to verify his opinion. See Table 5.

Monophyllus plethodon

Schwartz and Jones (1967) reported pregnant females from Dominica in March and April, perhaps indicating a distinct breeding season for this species.

Leptonycteris nivalis

Davis (1966) reported that the breeding season is restricted to April, May, and June. Easterla (1972) felt that young probably are born in México, possibly in June, prior to the time bats arrive in the Big Bend area of Texas. Records from Veracruz (Table 5) indicate a second pregnancy of the year for this migratory species.

Leptonycteris sanborni

Cockrum and Ordway (1959) and Hayward and Cockrum (1971) have reported on reproduction in *L. sanborni* in Arizona. They found that pregnant females arrive in southern Arizona in early May and the young are born shortly thereafter. By August there are subadult females containing embryos 10 mm. in crown-rump length; however, all bats have left for México by the early part of October. They hypothesized another birth peak in México in early November. In January females have small embryos and in February they begin to move to the northern part of their range where the young will be born. Hayward and Cockrum (1971) suggested, as an alternative hypothesis, that delayed development as described for *Macrotus waterhousii* might be involved. See Table 5.

Leptonycteris curasoae

Smith and Genoways (1974) found a large colony of this species on Margarita Island, Venezuela, which in July was estimated to contain 4000 females nursing nearly full-grown young. In November, seven of 34 females examined were pregnant, and no juveniles were present. In addition, adult males with large (6 to 8 mm.) testes were present in November, whereas males had been absent in July. This appears to be the only record of reproduction for this species.

Lonchophylla hesperia

Nothing is known about the reproductive pattern of this species.

Lonchophylla mordax

Thomas (1972) collected a reproductively inactive female of this species in Colombia in January. I can find no other literature records relating to reproduction in *L. mordax*.

Lonchophylla concava

Although there are few reports giving reproductive condition (Table 5), these are from sufficiently distinct times of the year as to suggest the possibility of more than one birth peak per year.

Lonchophylla robusta

Apparently, reproductively active individuals of this species have not been recorded. The capture of inactive females in several months of the year (Table 5) suggests an asynchronous reproductive cycle.

Lonchophylla thomasi

No data are available concerning the reproductive pattern of this species.

Lionycteris spurrelli

The only published record of reproductive activity in *L. spurrelli* is that of Tuttle (1970), who reported a pregnant female taken in August in Perú.

Anoura geoffroyi

Alvarez and Ramirez-Pulido (1972) netted 12 males but no females at the mouth of a cave in Michoacán and suggested that this species may form sexually segregated colonies. The data of Goodwin and Greenhall (1961) from Trinidad support this notion for certain times of the year. They reported 20 males and 25 females in June; 29 males and one female in October; and 32 males and 56 females in November—all from the same caves. Their data also recommend a discrete breeding season occurring late in the rainy season, a rather unusual pattern for phyllostomatids. See Table 5.

Anoura caudifer

Pregnancy records (Table 5) from several months throughout the year suggest an asynchronous reproductive cycle. Additional data from other months of the year would be useful in discerning the true reproductive patterns.

Anoura cultrata

Gardner *et al.* (1970) reported a pregnant female from Costa Rica taken in August. They also collected males in February, May, and July and gave testicular measurements.

Anoura werckleae

Nothing is known about the reproductive pattern of this species.

Anoura brevirostrum

When Carter (1968) described *A. brevirostrum* from Perú, he included data from a lactating female and two inactive females taken in August.

TABLE 5.—*Reproductive data for the genera* Monophyllus, Leptonycteris, Lonchophylla, Anoura, Lichonycteris, Hylonycteris, Choeroniscus, *and* Choeronycteris.

Place	Date	Pregnant	Lactating	Inactive	Reference
			Monophyllus redmani		
Jamaica	Feb	11			Osburn, 1865
	Feb	6		4	McNab, 1976
	Jan	2			Goodwin, 1970
	Dec	15		4	"
Caicos Is.	Jan	1			Homan and Jones, 1975
Hispaniola	Feb	1			"
	Dec	2			"
Puerto Rico	Feb	1			"
			Leptonycteris nivalis		
Texas	Jun		3		Easterla, 1972
Coahuila	Jul			20	Baker, 1956
Tamaulipas	Aug	12			Alvarez, 1963
Veracruz	Sep	6			Hall and Dalquest, 1963
			Leptonycteris sanborni		
Arizona	Aug		X		Hoffmeister and Goodpaster, 1954
Sonora	Mar	1			Cockrum and Bradshaw, 1963
	Apr	11			"
Sinaloa	Feb	1			Jones *et al.*, 1972
	Jul	1			"
	Nov	1			"
Jalisco	Jan			1	Watkins *et al.*, 1972
	Jul			1	"
	Oct			12	"
Morelos	Sep	1		2	Villa-R., 1966
México	Nov	1		2	"
			Lonchophylla concava		
Costa Rica	Mar	1		1	Davis *et al.*, 1964
	Aug	1			Gardner *et al.*, 1970
			Lonchophylla robusta		
Costa Rica	Mar			4	Mares and Wilson, 1971
Colombia	Mar			1	Thomas, 1972
	Apr			2	"
	Jul			1	"
	Sep			2	"
Perú	Aug			1	Tuttle, 1970
			Anoura geoffroyi		
Zacatecas	Jun			2	Matson and Patten, 1975
Sinaloa	Jul			6	Jones *et al.*, 1972
Colima	Nov		5		Villa-R., 1966
	Dec			X	"
Guerrero	Sep			3	"
Oaxaca	Jul			3	Baker and Womochel, 1966
	Nov		X		Schaldach, 1966
	Dec		X		"

TABLE 5.—*Continued.*

Nicaragua	Jul	1		1	Jones *et al.*, 1971*a*
Costa Rica	Mar	2		1	Mares and Wilson, 1971
Trinidad	Nov	56			Goodwin and Greenhall, 1961
Perú	Jun	2		14	Tuttle, 1970
		Anoura caudifer			
Colombia	Mar			1	Thomas, 1972
	May	1			"
	Nov	1			"
	Jun	1			Tamsitt and Valdivieso, 1966*a*
French Guiana	Jan	X			Brosset and Dubost, 1967
	Feb	X			"
Brazil	Feb		1		Kuhlhorn, 1953
	Jan	2			Peracchi and Albuquerque, 1971
		Lichonycteris obscura			
Guatemala	Feb	2		1	Carter *et al.*, 1966
Costa Rica	Jan		1		Gardner *et al.*, 1970
	Mar	1			"
		Hylonycteris underwoodi			
Jalisco	Jul			2	Phillips and Jones, 1971
	Sep	2		2	"
Tabasco	May		1		Villa-R., 1966
Oaxaca	Nov		1	1	"
	Jul			1	Baker and Womochel, 1966
Guatemala	Mar		1		Carter *et al.*, 1966
Costa Rica	Jan	1			LaVal, 1977
	Feb	1			"
	Mar	1			"
	Apr	1			"
	Apr			X	Gardner *et al.*, 1970
	May			X	"
	Jun			X	"
	Jul			X	"
	Aug	1			LaVal, 1972
	Oct	1			"
	Nov	1			"
		Choeroniscus godmani			
Sinaloa	Jul	1			Jones, 1964*b*
Oaxaca	May		1		Schaldach, 1965
Honduras	Jul			1	Valdez and LaVal, 1971
Nicaragua	Mar	1			Jones *et al.*, 1971*a*
	Apr			1	"
Costa Rica	Mar	1			Mares and Wilson, 1971
		Choeroniscus intermedius			
Trinidad	Aug	1			Goodwin and Greenhall, 1961
Perú	Jul			2	Tuttle, 1970

TABLE 5.—*Continued.*

		Choeronycteris mexicana			
Arizona	Jun		1		Campbell, 1934
	Jun	X			Barbour and Davis, 1969
	Jun		X		Walker, 1975
	Jul		X		"
	Aug			35	Hoffmeister and Goodpaster, 1954
New Mexico	Jun	2	4		Mumford and Zimmerman, 1962
	Jun		4		Mumford *et al.*, 1964
Coahuila	Mar	1			Baker, 1956
	Jun		4		"
	Aug			X	"
	Sep			X	"
	Jun		1		Axtell, 1962
Tamaulipas	Aug		X		Alvarez, 1963
Sonora	Jul			4	Villa-R., 1966
Sinaloa	Feb	1			Jones *et al.*, 1972
Jalisco	Jan			1	Watkins *et al.*, 1972
	Feb			1	"
	Mar			3	"
	Sep	1			"
	Oct			1	"
Guerrero	Feb	2			Villa-R., 1966

Scleronycteris ega

Nothing has been recorded about reproduction in this species.

Lichonycteris degener

Nothing is known about the reproductive pattern of *L. degener.*

Lichonycteris obscura

This species is reproductively active during the dry season in Middle America (Table 5), but until data are available from other months of the year, little can be said of the overall pattern.

Hylonycteris underwoodi

The data from Costa Rica (Table 5) fit the bimodal pattern common to many other species. The second birth peak appears to be later in the rainy season than for some other species.

Platalina genovensium

Nothing is known about reproduction in this species.

Choeroniscus godmani

Choeroniscus godmani (Table 5) seems to fit the usual pattern of weaning young during the early part of the rainy season, but the lack of data from later in the year makes this conclusion tentative.

Choeroniscus minor

The only apparent report of reproductive activity for this species is that of Tamsitt *et al.* (1965), who reported a lactating female from Colombia in December. Tuttle (1970) collected a juvenile in August in Perú.

Choeroniscus intermedius

The data in Table 5 are too few to provide much insight into the reproductive pattern of this species.

Choeroniscus inca

Goodwin and Greenhall (1961) noted a pregnant female taken in February in Trinidad.

Choeroniscus periosus

The only record is that of Thomas (1972), who captured two lactating females in Colombia in January.

Choeronycteris mexicana

These animals are pregnant in the early spring in México (Table 5), and those that migrate to Arizona and New Mexico give birth in June. The possibility of a second period of parturition, as suggested for *Leptonycteris sanborni*, is supported by the pregnancy record in September from Jalisco.

Musonycteris harrisoni

There are no published records of reproductive activity for this species, but Alfred L. Gardner has kindly made available to me his unpublished field notes, which record one inactive and two pregnant females taken in September in Colima.

Carollia castanea

Pine (1972) suggested that *C. castanea* is polyestrous, but cautioned that in any one locality there may be one or two more or less fixed seasons. This caveat is supported by Fleming (1973), who suggested that in Panamá *C. castanea* is bimodally polyestrous, with birth peaks occuring in March-April and July-August. Thomas' (1972) data show that females are pregnant during the period September-November in Colombia corresponding to a period of reproductive quiescence in

Panamá (Fleming, 1973). These differences probably reflect contrasts in the seasonality of the rainfall patterns at the different localities. See Table 6.

Carollia subrufa

Felten (1956*a*) suggested that *C. subrufa* breeds both in the dry and wet seasons in El Salvador. Pine (1972) felt that they either breed throughout the year or that possibly there is a period of inactivity in the early winter months, at least in some areas. The data from El Salvador, the most extensive for any one area, would seem to fit a bimodal pattern (Table 6).

Carollia brevicauda

Pine (1972) suggested that *C. brevicauda* breeds from midwinter to early spring. Three records of females both pregnant and lactating (Table 6) attest to the presence of polyestry in Central America. This species may exhibit the bimodal type of breeding season seen for other Central American phyllostomatids; however, data from late in the year are needed for clarification of this pattern.

Carollia perspicillata

Fleming (1973) and Heithaus *et al.* (1975) have shown that *C. perspicillata* fits the model of bimodal polyestry, and the data summarized here support this contention (Table 6). Birth peaks occur in the periods February-May and June-August in Panamá, and somewhat earlier in other areas, depending on seasonal rainfall patterns in the various localities. Several of the data sets from various localities show a distinct drop in reproductive activity during the latter part of the rainy season, usually in the period from October to December, but earlier in Colombia. Fleming *et al.* (1972) correlated testis size with spermatogenic activity and found that males had large testes just preceding those times when females were likely to be sexually active.

Rhinophylla pumilio

The data in Table 6 are too few to warrant speculation on the reproductive pattern of *R. pumilio.*

Rhinophylla alethina

Although the sample (Table 6) is admittedly small, the timing of the reproductive events recorded here suggests an extended or possibly asynchronous breeding season. Data from August-November would be useful for clarifying the pattern.

Rhinophylla fischerae

The lack of reproductive activity for animals taken in July and August seems striking when compared against what is known for other phyllostomatids. See Table 6.

TABLE 6.—*Reproductive data for the genera* Carollia *and* Rhinophylla.

Place	Date	Pregnant	Lactating	Inactive	Reference
			Carollia castanea		
Honduras	May	3			Pine, 1972
	Jul	1			"
Nicaragua	Feb			X	Jones *et al.*, 1971 *a*
	Mar	X		X	"
	Apr			X	"
	Jun			X	"
	Jul	X		X	"
	Aug			X	"
Costa Rica	Feb	5			"
	Mar*	1			"
	Aug	1			"
Panamá	Jan	5			"
	Feb	5			"
	Mar	5			"
	Jan	1		2	Fleming *et al.*, 1972
	Mar	3		3	"
	Apr	1			"
	Jun		1		"
	Jul	1			"
	Aug	4		1	"
	Oct			1	"
	Nov			3	"
	Dec			2	"
Colombia	Jan	5	2	5	Thomas, 1972
	Feb			1	"
	Mar	1		2	"
	Apr	2	1	7	"
	May		2		"
	Jun			2	"
	Jul			1	"
	Sep	1		3	"
	Oct	2		3	"
	Nov	3		1	"
	Dec			2	"
French Guiana	Jan	X			Brosset and Dubost, 1967
	Feb	X			"
	Mar	X			"
Perú	Jul			2	Tuttle, 1970
	Aug			1	"
			Carollia subrufa		
Puebla	Jun			3	LaVal, 1972
Guerrero	May			3	Pine, 1972
	Dec	1			"
Oaxaca	May	2	3		Villa-R., 1966
Chiapas	Feb	6			"
	May		1		Pine, 1972
	Jul	2			"

TABLE 6.—*Continued.*

Chiapas	Aug	5		1	Pine, 1972
	Oct		1	1	"
	Nov			1	"
Guatemala	Feb	6		1	"
	Nov		2		"
El Salvador	Jan	43		7	Felten, 1956*c*
	Feb	1		1	"
	Mar	4		1	"
	Sep			5	"
	Oct	3		21	"
	Nov			12	"
	Dec			2	"
Honduras	Jul			1	Pine, 1972
Nicaragua	Jul	1			"
	Aug	1		1	"
Panamá	Jan	X			Walker, 1975
	Feb	X			"
	Mar	X			"
	Dec	X			"
		Carollia brevicauda			
San L. Potosí	Apr	2			Pine, 1972
	Aug			1	"
Veracruz	Feb			2	"
	Mar	19		1	"
	Dec			1	"
Tabasco	Apr		2		"
	May		1		"
Campeche	Jan			4	"
Quintana Roo	Apr	1			"
	Aug			1	"
Oaxaca	Feb			1	"
	Mar	2		1	"
Chiapas	Jun	1	2	3	"
	Jul	6	1	2	"
	Nov			2	"
Guatemala	Feb	4		4	"
	Mar	1			"
	Aug	1		2	Jones, 1966
	Feb	1			Rick, 1968
Honduras	Apr		3	2	Pine, 1972
	May*	3	1	1	"
	Jun	2	4		"
Nicaragua	Jul*	1			"
Costa Rica	Mar	1	1	1	"
	Apr*	2			"
Panamá	Jan	1			"
	Feb	10	1		"
	Mar	9			"
Ecuador	Mar	1			"
Perú	Aug			3	"
	Oct	2			"

TABLE 6.—*Continued.*

		Carollia perspicillata			
Puebla	Jan			4	LaVal, 1972
Veracruz	May	3			Villa-R., 1966
	Jun	10		1	Lackey, 1970
	Jul	1		1	"
Campeche	May	2			Jones *et al.*, 1973
	Jul			1	Pine, 1972
Quintana Roo	Jul	4			"
	Jul	5			Jones *et al.*, 1973
	Aug	1			"
Oaxaca	Apr	X			Hahn, 1907
Chiapas	Aug		1		Pine, 1972
Guatemala	Mar	1			"
	Mar	3		1	Jones, 1966
El Salvador	Mar	1			Burt and Stirton, 1961
	Apr		1	2	Felten, 1956*c*
	Oct			4	"
	Nov			17	"
	Dec			4	"
	Mar	1			Pine, 1972
Honduras	May	2	6	3	"
	Jun	1			"
	Jul	2	1		"
Nicaragua	Feb	8		3	"
	Apr	1			"
	May		1	3	"
	Jun	2		1	"
	Jul	2			"
	Aug	3			"
Costa Rica	Feb	1	5		"
	Mar	6	1	1	"
	Apr	2	1	2	"
	Jul		4	1	"
	Aug	1	1		"
	Jan	1		3	Fleming *et al.*, 1972
	Feb	5		5	"
	Mar	17		3	"
	Apr	1	10	3	"
	May		12	7	"
	Jun	3			"
	Jul	4		7	"
	Aug	1	4	6	"
	Sep			1	"
	Oct			2	"
	Nov			3	"
Panamá	Jan	1		14	"
	Feb	15		4	"
	Mar	28	1	8	"
	Apr	10	16	13	"
	May	5	6	4	"
	Jun*	6	1		"
	Jul	10	3	4	"

TABLE 6.—*Continued.*

Panamá	Aug	20	10	15	Fleming *et al.*, 1972
	Sep	2	6	18	"
	Oct		4	27	"
	Nov			9	"
	Dec	1		19	"
	Mar	1			Enders, 1935
	May			2	Hall and Jackson, 1953
	Feb	10		1	Pine, 1972
	Mar	1		2	"
	Apr	1	3	4	"
	Jun	2			"
Trinidad	Jun	X			Hahn, 1907
	Feb	X			Goodwin and Greenhall, 1961
	Mar	X			"
	Apr	X			"
	May	X	X		"
	Jun	X	X		"
	Jul	X	X		"
	Aug	X	X		"
	Sep	X	X		"
	Oct	X	X		"
Venezuela	Jun	7	1	8	Pirlot, 1963
French Guiana	Jul	X			Brosset and Dubost, 1967
	Aug	X			"
	Sep	X			"
	Oct	X			"
	Nov	X			"
Colombia	Jul	1			Arata and Vaughn, 1970
	Aug	34	16	50	"
	Sep	20			"
	Jan	1		1	Tamsitt and Valdivieso, 1964
	Mar	1		3	"
	Apr		1	2	"
	Oct		1	1	"
	Jan	9	3	4	Thomas, 1972
	Feb		1	1	"
	Mar	2	2	5	"
	Apr	1	1	4	"
	May*	3	2	2	"
	Jun	3	4	8	"
	Jul	2		5	"
	Aug	2		4	"
	Sep		1	5	"
	Oct	2		5	"
	Nov	1	1	6	"
	Dec	4		9	"
	Jun	2			Pine, 1972
	Jul	4		3	"
Ecuador	Mar	2			"
	Jul			1	"
Bolivia	Aug	1			"
	Sep	1		1	"

TABLE 6.—*Continued.*

Perú	Aug	2		11	Pine, 1972
	Jun			12	Tuttle, 1970
	Jul			7	"
	Aug	3		12	"
Brazil	Jan	X			Peracchi and Albuquerque, 1971
	Sep	X	X		"
	Oct	X			"
			Rhinophylla pumilio		
Venezuela	Dec	1	1	1	Walker, 1975
Perú	Jun			4	Tuttle, 1970
	Jul			5	"
Colombia	Jan			1	Thomas, 1972
	Apr		1		"
	May	1			"
	Jun		1	2	"
	Jul	1			"
	Dec		1		"
			Rhinophylla fischerae		
Perú	Jul			8	Tuttle, 1970
	Aug			1	"
	Aug			7	Carter, 1966

*Pregnant and lactating.

Sturnira lilium

Jones (1966) and Jones *et al.* (1973) suggested that *S. lilium* probably breeds hrough the year. Actually, the data presented in Table 7 support the model of imodal polyestry as suggested by Fleming *et al.* (1972). Support for this model s provided by the data from Costa Rica and Colombia. In Costa Rica, birth peaks ccur in February-March and in June-July (Heithaus *et al.*, 1975); in Colombia, here appears to be much less synchrony in the cycle.

Sturnira thomasi

Genoways and Jones (1975) reported two lactating females, a subadult, and juvenile from Guadeloupe in July. This seems to be the only record of reproduction available for this species.

Sturnira tildae

The records listed in Table 7 provide no basis for speculation on the reproductive habits of *S. tildae*.

Sturnira magna

Tuttle (1970) provided testicular measurements on three Peruvian males aken in July. Gardner (1976) took one inactive and one lactating female in May and another inactive female in July in Perú.

TABLE 7.—*Reproductive data for the genus* Sturnira.

Place	Date	Pregnant	Lactating	Inactive	Reference
			Sturnira lilium		
Sonora	Sep	1			Findley and Jones, 1965
Sinaloa	Apr	1			Cockrum and Bradshaw, 1963
	May	1			Jones *et al.*, 1972
	Jun	1	2		"
	Aug	2			"
Durango	Jun		3	1	Jones, 1964*c*
	Jul	1	1		Baker and Greer, 1962
Jalisco	Jan	X			Watkins *et al.*, 1972
	Mar	X			"
	Apr	X	X		"
	Jun	X	X		"
	Jul	X	X		"
	Aug		X		"
	Sep	X	X		"
	Oct		X		"
	Nov			2	"
Querétaro	Jan	1			Spenrath and LaVal, 1970
Puebla	Jan			4	LaVal, 1972
Veracruz	Jun			21	Lackey, 1970
	Jul	4		1	"
Campeche	Jan	5			Jones *et al.*, 1973
	Jul	1			"
Quintana Roo	Aug	1			"
	Apr	2			Birney *et al.*, 1974
Oaxaca	Apr	1		1	USNM
	Jul			6	Baker and Womochel, 1966
	Dec		X		Schaldach, 1966
Chiapas	May		4		Villa-R., 1966
	Jun		1		"
Guatemala	Feb	X		X	Jones, 1966
	Mar	X		X	"
	Jun	X		X	"
	Jul	X		X	"
	Aug	X		X	"
	May	1*	2		Rick, 1968
El Salvador	Jul		1		Starrett and de la Torre, 1964
Nicaragua	Jul	1	1		"
Costa Rica	Jan	3	1		Fleming *et al.*, 1972
	Feb	1	5	2	"
	Mar		7	5	"
	Apr		5	5	"
	May	4	1	3	"
	Jun	1		2	"
	Jul		3	2	"
	Aug		2	6	"
	Dec	3			"

TABLE 7.—*Continued.*

ominica	Mar	7			Jones and Phillips, 1976
	Apr	4			"
	Aug		1	4	"
Iartinique	Mar	11		2	"
. Lucia	Aug	2	1		"
. Vincent	Aug			1	"
olombia	Jul	9	3	4	Arata and Vaughn, 1970
	Aug	1	1	13	"
	Jan	3		3	Thomas, 1972
	Feb		3		"
	Mar	3		2	"
	Apr	1	1	2	"
	May		2	3	"
	Jun		1	3	"
	Jul		2	2	"
	Aug		2	1	"
	Sep		4	4	"
	Oct	4	3	2	"
	Nov	7			"
	Dec	4	1	3	"
rench Guiana	Jun	X			Brosset and Dubost, 1967
	Jul	X			"
	Aug	X			"
erú	Jun			8	Tuttle, 1970
	Jul	1		8	"
razil	Jul	1			USNM
	Aug	X			Peracchi and Albuquerque, 1971
			Sturnira tildae		
rinidad	Mar	1			Goodwin and Greenhall, 1961
erú	Jul			2	Tuttle, 1970
razil	Jun			1	USNM
	Jul	1		1	"
			Sturnira mordax		
osta Rica	Feb	2		1	Gardner *et al.*, 1970
	May		1		"
	May		1		LaVal, 1977
	Aug	1			Armstrong, 1969
			Sturnira ludovici		
alisco	Apr	7		5	Watkins *et al.*, 1972
	May		2		"
	Jul	1		1	"
	Aug		1	13	"
	Sep			1	"
	Nov			5	"
	Dec			1	"
	Nov	5		5	Jones and Phillips, 1964
	Sep			12	Villa-R., 1966
olima	Nov			2	"
uerétaro	Jan			11	Schmidly and Martin, 1973
uebla	Jan			1	LaVal, 1972

TABLE 7.—*Continued.*

Oaxaca	Jul			4	Baker and Womochel, 1966
Chiapas	Aug	1			Villa-R., 1966
Costa Rica	Jul			1	Starrett and de la Torre, 1964
Colombia	Jan			2	Thomas, 1972
	Feb	1			"
	Mar	4		1	"
	Apr	4		1	"
	May*	12	9	6	"
	Jun		1		"
	Jul		1	1	"
	Aug	7	1		"
	Sep		1		"
	Oct	4		2	"
	Nov	2			"
	Dec	4		5	"
Perú	Jun			1	Tuttle, 1970
			Sturnira erythromos		
Colombia	May			2	Thomas, 1972
	Dec	2			"
Perú	Jun			1	Gardner and O'Neill, 1969
	Aug	10		5	"

*Pregnant and lactating.

Sturnira mordax

The presence of pregnant females both in February and in August suggests polyestry for *S. mordax* (Table 7).

Sturnira bidens

The only published record of reproductive activity for this species is that of Gardner and O'Neill (1969), who reported three pregnant females and one inactive female from Perú in August.

Sturnira nana

Nothing is known about the reproductive pattern of *S. nana.*

Sturnira aratathomasi

Thomas and McMurray (1974) reported pregnant females from Colombia in February and August. These pregnancy dates are not inconsistent with those for other, more common species of the genus *Sturnira* and may represent the familiar bimodal pattern.

Sturnira ludovici

Sturnira ludovici appears to me to be another species with a bimodal polyestrous pattern (Table 7). The data from Colombia are strikingly similar to those

resented for *S. lilium*. Starrett and de la Torre (1964) presented data on testis ze and spermatogenesis from two males from Costa Rica.

turnira erythromos

Speculation on the reproductive pattern of *S. erythromos* must await further ata. See Table 7.

Iroderma bilobatum

Davis (1968) suggested that *U. bilobatum* seemingly lacks a restricted breed-ng season based on his examination of 58 females from a variety of localities rom Oaxaca to Venezuela. Of these, three were pregnant in January, five in ebruary, and one each in May, July, and November (Table 8). Fleming (1973) ointed out that in Panamá this species is another example of bimodal polyestry nd much of the above data are in agreement with that conclusion. Again, the in-ormation from Colombia shows that the timing of reproductive peaks is quite ifferent from that in Panamá, with the second major pregnancy period in Colom-ia occurring in the late rainy season. Fleming *et al.* (1972) presented data on estis size and spermatogenesis, showing that males undergo active spermato-enesis in a bimodal fashion also.

Iroderma magnirostrum

Although the data are few and from widely scattered localities (Table 8), I uspect *U. magnirostrum* will prove to have a polyestrous pattern like that of its ongener, *U. bilobatum*.

/ampyrops infuscus

The only report of reproduction in this species appears to be that of Marinkelle 970), who collected one pregnant female and three lactating females in olombia in March.

/ampyrops vittatus

Pregnancies occur in the early part of the rainy season in Costa Rica (Table 8), ut data from other seasons are lacking.

/ampyrops dorsalis

The Colombian data (Table 8) show *V. dorsalis* to fit the pattern of bimodal olyestry common to several other species of Colombian phyllostomatids.

/ampyrops aurarius

No data are available about reproduction in this species.

/ampyrops nigellus

Nothing is known about the reproductive pattern of *V. nigellus*.

TABLE 8.—*Reproductive data for the genera* Uroderma, Vampyrops, *and* Vampyrodes.

Place	Date	Pregnant	Lactating	Inactive	Reference
		Uroderma bilobatum			
Veracruz	Jun			1	Lackey, 1970
	Jul			1	"
Chiapas	May		X		Villa-R., 1966
	Aug			1	"
Guatemala	Feb	1			Jones, 1966
El Salvador	Jan	4			Felten, 1956*a*
	Jan	3			Burt and Stirton, 1961
	May	1			"
Honduras	Jul	72	1	12	Baker *et al.*, 1975
Nicaragua	Feb	4			Jones, 1964*a*
	Aug		2		Davis *et al.*, 1964
Panamá	Jan	8			Davis, 1968
	Mar		X		Bloedel, 1955
	Jan	16		1	Fleming *et al.*, 1972
	Feb	7			"
	Mar	1	11	3	"
	Feb	X	X		Walker, 1975
	Mar	X	X		"
	Apr	X	X		"
	Apr	10	15		Fleming *et al.*, 1972
	May	12	3	2	"
	Jun	4		1	"
	Jul	4	9	6	"
	Aug		1	2	"
	Sep			24	"
	Oct			10	"
	Nov			1	"
	Dec	2			"
Trinidad	Feb	1		1	Goodwin and Greenhall, 1961
	May	3	3	2	"
Colombia	Jan	1			Tamsitt and Valdivieso, 1964
	Mar		1	1	"
	Jul	3			"
	Sep	1			"
	Nov	1		1	"
	Nov			1	Thomas, 1972
Perú	Aug	1		2	Tuttle, 1970
Brazil	Jul	3			USNM
		Uroderma magnirostrum			
El Salvador	Jun	1			Davis, 1968
Nicaragua	Mar	1			Jones *et al.*, 1971*a*
	Jul	1			Davis, 1968
Bolivia	Sep	10		7	"
Brazil	Jun	1			USNM

TABLE 8.—*Continued.*

		Vampyrops vittatus			
Costa Rica	Mar	X			LaVal, 1977
	Apr	2			Davis *et al.*, 1964
	Jan			1	Gardner *et al.*, 1970
	May		4		"
	Jun	1	1	1	"
	Jul		1		"
	Jul			1	Tamsitt and Valdivieso, 1961
Colombia	May	1		3	Thomas, 1972
	Oct	1			"
	Dec			1	"
Perú	Jun			4	Tuttle, 1970
	Aug			9	"
		Vampyrops dorsalis			
Colombia	Aug		3	18	Arata and Vaughn, 1970
	Jan	8		8	Thomas, 1972
	Feb	2	5		"
	Mar*	12	3		"
	Apr	4		2	"
	May	5	2	10	"
	Jun	2	5	8	"
	Jul*	2	2	8	"
	Aug			9	"
	Sep			7	"
	Oct		1	4	"
	Nov	3			"
	Dec	7		2	"
		Vampyrops brachycephalis			
Venezuela	Feb	1			Rouk and Carter, 1972
	Jul			1	"
	Oct		1	3	"
Colombia	Jul			1	"
Perú	Aug	2		5	"
		Vampyrops helleri			
Tabasco	May		1		Villa-R., 1966
Chiapas	May		1		"
	Jul	1			Davis *et al.*, 1964
Guatemala	May		1		Rick, 1968
El Salvador	Jun	2			LaVal, 1969
Honduras	Aug	1			"
Nicaragua	Mar	X			Jones *et al.*, 1971*a*
	Apr	X			"
	Jun	X			"
	Jul	X			"
	Aug	X			"
Costa Rica	Mar	1			Mares and Wilson, 1971
	Aug			1	Starrett and de la Torre, 1964
Panamá	Jan	1			Fleming *et al.*, 1972

TABLE 8.—*Continued.*

Panamá	Apr	1	1		Fleming *et al.*, 1972
	Jul	1			"
	Sep		1		"
	Oct			1	"
	Nov			1	"
	Dec	1			"
Colombia	Aug	2	2	9	Arata and Vaughn, 1970
	Jan*	3	13	6	Thomas, 1972
	Feb	2		7	"
	Mar	7		3	"
	Apr*	3	5	8	"
	May	1	9	5	"
	Jun*	2		7	"
	Jul			6	"
	Aug			6	"
	Sep			14	"
	Oct	7		3	"
	Nov	5		1	"
	Dec	5	2		"
French Guiana	Aug	X			"
	Sep	X			"
Perú	Jul	1			Tuttle, 1970
	Aug	2		2	"
			Vampyrodes caraccioli		
Veracruz	Apr			1	Villa-R., 1966
Chiapas	Jun	1			Jones, 1964*b*
	Jul	1			Davis *et al.*, 1964
Honduras	May		1		"
	Aug	14		2	Valdez and LaVal, 1971
Nicaragua	Jul	2			Jones *et al.*, 1971*a*
	Aug	1		1	"
Panamá	Jan	2			Fleming *et al.*, 1972
	Apr			1	"
Tobago	Sep			1	Goodwin and Greenhall, 1961
Colombia	Jan	4	2	1	Thomas, 1972
	Feb	1	1		"
	Mar*	1	2		"
	Apr	1	1		"
	May		1		"
	Jun		6	3	"
	Jul	1		7	"
	Aug		1	5	Thomas, 1972
	Sep			2	"
	Oct	2		1	"
	Nov	4			"
Perú	Jun			2	Tuttle, 1970
	Jul	1			"

*Pregnant and lactating.

Vampyrops brachycephalis

It is fruitless to speculate on the reproductive pattern of *V. brachycephalis* on the basis of the few known records (Table 8).

Vampyrops helleri

Jones *et al.* (1971*a*) suggested that Nicaraguan *V. helleri* probably breed throughout much of the year. Fleming *et al.* (1972) thought that this species might be bimodally polyestrous based on their evidence from Panamá. Thomas' (1972) work in Colombia, by far the most extensive, indicated a single period of nonpregnancies from July through September. This is also suggestive of a bimodal polyestrous pattern. See Table 8.

Vampyrops lineatus

Peracchi and Albuquerque (1971) reported pregnant females in January, March, and December in Brazil.

Vampyrops recifinus

Nothing is known about the reproductive pattern of *V. recifinus.*

Vampyrodes caraccioli

The data from Colombia (Table 8) suggest the familiar pattern of two sequential breeding periods followed by a quiescent period, as indicated here by fewer pregnancies during the July-September period.

Vampyressa pusilla

Although the data are not complete (Table 9), they suggest a pattern of bimodal polyestry. Panamanian females have been recorded as pregnant and lactating during the early part of the rainy season, whereas records from Colombia indicate the mid-rainy season break seen in other species in this area.

Vampyressa melissa

Nothing is known about the reproductive pattern of this species, although Gardner (1976) reported three reproductively inactive females from Perú in May.

Vampyressa nymphaea

Colombian samples (Table 9) are substantial, and indicate the familiar pattern of two periods of activity followed by a quiescent period. The time of inactivity seems to be slightly later in *V. nymphaea* than in other species.

TABLE 9.—*Reproductive data for the genera* Vampyressa, Chiroderma, *and* Ectophylla.

Place	Date	Pregnant	Lactating	Inactive	Reference
		Vampyressa pusilla			
Campeche	Feb	1			Jones *et al.*, 1973
Chiapas	Jul	1			Davis *et al.*, 1964
Guatemala	Jul	1			Rick, 1968
Honduras	Aug	1			Valdez and LaVal, 1971
Nicaragua	Mar	4			Jones *et al.*, 1971*a*
	Jul	1			Starrett and de la Torre, 1964
Costa Rica	Feb	2			Mares and Wilson, 1971
	Mar			1	"
	Jul		1		Armstrong, 1969
	Aug			1	"
Panamá	Jan	1			Fleming *et al.*, 1972
	Mar		1		"
	Apr	1	2		"
	Apr		1		Hall and Jackson, 1953
Colombia	Mar	1			Thomas, 1972
	Apr	1		1	"
	May	2		2	"
	Jul		1	1	"
	Aug	1		1	"
	Nov	1		1	"
	Aug	1	3		Arata and Vaughn, 1970
		Vampyressa nymphaea			
Nicaragua	Feb	1			Jones *et al.*, 1971*a*
Costa Rica	Apr	2			Gardner *et al.*, 1970
Panamá	May			1	Hall and Jackson, 1953
Colombia	Jan	29	1	2	Thomas, 1972
	Feb	4	8		"
	Mar*	9	25	1	"
	Apr*	8	3	2	"
	May	4	1	2	"
	Jun	6	5	4	"
	Jul*	15	40	13	"
	Aug*	17	13	4	"
	Sep			2	"
	Oct	1			"
	Nov	6			"
	Dec	12		1	"
		Chiroderma villosum			
Chiapas	May		1		Davis *et al.*, 1964
	Jul	3		2	"
	Dec	2		3	"
Nicaragua	Mar	4		1	Jones *et al.*, 1971*a*
	Jul	4			"
Panamá	Mar		1		Fleming *et al.*, 1972
	Apr	1	3		"

TABLE 9.—*Continued.*

Trinidad	Aug	1			Goodwin and Greenhall, 1961
	Sep	1			"
Colombia	Jan	1			Thomas, 1972
Perú	Aug			1	Tuttle, 1970
			Chiroderma salvini		
Chihuahua	Jul			2	Anderson, 1972
Sinaloa	Jan	1			Jones *et al.*, 1972
Jalisco	Feb	2			Watkins *et al.*, 1972
Colima	Sep			2	Villa-R., 1966
Honduras	Jul	1			Carter *et al.*, 1966
	Jul	1	1		LaVal, 1969
	Aug	1	1		"
Colombia	Jan	2		1	Thomas, 1972
	Mar*	1	2		"
	Apr*	1	1		"
	May	1			"
	Jun	2		1	"
	Jul		3	3	"
	Oct	1			"
	Nov			1	"
	Dec	3			"
			Chiroderma trinitatum		
Panamá	Feb	2			Fleming *et al.*, 1972
	May	1	1		"
	Sep		1		"
Trinidad	Mar	1			Goodwin and Greenhall, 1961
Colombia	Jul	1			Thomas, 1972
Perú	Jul			1	Tuttle, 1970
Brazil	Jun	1			USNM
	Jul	1			"
			Ectophylla macconnelli		
Colombia	Jan	1		1	Thomas, 1972
Perú	Aug	1			Tuttle, 1970

*Pregnant and lactating.

Vampyressa brocki

The only published record of reproductive activity in *V. brocki* is that of Baker *et al.* (1972), who reported one lactating and two pregnant females from Colombia that were taken in June and July.

Vampyressa bidens

Davis (1975) reported two of 14 females pregnant in December in Perú. This appears to be the only published record of reproductive activity for this species.

Chiroderma doriae

Nothing is known about the reproductive pattern of *C. doriae*.

Chiroderma improvisum

No information is available on reproduction in this species.

Chiroderma villosum

Although the records listed in Table 9 are diverse, they are too insufficient to have much predictive value. Davis *et al.* (1964) suggested that this species breeds throughout the year on the basis of their specimens from Chiapas. These data also fit the pattern of bimodal polyestry fairly well, but unfortunately there are no records from late in the rainy season.

Chiroderma salvini

This species is obviously polyestrous in Colombia, and when further data are available, may prove to have a bimodal pattern similar to that found in other species of Colombian phyllostomatids. See Table 9.

Chiroderma trinitatum

Analysis of the reproductive pattern of *C. trinitatum* must await further data (see Table 9). Pregnancy records are all from early in the rainy season and late the dry season.

Ectophylla alba

Gardner *et al.* (1970) reported a pregnant female in March and a lactating female in April from Costa Rica. LaVal (1977) recorded pregnant females in February and August in Costa Rica. He also found one lactating female in March, and postlactating animals in September and November.

Ectophylla macconnelli

In addition to the records shown in Table 9, A. L. Gardner (personal communication) collected a lactating female in May and a pregnant female in July from Perú.

Artibeus cinereus

The records for Colombia (Table 10) are in accord with the pattern of bimodal polyestry as suggested for several other Colombian species. Larger samples would help to define pregnancy and birth peaks.

Artibeus glaucus

I can find no published records of reproductive activity for *A. glaucus*, but there is a USNM specimen from Venezuela recorded as lactating in August.

Alfred L. Gardner (personal communication) has collected inactive females in Perú in April and May.

Artibeus watsoni

In addition to the data in Table 10, Davis (1970) recorded pregnant females from the months of February, March, April, July, August, and November from throughout the range of *A. watsoni* (southern México-Panamá). Fleming (1973) suggested that this species provides an example of bimodal polyestry in Panamá. The few data from Nicaragua also fit this pattern.

Artibeus phaeotis

Davis (1970) reported pregnant females in January, February, April, June, July, and August, and inactive females from all other months except November from throughout the range of *A. phaeotis* (Sinaloa to Panamá). Fleming (1973) reported *A. phaeotis* as seasonally polyestrous in Panamá, and the data from México seem to support this. Heithaus *et al.* (1975) suggested bimodal polyestry as the pattern in Costa Rica as well. See Table 10.

Artibeus toltecus

Davis (1969) recorded pregnant females in each month from January through August in México and Central America (Table 10). Davis *et al.* (1964) suggested an extended breeding season for *A. toltecus* and mentioned the possibility of their having two births per year. The data support this assertion.

Artibeus aztecus

Davis (1969) mentioned three pregnant and two inactive females taken in March and April in either southern México, Guatemala, or Honduras. The data in Table 10 from northern México suggest that these bats are pregnant during the summer months. Additional information from other times of the year would be useful in clarifying the reproductive cycle.

Artibeus hirsutus

Anderson (1960) suggested that *A. hirsutus* lacks a restricted breeding season. In support of this claim, Findley and Jones (1965) found in Sonora that two of the lactating females had placental scars while a third had sperm in the uterus. They also found three males with sperm and eight without in the same sample. As they pointed out, spermatogenesis, copulation, lactation, and parturition all were occurring at the same time. See Table 10.

Artibeus inopinatus

Reproductive information for *A. inopinatus* seems to be lacking, but in the description of the species, Davis and Carter (1964) mentioned five young animals taken in August in Honduras. Two of the young bats appeared to be about one

TABLE 10.—*Reproductive data for the genus* Artibeus.

Place	Date	Pregnant	Lactating	Inactive	Reference
			Artibeus cinereus		
Trinidad	Sep			X	Goodwin and Greenhall, 1961
	Oct			X	"
Venezuela	Jul	1	2		USNM
	Aug		1		"
Colombia	Jan	9	1*	2	Thomas, 1972
	Feb			1	"
	Mar		1		"
	Apr	2		3	"
	May	1	1	1	"
	Jul	1		2	"
	Aug	1	1	2	"
	Sep		1	4	"
	Oct	1		2	"
	Nov	2		2	"
	Dec	3		6	"
	Aug	1	5	9	Arata and Vaughn, 1970
Perú	Jul			1	Tuttle, 1970
Brazil	Jun	1			USNM
	Jul	1		4	"
			Artibeus watsoni		
Guatemala	Mar	1			Jones, 1966
Nicaragua	Feb	1		1	Jones *et al.*, 1971 *a*
	Aug	1		1	"
Panamá	Jan	1			Fleming *et al.*, 1972
	Feb	1			"
	Apr		2		"
	Jun	1			"
	Aug		2		"
	Dec	1		3	"
			Artibeus phaeotis		
Sinaloa	Jul	4			Jones *et al.*, 1972
	Oct			1	"
Jalisco	Jan	6			Watkins *et al.*, 1972
	Apr	1			"
	Jun	11			"
	Aug		1		"
Campeche	Jan	2			Jones *et al.*, 1973
	Feb	7			"
	Mar	1	1		"
Quintana Roo	Aug	2			"
	Apr		1		Birney *et al.*, 1974
So. Mexico	Jan			X	Villa-R., 1966
	Feb			X	"
	Apr	X			"
	Jun		X		"
	Aug	X			"

TABLE 10.—*Continued.*

So. Mexico	Sep	X			Villa-R., 1966
	Oct		X		"
Guatemala	Mar	1			Jones, 1966
	Apr	1			Murie, 1935
	May*	2			Rick, 1968
Panamá	Jan	1			Fleming *et al.*, 1972
	Feb	9		1	"
	Mar	2			"
	Apr	1		1	"
	Jun	1			"
	Aug	1		2	"
			Artibeus toltecus		
Tamaulipas	Jul	1			de la Torre, 1954
Sinaloa	Jan	X			Jones *et al.*, 1972
	May	X	X		"
	Oct	X			"
Jalisco	Jan	9	X		Watkins *et al.*, 1972
	Feb	7			"
	Mar	1			"
	Apr	5			"
	Jun	10	X		"
	Jul	1	X		"
	Aug		X		"
	Sep		X		"
Puebla	Jan	2		1	LaVal, 1972
Chiapas	May		3		Davis *et al.*, 1964
	Jun	4			"
	Aug	1			"
El Salvador	Jan	7			Burt and Stirton, 1961
Nicaragua	Apr	8			Jones *et al.*, 1971*a*
	Jun	1			"
			Artibeus aztecus		
Tamaulipas	Jul	1			Alvarez, 1963
	Aug	1			"
Durango	Jul	1			Baker and Greer, 1962
Sinaloa	Jul	18		5	Jones *et al.*, 1972
Querétaro	Jan			5	Schmidly and Martin, 1973
México	Sep		1		Villa-R., 1966
			Artibeus hirsutus		
Chihuahua	Jul	1			Anderson, 1972
Sonora	Apr	1			Cockrum and Bradshaw, 1963
	May	2			Cockrum, 1955
	May	8			Anderson, 1960
	Sep	15	6	4	Findley and Jones, 1965
Sinaloa	Jun		1	1	Jones *et al.*, 1972
	Jul			1	"
	Aug	5		2	"
	Dec			1	"
Jalisco	Feb	2		2	Watkins *et al.*, 1972
	Jun	5	X	15	"
	Aug	1	X	1	"

TABLE 10.—*Continued.*

Guerrero	May	2		11	Anderson, 1960
			Artibeus jamaicensis		
Tamaulipas	Mar	6			de la Torre, 1954
	May	1			Alvarez, 1963
San L. Potosí	Jun	3			Cockrum, 1955
Sinaloa	Jan	X			Jones *et al.*, 1972
	Feb	X			"
	Apr	X			"
	May	X			"
	Jun	X			"
	Jul	X			"
	Sep		X		"
	Nov		X		"
	Jun	3			Anderson, 1960
Nayarit	Apr	X			Villa-R., 1966
Jalisco	Jul			1	Anderson, 1960
	Jan	X			Watkins *et al.*, 1972
	Feb	X			"
	Mar	X			"
	Apr	X	X		"
	May	X	X		"
	Jun	X			"
	Jul		X		"
	Oct		X		"
Guerrero	Feb	1			Villa-R., 1966
Morelos	Jul	4			Novick, 1960
Querétaro	Jan			13	Schmidly and Martin, 1973
Puebla	Jan			2	LaVal, 1972
Veracruz	Feb	X			Hall and Dalquest, 1963
	Jul	6		3	Webb *et al.*, 1967
	Aug**	1			Barlow and Tamsitt, 1968
Yucatan Pen.	Apr	1			Bowles, 1973
	May			2	"
	Feb	1	1		Jones *et al.*, 1973
	Apr	1			"
	May		1		"
	Jul	X	X	X	"
	Aug		X		"
	Mar	4		X	Birney *et al.*, 1974
	Apr	3		X	"
Isla Cozumel	Aug	5		6	Jones and Lawlor, 1965
Oaxaca	Apr			1	USNM
Guatemala	Jan			6	Jones, 1966
	Feb	4		1	"
	Mar	1		2	"
	Aug			4	"
	May	1			Rick, 1968
El Salvador	Dec	16			Burt and Stirton, 1961
Costa Rica	Jan	2		2	Fleming *et al.*, 1972
	Feb	16	5	14	"
	Mar	1	20	2	"

TABLE 10.—*Continued.*

Costa Rica	Apr	7	12	4	Fleming *et al.*, 1972
	May	10	1	2	"
	Jun	1		1	"
	Jul	2	9		"
	Sep	1		1	"
	Oct			51	"
	Nov	1		15	"
	Dec	1	1	16	"
	Aug*	X	X	4	Tamsitt and Valdivieso, 1961
Panamá	Jan	41		7	Fleming *et al.*, 1972
	Feb	15		2	"
	Mar	23	42	11	"
	Apr*	12	18		"
	May*	22	5		"
	Jun	14	4	4	"
	Jul	10	21	21	"
	Aug		19	15	"
	Sep		21	26	"
	Oct		4	20	"
	Nov			15	"
	Dec	1		4	"
Jamaica	Dec	6		4	Goodwin, 1970
	Feb	6	1	2	McNab, 1976
Providencia	Jan	4		5	Tamsitt and Mejia, 1962
Puerto Rico	Feb		X		Fenton, 1969
	Feb	X			Tamsitt, 1970
	Mar	X	X		"
	Apr		X		"
	Jun	X			"
	Jun	X	X		Anthony, 1918
	Aug			2	Tamsitt and Valdivieso, 1970
Virgin Is.	Apr**	X			Barlow and Tamsitt, 1968
	Jul**	X			"
Trinidad	Feb	X	X		Goodwin and Greenhall, 1961
	Mar	X	X		"
	Apr	X	X		"
	May	X	X		"
	Jun		X		"
	Jul	X	X		"
	Sep		X		"
	Jun	X			Jones, 1946
Colombia	Jun	1			Tamsitt and Valdivieso, 1963*b*
	Jul	1	1	6	Arata and Vaughn, 1970
	Aug		3	14	"
	Jan	14	4	8	Thomas, 1972
	Feb		3		"
	Mar*	1	3	1	"
	Apr*		3		"
	May	2		5	"
	Jun	1	2	2	"
	Jul*	2	10	13	"
	Aug	1	3	16	"

TABLE 10.—*Continued.*

Colombia	Sep	1		15	Thomas, 1972
	Oct		1	2	"
	Nov	3		2	"
	Dec	9		5	"
Venezuela	Jul	4	2	1	Smith and Genoways, 1974
Perú	Jun			14	Tuttle, 1970
	Jul			4	"
	Aug			3	"
			Artibeus lituratus		
Tamaulipas	Mar	2			de la Torre, 1954
	May	10			Alvarez, 1963
Durango	Jun		2	3	Jones, 1964*c*
Sinaloa	Feb	X			Jones *et al.*, 1972
	Apr	X			"
	Jun	X			"
	Jul	X	X		"
	Oct		X		"
	Nov			13	Anderson, 1960
Jalisco	Mar	2	X		Watkins *et al.*, 1972
	Apr	2	X		"
	Jun	3			"
	Jul	1	X		"
	Aug		X		"
	Sep		X		"
	Oct		X		"
Morelos	May	1			Cockrum, 1955
Querétaro	Jan	1			Spenrath and LaVal, 1970
Veracruz	Feb			1	Hall and Dalquest, 1963
Yucatan Pen.	Jan	2			Jones *et al.*, 1973
	Feb	1			"
	Apr	2			"
	Jul	1			"
Oaxaca	Apr		5		Villa-R., 1966
Guatemala	Feb	2			Jones, 1966
	Mar	3		1	"
	May		2		Rick, 1968
El Salvador	Jul		1		Starrett and de la Torre, 1964
Costa Rica	Jul	1			"
	Jan	1		1	Fleming *et al.*, 1972
	Feb	1			"
	Apr		2		"
	May	1	1		"
	Jul	2	2		"
	Sep			3	"
	Oct			1	"
	Nov			3	"
	Dec			10	"
Panamá	Jan	9		3	"
	Mar	1	2		"
	Apr	2	2	1	"
	May	1			"

TABLE 10.—*Continued.*

Panamá	Aug	1			Fleming *et al.*, 1972
	Sep		6		"
	Oct		1		"
	Mar	3		1	Bloedel, 1955
	Apr			1	Hall and Jackson, 1953
	May	2			"
Trinidad	Feb	X			Goodwin and Greenhall, 1961
	Mar	X			"
	Apr	X	X		"
	May	X	X		"
	Jun	X	X		"
	Jul	X	X		"
	Aug		X		"
	Sep		X		"
	Oct		X		"
Venezuela	Aug	1			USNM
	Jul	1		1	Smith and Genoways, 1974
French Guiana	Aug	X			Brosset and Dubost, 1967
	Sep	X			"
Colombia	Jan	9		1	Tamsitt and Valdivieso, 1965*a*
	Feb			1	"
	Mar*	1	1		"
	Apr	1			"
	May	3	1	3	"
	Jun*	4	5	6	"
	Jul		1	1	"
	Aug	1		1	"
	Sep*			4	"
	Oct*	4	1	9	"
	Nov*	8	2	8	"
	Jan	18	24	21	Thomas, 1972
	Feb	14	12		"
	Mar	9	5	10	"
	Apr*	13	4	9	"
	May*	22	10	16	"
	Jun	8	13	18	"
	Jul*	7	4	13	"
	Aug*	3	9	23	"
	Sep	3	7	19	"
	Oct	23	4	32	"
	Nov	33	1	27	"
	Dec	30	7	33	"
	Jul	5	10	32	Arata and Vaughn, 1970
	Aug			3	"
Perú	Jul			2	Tuttle, 1970
Brazil	Jun			1	USNM
	Jul	2		6	"
	Jul	X			Peracchi and Albuquerque, 1971
	Aug	X			"

*Pregnant and lactating.
**Twins.

month old and the others were older, but still in subadult pelage. Baker and Jones (1975) also recorded August-taken young from Nicaragua.

Artibeus concolor

The only record of reproduction in *A. concolor* is that of Thomas (1972), who collected a pregnant female in February in Colombia.

Artibeus jamaicensis

Artibeus jamaicensis is one of the few species for which adequate information on reproduction is available (Table 10). Goodwin (1970) reported that breeding is generally synchronized in Jamaica; Tamsitt and Mejia (1962) discussed a restricted season on Providencia; and Felten (1956*a*) suggested that breeding occurs in the dry season in El Salvador. On the other hand, Tamsitt (1966) and Jones *et al.* (1973) argued for continuous or acyclic breeding behavior in Colombia and the Yucatan Peninsula, respectively. Fleming *et al.* (1972) and Fleming (1973) have shown this species to be seasonally polyestrous in Panamá and Costa Rica. Fleming *et al.* (1972) also presented data on testis size correlated with spermatogenic activity in males. Heithaus *et al.* (1975) supported the case for bimodal polyestry in Costa Rica, pointing out that the two birth peaks occur at times of peak flower and fruit availability.

Fleming (1971) has shown that *A. jamaicensis* has a unique seasonally polyestrous cycle in Panamá. A peak in parturition occurs in March and April, followed by postpartum estrous and a second peak in parturition in July and August. "Blastocysts conceived after the second birth implant in the uterus but are dormant from September to mid-November, when normal development again resumes" (Fleming, 1971:402). Embryos then develop and young are born during the March-April birth peak.

Artibeus lituratus

In the northern part of its distribution, *A. lituratus* produces only one young per year, but farther southward, the period of reproductive activity is extended (Table 10). In Costa Rica and Panamá, these bats probably are on a bimodal cycle with a quiescent period after the second birth peak in the rainy season (Heithaus *et al.*, 1975). In Colombia, breeding proceeds throughout the year (Tamsitt and Valdivieso, 1963*a*). Tamsitt (1966) noted that *A. lituratus* is an acyclic or continuous breeder in Colombia. Tamsitt and Valdivieso (1965*b*) studied the reproductive cycle of males in Colombia and their data, based on presence of sperm, length and tubule diameter of the testes, and diameter of the epididymides, indicate that males are capable of reproductive activity at any time of the year, and that the reproductive pattern is acyclic without any suggestion of seasonal variation.

Thomas (1972) presented a much more extensive sample from Colombia and, although he has confirmed year-round activity with the presence of pregnant,

lactating, and inactive females in every month of the year, his data indicate bimodal activity peaks. Pregnancy peaks occur in December and May, with lactation peaks lagging about a month behind, as would be expected.

Enchisthenes hartii

Gardner *et al.* (1970) suggested that *E. hartii* is reproductively active throughout the year in Costa Rica. The only inactive animals they found were subadults, one in May and three in July. This species may be found to undergo a period of reproductive inactivity when data become available from later in the year. See Table 11.

Ardops nichollsi

I can find no records other than those of Jones and Schwartz (1967) who reported four pregnant females in March and one lactating and two pregnant females in April from Dominica.

Phyllops falcatus

No information is available on reproduction in this species.

Phyllops haitiensis

Nothing is known about the reproductive pattern of *P. haitiensis.*

Ariteus flavescens

No data are available concerning the reproductive pattern of this species.

Stenoderma rufum

Tamsitt and Valdivieso (1966*b*) described parturition in *S. rufum.* This species seems to be polyestrous on Puerto Rico, but data from the period September through December are needed in order to clarify their reproductive pattern. See Table 11.

Pygoderma bilabiatum

Peracchi and Albuquerque (1971) reported a pregnant female collected in August in Brazil.

Ametrida centurio

Nothing is known about the reproductive pattern of this species.

Sphaeronycteris toxophyllum

Nothing has been published about the reproductive pattern of *S. toxophyllum.*

TABLE 11.—*Reproductive data for the genera* Enchisthenes, Stenoderma, *and* Centurio.

Place	Date	Pregnant	Lactating	Inactive	Reference
		Enchisthenes hartii			
Honduras	Aug*				LaVal, 1969
Costa Rica	Jan	1			Gardner *et al.*, 1970
	May	1	X		"
	Jun	1	X		"
	Jul		X		"
	Aug		1		Armstrong, 1969
	Aug			1	LaVal, 1977
Colombia	Apr	7		5	Thomas, 1972
	May	12		13	"
	Jul		1	3	"
	Aug			7	"
	Sep		1		"
Perú	Nov			1	Gardner, 1976
		Stenoderma rufum			
Puerto Rico	Feb	X	X		Tamsitt, 1970
	Mar	X			"
	May	X			"
	Jul	X			"
	Aug	X			"
	Nov		X		"
	Jul	6	1	9	Jones *et al.*, 1971*b*
	Jul	1			Genoways and Baker, 1972
	Aug	1			"
	Aug	1			Tamsitt and Valdivieso, 1966*b*
		Centurio senex			
Tamaulipas	Jun	1			Alvarez, 1963
Jalisco	Mar	2	1		Watkins *et al.*, 1972
	Aug		1		"
	Apr			1	Jones, 1964*b*
Veracruz	Apr		5		Villa-R., 1966
Yucatan Pen.	Jan			1	Jones *et al.*, 1973
	Feb	1			"
	Jul	1			"
Oaxaca	Mar	1			Villa-R., 1966
	Mar	1	1		USNM
Chiapas	Apr	1			Davis *et al.*, 1964
	Jul	1			"
Honduras	Aug	2			LaVal, 1969
Nicaragua	Feb	1			Jones *et al.*, 1971*a*
	Mar	2		1	"
Costa Rica	Mar			1	Mares and Wilson, 1971
Trinidad	Jan	1			Goodwin and Greenhall, 1961
	Oct			1	"

*Pregnant and lactating.

Centurio senex

Although there are a fair number of records for *C. senex* (Table 11), the data from any given area are too few to decipher reproductive patterns. Pregnancies from February and July on the Yucatan Peninsula suggest the possibility of either polyestry or asynchrony.

Brachyphylla cavernarum

Anthony (1918) reported lactating females in July in Puerto Rico, and Nellis (1971) found a lactating female in April on St. Croix. Walker (1975) mentioned pregnant females in February on Puerto Rico, March on St. Croix, and a lactating female in April on Puerto Rico.

Buden (1977) collected 12 females, all of which were pregnant, in March on the Island of Caicos in the West Indies. All fetuses were 24 to 34 mm. in length, suggesting a synchronized cycle. The females lactating in July (Anthony, 1918) suggest the possibility of a second period of parturition as well.

Brachyphylla nana

Nothing is known about the reproductive pattern of this species.

Erophylla bombifrons

Although the data are sparse (Table 12), they suggest a restricted breeding season. Females are pregnant from February to June and lactating in July. This would result in the production of young early in the rainy season, a time when resources should be most plentiful.

Erophylla sezekorni

Buden (1976) summarized data based on 91 pregnant or lactating females and immatures. He suggested a gestation period during the first part of the year with parturition in early summer. He found females carrying small fetuses in February and larger fetuses in April and May. Lactating females were taken in June and many juveniles in July. Immature animals approaching adult size were taken in August. Thus, the pattern appears identical to that described above for *E. bombifrons*. See Table 12.

Phyllonycteris poeyi

Miller (1904) reported that all of the females he examined from Cuba were pregnant in June.

Phyllonycteris major

Nothing is known about reproductive patterns of *P. major*, a bat which is likely extinct.

TABLE 12.—*Reproductive date for the genus* Erophylla.

Place	Date	Pregnant	Lactating	Inactive	Reference
		Erophylla bombifrons			
Hispaniola	Feb	1			Buden, 1976
Puerto Rico	Jul		1		"
	Apr	X			Barlow and Tamsitt, 1968
	Jun	X			Valdivieso *et al.*, 1968
	Mar	X			Walker, 1975
	Apr	X			"
	May		X		"
	Jul		X		"
		Erophylla sezekorni			
Cuba	Feb	11			Buden, 1976
Bahamas	Apr	11			"
	May	6			"
	Jun		4		"
	Jul		1*		"
	Jun		8	2	Blake, 1885

*Plus many immatures.

Phyllonycteris aphylla

The only record of reproductive activity in this species is that of Goodwin (1970), who reported a pregnant female taken in January on Jamaica.

Desmodus rotundus

More is known about the reproduction of *D. rotundus* than about any other phyllostomatid (Table 13). DeVerteiul and Urich (1936) apparently were the first to suggest that *D. rotundus* breeds year-round, based on their work on Trinidadian populations. Wimsatt and Trapido (1952) confirmed this in Panamá by presenting data on both males and females, and suggested a gestation period of five to six months. Burt and Stirton (1961) reported continuous breeding in El Salvador. Goodwin and Greenhall (1961) recorded the same thing for populations on Trinidad and reported pregnant females, lactating females, and young animals in every month, although the highest incidence of young was in April and May and again in October and November. They also suggested that males may roost separately from females when the young are born.

Crespo *et al.* (1961) gave a detailed account of reproduction in vampires based on their work in Argentina during September and November. They found that in males both testes are active and coincide in their activity rhythm. Sexually active males with well-developed epididymides containing spermatozoa and inactive males with small epididymides and no spermatozoa were found in the same population at the same time of year. Sexually active males were present in September and November. In some instances, adult males have epididymides with few spermatozoa mixed with resting cells, which could be interpreted as the beginning of a new cycle of activity.

For females, Crespo *et al.* (1961) found that both ovaries are functional, with only a slight difference in degree of development of follicles. Ovaries are in a periovarian capsule, and the fallopian tubes begin in the walls of the capsules. There is always only one embryo, which occupies one uterine horn first but, with development extends into both horns and the body of the uterus, obliterating the partitioning of the uterus. At the end of a pregnancy, the ovary without the corpus luteum is in early proestrous and will produce the next ovum. One postpartum specimen had a corpus luteum in one ovary and a corpus albicans representing a previous pregnancy in the other ovary.

In September and November, there are proestrous immature animals bearing primary and secondary follicles. None of the animals examined had vaginal plugs or sperm in the uteri.

Hall and Dalquest (1963) mentioned that these animals seem to have no regular breeding season in Veracruz. They found a few young in various stages of development, pregnant females, and inactive females in all of the colonies examined. Dalquest (1955) had earlier pointed this out for San Luis Potosí populations, and suggested that young are born in all months of the year.

Villa-R. (1966) found pregnant females, lactating females, and newborn young at all times of the year during 15 years work in México.

Greenhall (1965) described mating behavior (including copulation), pregnancy, and young animals in captivity. Schmidt and Manske (1973) found a gestation period of seven months and lactation period of three to nine months for captive animals. Linhart (1971) compiled a useful bibliography of vampire bats.

Diaemus youngii

The only recorded reproductive information for this species is that of Goodwin and Greenhall (1961) for Trinidad. They found two lactating females in August and in October they took one immature male, four pregnant females, one lactating female, and two inactive females.

Diphylla ecaudata

Dalquest (1955) reported that *D. ecaudata* seems to have a well-defined breeding season and may have a single young per year in eastern México. Felten (1956*a*), however, felt that they breed in both dry and wet seasons in El Salvador and postulated two litters per year. From the scatter in the records listed in Table 13, I am inclined to agree with Felten.

Summary

The three most obvious reproductive strategies found in the family Phyllostomatidae are summarized in Fig. 1. The most critical environmental parameter is the seasonality of the rainfall pattern. Although a great deal of geographic variation exists, the pattern of a dry season during the months of January to April or May is common in Middle America and in many areas in northern South America. In tropical México, the rains often begin as late as June, but as one

TABLE 13.—*Reproductive data for the genera* Desmodus and Diphylla.

Place	Date	Pregnant	Lactating	Inactive	Reference
		Desmodus rotundus			
Tamaulipas	Mar	1			Alvarez, 1963
	May	2			"
	Jun	1	5		"
	Aug		9		"
Chihuahua	May	4		4	Anderson, 1972
Durango	Jun	1			Jones, 1964*c*
Sinaloa	Jan	1			Jones *et al.*, 1972
	Mar	1			"
	May	1			"
	Dec	1			"
Nayarit	Jan	1			Cockrum, 1955
Jalisco	Jan	X			Watkins *et al.*, 1972
	Feb	X			"
	Mar	X			"
	Apr	X			"
	May	X			"
	Jun	X			"
	Jul	X			"
	Aug		X		"
	Sep	X			"
Colima	Mar	52	1	39	Burns and Crespo, 1975
	May	36	9	23	"
	Jul	2	23	1	"
Zacatecas	Oct	1			Cockrum, 1955
Michoacán	Jul	1			Hall and Villa-R., 1949
Guerrero	Jun	22		7	Forment *et al.*, 1971
	Aug	16		31	"
	Sep	21		43	"
	Nov	10		12	"
Querétaro	May	1		3	Schmidly and Martin, 1973
	Jun	1		1	"
	Dec	3		2	"
Puebla	Jan	2			LaVal, 1972
Morelos	Jan	1			Burns, 1970
México	Jan*	1			"
Veracruz	Feb	X			Hall and Dalquest, 1963
	Jun	4		12	Lackey, 1970
	Jul	1		1	"
Yucatan Pen.	Jan	1			Jones *et al.*, 1973
	Feb	1			"
	Mar	2			"
	Apr	4	X		"
	Jun	1			"
	Jul	1	X		"
	Aug		X		"
	Apr	2			Birney *et al.*, 1974

TABLE 13.—*Continued.*

Guatemala	Mar	3			Jones, 1966
El Salvador	Feb			X	Felten, 1956*c*
	Mar	5			"
	May	2			"
	Jul	1			"
	Aug	1			"
	Oct	1			"
	Nov			X	"
Costa Rica	Jan	4		6	Fleming *et al.*, 1972
	Feb	7	2	15	"
	Mar	1	1	5	"
	Apr	1		2	"
	May	2		2	"
	Jul	1		4	"
	Aug			4	"
	Oct			1	"
	Nov	1		2	"
	Dec			4	"
Panamá	Apr	2	1		"
	May	1	1		"
	Feb	6		4	Wimsatt and Trapido, 1952
	Apr	5			"
	May	1		3	"
	Jul	1		2	"
	Nov	2	1		"
Trinidad	Jan	X			DeVerteiul and Urich, 1936
	Jun	X			"
	Nov	X			"
	Dec	X			"
Colombia	Nov	X			Tamsitt and Valdivieso, 1963*b*
	Jul	3	3	12	Arata and Vaughn, 1970
	Apr		1		Thomas, 1972
	May	1			"
	Oct	1	1	1	"
Venezuela	Apr	1		6	Pirlot and Leon, 1965
Brazil	Jan	X	X		Peracchi and Albuquerque, 1971
			Diphylla ecaudata		
Tamaulipas	Nov	2	1		Alvarez, 1963
San L. Potosí	Mar	3			Dalquest, 1953
	Jul		X		"
Yucatán	Nov	1	2		Hatt, 1938
	May		1		Birney *et al.*, 1974
México	Aug	1			Villa-R., 1966
	Oct	7			"
	Nov	2	2		"
El Salvador	Aug			1	Felten, 1956*c*
Honduras	Jul	2	1	3	Valdez and LaVal, 1971
Nicaragua	Apr			2	Jones *et al.*, 1971*a*

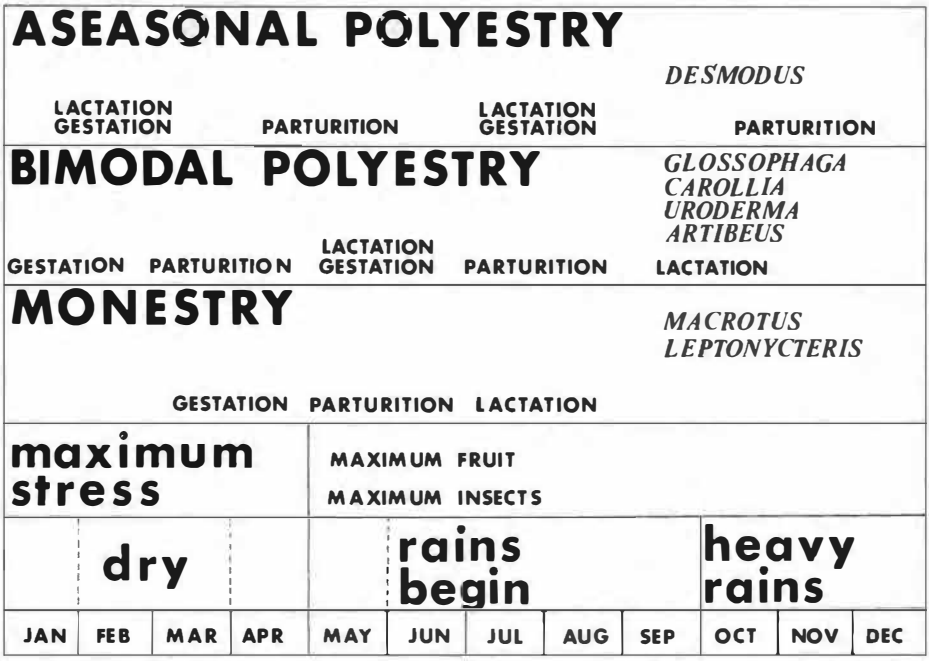

FIG. 1.—Summary of the three common reproductive patterns and of the environmental events affecting them.

moves southward, the length of the dry season generally decreases, and in some areas may be only a month or less in duration. Also, annual variations occur in any given locality. Nevertheless, for purposes of this discussion, the pattern represented in Fig. 1 may be taken as representative.

This environmental seasonality affects reproductive cycles of bats through the food supply. The time of maximum abundance of a wide variety of both fruits and insects is just after the beginning of the rainy season. Thereafter, a general decline is seen, culminating in a period of minimal abundance during the dry season.

The critical time for most bat populations seems to be the period of weaning of the young (Wilson and Findley, 1970; Fleming *et al.*, 1972). Thus, although it may be possible for females to undergo gestation and lactation during the stressful time of year, the young are usually weaned during the most energetically favorable periods.

In monestrous species of the Phyllostomatidae, there is a distinct period of reproductive activity culminating with weaning of the young shortly after the beginning of the rainy season when food is plentiful. This pattern is seen in some species at the northern limit of the range of the family, where the time of maximum food availability is fairly short. The nectarivorous bats of the genus *Leptonycteris* show this pattern in the southwestern United States, where they migrate northward from México and have their young in May or June. These young are weaned in July or August, the peak of the rainy season and the period

TABLE 14.—*Reproductive patterns of the 20 species for which adequate data exist.*

Macrotus waterhousii	delayed development and monestry
Glossophaga soricina	continuous or bimodal polyestry
Leptonycteris sanborni	monestry or bimodal polyestry
Choeronycteris mexicana	monestry
Carollia castanea	bimodal polyestry
Carollia subrufa	continuous or bimodal polyestry
Carollia brevicauda	bimodal polyestry
Carollia perspicillata	bimodal polyestry
Sturnira lilium	bimodal polyestry
Uroderma bilobatum	bimodal polyestry
Vampyrops helleri	bimodal polyestry
Vampyrodes caraccioli	bimodal polyestry
Vampyressa pusilla	bimodal polyestry
Vampyressa nymphaea	bimodal polyestry
Artibeus cinereus	bimodal polyestry
Artibeus watsoni	bimodal polyestry
Artibeus phaeotis	bimodal polyestry
Artibeus jamaicensis	bimodal polyestry and delayed development
Artibeus lituratus	geographically variable
Desmodus rotundus	continuous polyestry

of peak flower abundance. In October, individuals migrate back to México for the winter. A variation of this pattern is found in *Macrotus californicus*, where the embryos undergo delayed development during the autumn and winter months and begin developing at a more normal rate in spring. This results in parturition and weaning periods similar to those of *Leptonycteris*. There is a possibility that some individuals of *Leptonycteris sanborni* have a second period of reproductive activity resulting in the production of offspring in México in November. If so this species would more properly belong in the next category, that of bimodal polyestry.

The majority of species of phyllostomatids for which there is ample data show a reproductive pattern involving an extended breeding season with two birth peaks a year. In these species (for example, some members of the genera *Glossophaga*, *Carollia*, *Uroderma*, and *Artibeus*), the young from the first birth peak are weaned at the beginning of the rainy season, and those from the second pregnancy of the year are weaned well into the rainy season. These two peaks are followed by an inactive period, which results in no young being weaned during the stressful dry season.

At the other extreme from monestry are those animals that are completely polyestrous and produce young continuously and asynchronously throughout the year. The evidence to date shows only the vampire bat *Desmodus rotundus* to be in this category. These animals are adapted to a food supply (primarily blood from domestic cattle) that is available throughout the year over much of their range. However, because their gestation period is five or six months long, the net result still is only two young per year.

Table 14 summarizes the type of reproductive pattern for the 20 species for which there is a reasonable amount of data. It should be noted that many of these species will show geographic variation in the timing of reproductive events, and, in some cases (*Artibeus lituratus*, for example), the species may have completely different patterns in different areas. This is hardly surprising in view of the wide geographic and ecologic range of many of the species.

All of these patterns may be thought of as variations on a single theme—maximizing the production of offspring with available environmental energy resources. Further study will undoubtedly add a wealth of data on the fine tuning of the various mechanisms involved in selecting for a particular reproductive strategy for a given species.

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EMBRYOLOGY

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Over the years, there have been numerous reports concerning reproduction in the phyllostomatid bats, but a survey of the literature reveals that data on the embryology of the Phyllostomatidae are limited to gross morphological observations of reproductive tissues, embryos, and mammary glands of individuals from natural populations. These reports have provided useful information concerning times of pregnancy, lactation, and spermatogenesis. Thus, a basic knowledge of reproductive cycles for a number of the phyllostomatid bats has been accumulated (for review, see Wilson, this volume).

However, there have been few microscopic studies of reproduction and embryological development in the Phyllostomatidae. With respect to the details of the embryology of these bats, only seven species representing five genera have been studied microscopically. Some of these works are based on tissues collected from natural populations; others, on tissues from laboratory colonies.

This paper reviews the data now available on the embryology of the Phyllostomatidae. In order to facilitate this presentation, developmental events will serve as major subdivisions, and, within these subdivisions, the data available on the various species will be presented. The subdivisions to be considered are ovulation, fertilization, preimplantation embryonic development, implantation, postimplantation embryonic development, and placentation.

OVULATION

Macrotus californicus.—Studies of *M. californicus* indicate that ovulation is from the right ovary only (even though both ovaries develop Graafian follicles), and, typically, that only one ovum is released. It is not known if ovulation is spontaneous in *Macrotus* (Bradshaw, 1961).

Glossophaga soricina.—Ovulation in *G. soricina* may occur from either ovary, and there is a tendency for it to alternate between the two. Ovulation is spontaneous and usually only one ovum is released per cycle. Menstruation occurs in *G. soricina* and ovulation takes place at, or very close to, the time of menstruation (Hamlett, 1935; Rasweiler, 1972).

Carollia perspicillata, C. brevicauda, and *Desmodus rotundus.*—Ovulation in these three species is basically the same as in *G. soricina.* However, it is not known if ovulation is spontaneous. Menstruation in *Carollia* and *Desmodus* is similar to that of *G. soricina.*

Artibeus lituratus.—Ovulation in *Artibeus lituratus* may occur from either ovary (Tamsitt and Valdivieso, 1963, 1965).

Fertilization

Because there is no evidence for sperm storage in the female reproductive tracts of phyllostomatid bats, it appears that fertilization occurs shortly after copulation. Hence, the phenomenon of delayed fertilization that has been observed in some of the Vespertilionidae (Wimsatt, 1942) has not been reported in any of the Phyllostomatidae.

Preimplantation Embryonic Development

Macrotus californicus.—Studies on *M. californicus* have revealed the sequence of events prior to implantation; however, the timing of these events has not been determined (Bleier, 1975*a*). Development to a blastocyst occurs in the oviduct and was predicted to require 10 to 20 days (Bleier, 1975*b*). Embryonic development follows the pattern typical for other therian mammals. There is no information concerning the loss of the zona pellucida in *Macrotus.*

Glossophaga soricina.—In studies of a laboratory colony, Rasweiler (1972) was able to time the sequence of events in embryonic growth of *G. soricina.* The two-celled stage of development is attained by day 2 or 3 post-ovulation. The eight-celled stage is reached by days 5 to 7; the 32-celled stage, by day 8; the blastocyst stage, by day 10. Compared to development in other mammals, cleavage rate in *Glossophaga* is slow. The zona pellucida is usually lost on day 12 or 13, and, prior to its loss, the embryo has been contained within the ampulla of the oviduct. Upon loss of the zona pellucida, the embryo is located in the intramural uterine cornu, which is the site of implantation. There is no evidence of differentiation of germ layers during this preimplantation period.

Carollia perspicillata and *C. brevicauda.*—Cleavage in *C. perspicillata* and *C. brevicauda* also proceeds slowly. De Bonilla and Rasweiler (1974) reported that the first blastocyst was observed on day 10 postcoitum. Again, development to the blastocyst stage and loss of the zona pellucida occurs in the oviduct. Earliest loss of the zona pellucida was day 10.

Artibeus jamaicensis.—The only information available on early embryonic development in *A. jamaicensis* was reported by Fleming (1971), who found two reproductive cycles per year in Panamanian populations and noted that the embryo reaches the blastocyst stage before entering the uterus. An unusual feature is that during one of the cycles (August to March) there is a 2.5-month period of delayed embryonic development. During this period of retarded development, the only noticeable morphological change is an increase in the size of the blastocyst.

Desmodus rotundus.—Slow cleavage also is characteristic of *D. rotundus.* Quintero and Rasweiler (1974) observed a two-celled embryo as late as day 7 postcoitum in an individual from a laboratory colony. A blastocyst was not observed until day 15. Loss of the zona pellucida occurred in the oviduct, and the earliest date of this loss was day 15. Wimsatt (1954) noted that endoderm differentiation in the blastocyst begins while the blastocyst is still in the oviduct.

Implantation

Macrotus californicus.—Several reports are available concerning implantation in *M. californicus.* Bradshaw (1962) noted that implantation occurs during early gestation. Later studies by Bodley (1974) and Bleier (1975*a*, 1975*b*) have provided more details concerning the process in *Macrotus.* Central implantation is initiated shortly after the arrival of the blastocyst into the uterus. Early stages are characterized by a deterioration of the uterine epithelium such that the invading trophoblast comes into contact with the basal lamina of the uterine epithelium. Endoderm differentiation is initiated at this time. By the end of October, implantation has progressed to the point that the entire uterine epithelium that once surrounded the embryo has now been obliterated. The trophoblast is largely multilayered at this time, but unilaminar portions may be observed in the abembryonic regions. Reichert's membrane separates the trophoblast from the remaining fetal tissue and becomes continuous throughout the embryonic and abembryonic regions. The age of an embryo at this stage is estimated to be 20 to 30 days (Bleier, 1975*b*). By mid December, syncytiotrophoblast has differentiated; there is considerable proliferation of the syncytiotrophoblast by the end of January. At this time, an interstitial membrane (presumptive intrasyncytial lamina) is conspicuous between the maternal tissue and the syncytiotrophoblast. Reichert's membrane, which reaches its greatest thickness in late January, disappears by mid February. Endoderm completely surrounds the yolk sac cavity at this stage. By mid February all the layers that comprise the definitive placenta are present (Bodley, 1974; Bleier, 1975*b*).

Glossophaga soricina.—Implantation in *G. soricina* is initially central and secondarily interstitial (Rasweiler, 1974). Rasweiler (1974) divided this process of implantation into eight stages. Stage I (12 to 14 days postcoitum) blastocysts resemble ampullary blastocysts; however, there is some hypertrophy of the trophoblast in Stage I embryos. The uterine epithelium is intact but at times flattened. The blastocyst is oriented such that the inner cell mass is toward the cephalic side of the blastocystic cavity. The first appearance of endoderm differentiation is at this stage. Stage II blastocysts (days 13 to 15) are characterized by a bilaminar and multilaminar trophoblast in the embryonic polar region, whereas the trophoblast of the abembryonic region remains unilaminar. Necrosis of the maternal epithelium has begun in the bilaminar and multilaminar regions and the trophoblast has penetrated the basal lamina of the uterine epithelium. Stage III blastocysts (days 14 to 16) resemble Stage II blastocysts, but the uterine epithelium has deteriorated further. In some areas, the trophoblast has penetrated to the maternal basal lamina. Endoderm is clearly recognized in all specimens from Stage III. Stage IV specimens (days 15 to 17) are characterized by complete obliteration of the uterine luminal epithelium with encroachment of the trophoblast to the uterine glands. A decidual reaction first appears at this stage. During Stage IV, the endoderm and inner cell mass

fill almost the entire space of the blastocystic cavity. Solid multilayered masses of endoderm occur on the ventral side of the inner cell mass, and, by days 16 to 17, pockets have begun to develop in the endoderm. Endoderm appears on the lateral and dorsal surfaces of the inner cell mass. Stage V (days 16 to 21) is recognized by the presence of syncytiotrophoblast in the region of the embryonic pole. Cytotrophoblast at this stage is present outside of the syncytiotrophoblast, in addition to its position inside the syncytiotrophoblast, and in some regions has penetrated the glandular epithelium. The fluid-filled pockets in the endoderm are more pronounced, and in one specimen had coalesced to form a unilocular condition. By Stage VI (days 20 to 22) and Stage VII (days 23 to 25), the syncytiotrophoblast has proliferated further and has begun to penetrate the decidua basalis. There is an increase in vascular lacunae and a decrease in maternal endothelium in Stage VII individuals. A lamina that is probably an extension of the abembryonic portion of Reichert's membrane is interposed between the inner cell mass and the endoderm dorsal and lateral to the inner cell mass. Coalescence of the pockets in the endoderm has continued so that most embryos are unilocular. In Stage VIII (days 26 to 30), the cytotrophoblast has penetrated deep into the syncytiotrophoblast. During this stage, the intrasyncytial lamina is observed and significant quantities of maternal blood in the labyrinth first appear. Amniogenesis by cavitation has begun at this stage. By day 32, differentiation of ectoderm has been initiated, and thinning of the roof of the amnion has begun. The endoderm and Reichert's membrane, in the region of the embryonic pole, have disappeared. The fate of Reichert's membrane is currently unknown.

Carollia perspicillata and *C. brevicauda.*—Little is known about implantation in *Carollia.* De Bonilla and Rasweiler (1974) found that the site of implantation in *C. perspicillata* and *C. brevicauda* is similar to that reported for *G. soricina*; that is, implantation occurs in the segment between the end of the oviduct and the main cavity of the uterus.

Artibeus jamaicensis.—The only report on *A. jamaicensis* is that of Fleming (1971). Implantation is similar to that observed for *Glossophaga soricina* and *Desmodus rotundus,* including "(i) precocious development of the blastocyst, which by the time it reaches the uterus, has differentiated into a trophoblast thickened at the embryonic pole and an embryonic cell mass . . . and (ii) implantation that is interstitial and cytolytic."

Desmodus rotundus.—The only observations of implantation in *D. rotundus* were reported by Wimsatt (1954): implantation is "cytolytic and completely interstitial," occurring antimesometrially in the middle of the uterine cornu and on the same side as is the ovary from which ovulation occurred. During early implantation, the embryo is secured to the uterus only in the region of the embryonic cell mass, thereby exposing the abembryonic surface to the uterine cavity. The trophoblast near the embryonic pole is multilaminar, whereas the trophoblast associated with the free surface (abembryonic) is unilaminar. Beneath the inner cell mass, the endoderm has hypertrophied;

in other regions it remains flattened. Wimsatt (1954) also observed precocious formation of mesoderm, but Rasweiler (1974) speculated that this may actually be endoderm.

In a second, older specimen, Wimsatt (1954) noted that implantation was complete. By this stage, the embryo is completely embedded in the endometrium, and the trophoblast is multilayered in the embryonic region but still largely unilaminar in the abembryonic region. In both specimens, there is a marked decidual reaction but it is most pronounced in the older specimen. Amniogenesis is accomplished by cavitation.

Postimplantation Embryonic Development

Macrotus californicus.—Embryonic growth in *M. californicus* to the end of implantation is slow. Fertilization in *Macrotus* most often occurs during October, and, by the end of implantation (mid February), amniogenesis by cavitation has begun. Therefore, the embryo requires approximately four months to reach the embryonic-disc stage (Bleier, 1975*a*). Growth accelerates during March, and embryos at the limb-bud stage (crown-rump length approximately 4.5 millimeters) of development are observed. Embryonic growth continues at a rapid rate, and most parturitions occur during June. Growth and differentiation of the embryonic tissues and organs, following the period of slow development, are similar to the pattern that has been described for other therian mammals.

Glossophaga soricina.—Hamlett (1935) described the embryonic growth in *G. soricina* following implantation. His description included a discussion of the primitive streak and mesoderm formation. Primary mesoderm is formed early; however, Rasweiler (1974) provided evidence that this "primary mesoderm" is most likely endoderm. Formation of secondary mesoderm (that derived from the primitive streak) and subsequent primitive streak activity are similar to that of any typical mammal. By the six-somite stage the coelom is present (but absent at the medullary-fold stage) and the mesoderm has split into splanchnic and somatic layers. The yolk sac remains large, but the yolk stalk disappears before the 2.5-millimeter stage. There is no evidence of the allantois in the six-somite specimen (length is one millimeter from head fold to end of primitive streak), but by the time the embryo reaches 2.5 in length, the allantois has attained its maximum relative size.

Placentation

Macrotus californicus.—Bradshaw (1961) noted that the definitive placenta in *M. californicus* is hemochorial. Recently, Bodley (1974) used electron microscopic techniques that revealed the definitive placenta to be hemodichorial. Development of the placenta is such that it is large enough to be readily visible with the naked eye by late March. At this time, reduction of the cytotrophoblast to a single cell layer begins and syncytial blocks

(derivatives of the syncytiotrophoblast) replace the maternal endothelium (Bodley, 1974; Bleier, 1975*b*). Changes from March to June involve maturation of the placenta, but there is no change in the number of cell layers. The layers of the hemodichorial placenta in *Macrotus* include syncytial blocks, intrasyncytial lamina, syncytiotrophoblast, cytotrophoblast, fetal basal lamina, and fetal capillary endothelium (Bodley, 1974).

Glossophaga soricina.—Hamlett (1935) and Rasweiler (1974) classified the placenta in *G. soricina* as discoidal and hemochorial, and Rasweiler (1974) indicated that formation was rapid. There is an interstitial lamina present, but its origin is uncertain—Rasweiler (1974) suggested that it is derived from the trophoblast. The trophoblast differentiates into cytotrophoblast and syncytiotrophoblast; however, the cytotrophoblast disappears by midgestation. In addition, the walls and endothelium of the maternal blood vessels are eroded (Hamlett, 1935) so that there are three cell layers that separate the fetal and maternal blood streams. These layers are fetal endothelium, loose mesenchyme, and syncytiotrophoblast.

Carollia perspicillata.—Little is known concerning the placenta in *C. perspicillata.* Wimsatt (1958) noted that the placenta is discoidal and endotheliochorial. Also, he implied that the cytotrophoblast does not persist to the end of gestation. There is a conspicuous interstitial membrane between the syncytiotrophoblast and maternal endothelium. However, this observation was made by using light microscopy. Recent studies indicate that other phyllostomatid bats have a hemodichorial type placenta and that the "maternal endothelium" is actually syncytiotrophoblast (Björkman and Wimsatt, 1968; Rasweiler, 1974; Bodley, 1974; Bleier, 1975*b*). Therefore, it would not be surprising if it were determined that the "maternal endothelium" in the placenta were syncytiotrophoblast. If this were true, and if the cytotrophoblast is lost, then the placenta of *Carollia* would be a hemochorial type. Further investigations are needed to confirm the type of placental barrier characteristic of *Carollia.*

Artibeus jamaicensis.—Wislocki and Fawcett (1941) stated that the placenta is discoidal and hemochorial.

Desmodus rotundus.—Initial reports indicated that the placenta in *D. rotundus* is discoidal and endotheliochorial (Wimsatt, 1954, 1958). However, by using electron microscopic methods, Björkman and Wimsatt (1968) concluded that the definitive placenta is hemodichorial, but in earlier stages before the loss of the maternal endothelium it is endotheliochorial. Thus, the definitive placenta consists of the following layers: intrasyncytial lamina, syncytiotrophoblast, cytotrophoblast, a thick basement membrane, mesenchyme, and fetal endothelium.

Summary and Conclusions

From the data summarized in this paper, several trends can be seen in the embryology of the Phyllostomatidae. In general, ovulation may occur from

either ovary, except in *Macrotus californicus*, and fertilization follows immediately after ovulation and copulation. Embryonic development to the blastocyst stage appears to be similar to that reported for other therian mammals; however, the process seems to be considerably slower in the phyllostomatid bats studied thus far. Implantation is interstitial except in *M. californicus*. The placenta is discoidal, and it is likely that the placental barrier is either hemodichorial or hemochorial.

There are several features of phyllostomid embryology that should stimulate further investigations of the species reported in this paper. In addition, studies of other species should be encouraged for they might reveal embryological strategies other than the ones presently known. Some of the areas deserving the application of sophisticated research techniques include ovulation from only the right ovary in *M. californicus*, delayed embryonic development in *M. californicus* and *Artibeus jamaicensis*, the length of gestation in *Desmodus*, and menstruation and interstitial implantation in *Glossophaga*, *Carollia*, and *Desmodus*.

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ONTOGENY AND MATERNAL CARE

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Although many aspects of phyllostomatid biology have received increasing attention in recent years, there is still a dearth of information on the growth and behavioral ontogeny of this diverse family of bats. This is in contrast with studies of the Vespertilionidae, where both field and laboratory investigations of development have been common, although by no means numerous (Jones, 1967; Pearson *et al.*, 1952; Kleiman, 1969; Orr, 1970; Gould, 1971). The lack of interest in chiropteran ontogeny is discouraging because the special adaptations for flight, including echolocation, and diverse feeding strategies should provide fertile ground for developmental studies, as Gould (1970) has pointed out.

In this chapter we will attempt to review some aspects of ontogeny in the phyllostomatid bats, concentrating on growth and development in *Carollia perspicillata*, which we have studied in captivity. Field and laboratory observations of other species will be included where they are available. The vampire bat, *Desmodus rotundus*, is the only other phyllostomatid for which detailed information is available (Schmidt and Manske, 1973).

The colony of *Carollia perspicillata* was originally captured in Trinidad in April 1972 and maintained at Johns Hopkins University for six months by E. Gould. During this period, several births occurred. Sixteen *Carollia* were brought to the National Zoological Park, Washington, D.C., in October 1972. At this time, one female had a small infant; a second female gave birth three days after the arrival of the colony. Both young were reared. Table 1 presents the history of the colony between January 1973 and January 1974. Three *Glossophaga soricina* (two males, one female) were acquired with the *Carollia*, of which one adult male died and one male was born. Nine *Anoura geoffroyi* (four males, five females) also were received, but all but a pair died within the first three days. No breeding of *Anoura* occurred.

The colony was housed in a climate-controlled room measuring approximately 3 by 3 by 2.5 meters. Temperatures averaged 29°C (range 27 to 31°C); relative humidity, 70 per cent (range 50 to 80 per cent). A light cycle of 12 hours of light to 12 hours of dark was used. Two wire mesh cages with wooden frames and burlap covers were provided for roosts in an elevated position. Several branches were placed between the roosts and from the roosts to the floor.

Bats were fed a peach-nectar mixture developed by Rasweiler and De Bonilla (1972) for nectarivorous phyllostomatids, although there is evidence that *Carollia* also feeds on insects (Pine, 1972; Ayala and D'Alessandro, 1973). Water was available *ad libitum*, as were ripe, peeled bananas that were suspended from branches. Dishes with the nectar diet were placed in brackets

TABLE 1.—*History of* Carollia perspicillata *colony from January 1973 to January 1974.*

	Males	Females	Total
Number of original adults	6	11	17
Number of births	17	13	30
Number of deaths:			
Adults	0	1*	1
Juveniles	1	5*	6

*One mother and young died accidentally.

attached to the outside of the roosts so that bats could feed while in flight or while hanging on the roost.

Bats were caught with butterfly nets; adults initially were examined bimonthly beginning in January 1973, but weekly examinations were instituted in April 1973. Young were weighed and measured every two to four days. Individuals were identified by a number punch marked on the wing membrane (Bonaccorso and Smythe, 1972; Kleiman and Davis, 1974). Behavioral observations and retrieval tests were conducted at irregular intervals.

REPRODUCTIVE CYCLE

After the two births in October 1972, there were three birth peaks in *Carollia*: February 1973, June and July 1973, and November and December 1973 (Table 2). Known interbirth intervals ranged from 115 to 173 days. During the first peak of parturition, females were highly synchronized—nine of 11 females gave birth within a 17-day period. The births were more scattered

TABLE 2.—*Dates of birth and interbirth intervals for 12* Carollia perspicillata *females, between January 1973 and January 1974.*

No. of females	Birth no. 1	Birth no. 2	Birth no. 3	Interbirth interval (days)
4	12 Feb. 73	1 July 73	25 Oct. 73	138, 116
6	26 Jan. 73	29 May 73	18 Nov. 73	123, 173
7	28 Feb. 73*	23 June 73	6 Dec. 73*	115, 165
10	20 Feb. 73*	21 June 73*		121
11	14 Feb. 73*			
16	5 Mar. 73	21 July 73*	10 Dec. 73	138, 142
17	16 Feb. 73*	3 Aug. 73*		168
19	12 Feb. 73	24 June 73	8 Nov. 73*	132, 137
20	18 Feb. 73*	1 July 73	15 Nov. 73*	133, 137
25	22 Feb. 73*	12 July 73*	7 Dec. 73*	140, 148
26	22 Feb. 73*	20 June 73*	10 Dec. 73	118, 173
35	14 Jan. 74*			

*Indicates accurate birth date. Other dates are estimated and parturition might have occurred a maximum of three days earlier.

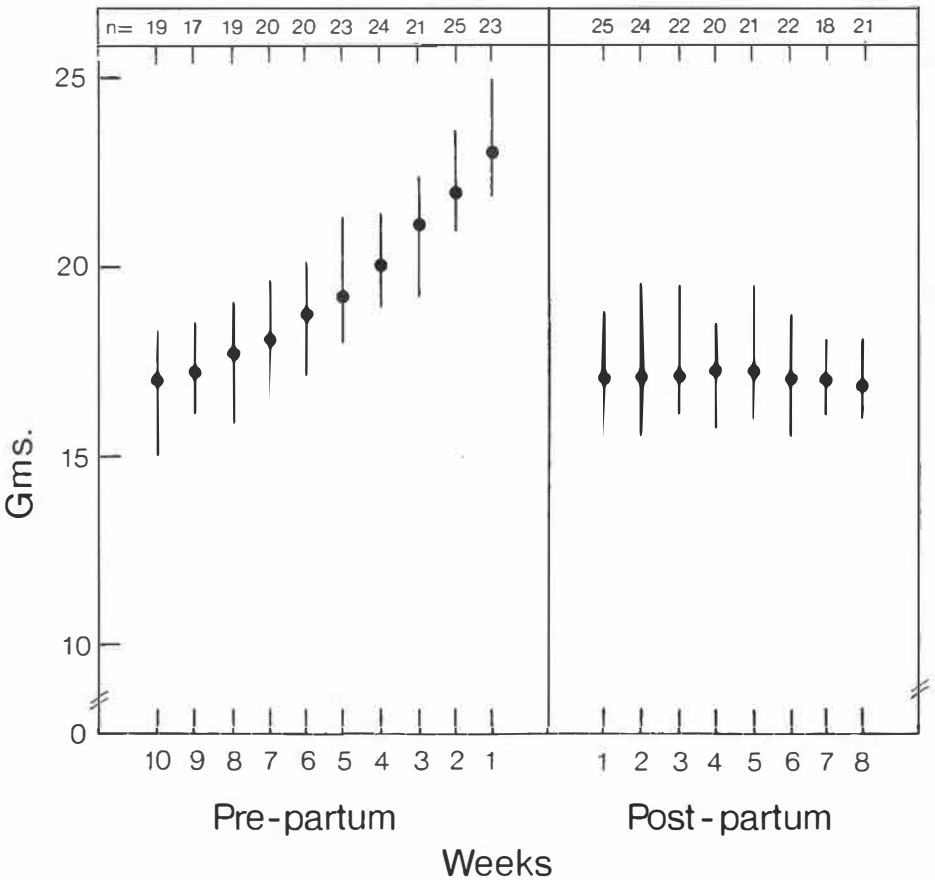

FIG. 1.—Average weights and ranges of weights in pre and postpartum *Carollia perspicillata*, based on 25 births of 11 females.

during the succeeding two parturition periods. The shortest interbirth intervals ranged from 115 to 123 days ($N = 5$). Rasweiler and De Bonilla (1972) found an implanting blastocyst in a female killed 21 days postpartum, suggesting that estrus may occur shortly after parturition. If an immediate postpartum heat occasionally occurs, the gestation period for *Carollia perspicillata* may be approximately 115 to 120 days. The single *Glossophaga soricina* female gave birth in March 1973 and did not become pregnant again for a full year.

A total of 30 *Carollia* young were born (see Table 1), of which 24 survived through weaning. No females aborted nor were any infants rejected after birth. The majority of juvenile deaths occurred at weaning, and at least four of these might have resulted from feeding on spoiled food or a disfunction in the humidity control, which caused a rapid drop in humidity in the flight room. Adult losses were limited to a single female and her young, which died accidentally.

Females gained approximately one-third of their initial weight during pregnancy (see Fig. 1). Average weight during the last week of pregnancy was 22.9 grams as compared with 17.3 grams during the first week postpartum. During the final weeks of pregnancy, females were reluctant to fly and maneuvered less efficiently when they flew. Fetuses were palpable from about five to six weeks before birth, and were in a transverse position.

The nipples of pregnant females were not obvious prior to birth, but within two days of parturition the surrounding fur had been shed and the mammary region had become pink in color. Thick milk could be expressed from the nipples up until approximately 33 days postpartum (range 21 to 49 days). Thereafter, the milk began to thin, but fluid could be expressed until approximately 56 days after birth (range 42 to 72 days). The area around the nipples began to assume a darker pigmentation and the fur began to reappear from 48 days postpartum (range 37 to 66 days); however, the mammary region did not assume prepartum condition until 72 days postpartum (range 64 to 87 days). From these observations, it would appear that heavy lactation continues for slightly over one month after birth, but females continue to produce milk until approximately 1.5 to 2 months postpartum.

Data available for length of lactation in other phyllostomatids indicate a lactation period of one to two months (Jenness and Studier, 1976). In the vampire bat, *Desmodus*, nursing may continue for nine months although weaning is initiated at three (Schmidt and Manske, 1973). In *Macrotus* and *Leptonycteris*, lactation continues for one month and four to eight weeks, respectively (see Jenness and Studier, 1976). A single *Glossophaga soricina* female in our colony continued lactating for approximately two months.

Maternal Care

No births were observed in *Carollia* although females were seen eating placentas and licking newborn young. The umbilical cord was rarely severed at the base, but usually dried up and fell off within a day following birth.

Parturition has been described for *Stenoderma rufum* (Tamsitt and Valdivieso, 1966*b*), *Artibeus lituratus, Glossophaga soricina, Vampyrops helleri* (Tamsitt and Valdivieso, 1965), and *Choeronycteris mexicana* (Barbour and Davis, 1969). In all species, parturition occurred in the normal head-down position; this seems to be typical of phyllostomatids but rare in vespertilionids (Wimsatt, 1960), except for *Nyctalus noctula* (Kleiman, 1969).

In the species observed by Tamsitt and Valdivieso (1965, 1966*b*), a head presentation was found. Placentophagia has not been reported for the above-mentioned species, nor for *Desmodus* (Schmidt and Manske, 1973).

During the first few days, young *Carollia* were carried parallel to the mother's body and held under the wing. Thereafter, the typical carrying position, both at rest and in flight, was cross-wise on the mother's ventral surface, just posterior to the throat. *Carollia* infants (up to 14 days) were rarely observed hanging alone. Young attached themselves primarily with the mouth and hind feet;

the wings were tightly closed and partially covered the infant's body. Claws on the thumbs were not used for clinging because the distal portion of the forearm was pressed tightly against and covered the infant's head and ears. Young removed from the mother's nipple occasionally remained in this carrying posture for several seconds, even when placed on their back. The cross-wise carrying posture was also seen in our individual of *Glossophaga soricina*, *Desmodus* (see fig. 2 *in* Schmidt and Manske, 1973), and might be present in *Choeronycteris* (see fig. 8 *in* Barbour and Davis, 1969). It appears to be an adaptation for carrying young while the female is flying. For the first 10 days, captive young of *Artibeus* were reported (Novick, 1960) to hang head down under the mother's wing with the hindfeet around the mother's thigh.

Carollia mothers preferred to hang freely from a horizontal ceiling when carrying attached young. Thus, it was impossible for infants to be attached simultaneously to the nipple and support themselves by the hind feet until they were about half the size of the mother. Young were capable of hanging from the ceiling by the age of 18 days, but still remained attached to a nipple. Similar observations were made of a young *Glossophaga*. In *Desmodus*, young do not support themselves until at least two weeks of age (Schmidt and Manske, 1973).

From our observations, it appeared that resting *Carollia* females supported the bulk of their infant's weight for at least 14 days. An added advantage to the cross-wise carrying position assumed by the young, other than providing balance, was that they did not need to readjust their position when a female flew. Young were last observed attached to the mother approximately 23.5 days postpartum (range 19 to 31; $N = 15$), when they were approximately 57 per cent of the mother's weight.

Because we were unable to observe the bats without disturbing them, especially at night, we do not know whether females foraging in the wild carry their young or, if they do, for how long. One 11-day-old young was seen hanging alone next to its mother approximately 45 minutes after the lights went out, but the infant attached to the nipple and moved back into a cross-wise carrying position immediately after we entered the room. The mother flew as soon as the young attached. This suggests that mothers may detach from the young at night, but we had no evidence that young were ever left in a crèche. Mothers with attached young were more reluctant to fly when disturbed than were unencumbered bats but did so, nevertheless, and seemed able to maneuver efficiently.

Observations of development in a single young *Glossophaga soricina* were similar to those for *Carollia*. The young was last seen attached to the mother when it was 20 days old.

Both from our *Carollia* observations and some field reports, it appears as though some species of phyllostomatid bats commonly carry their young and, unlike vespertilionids (see Fenton, 1969; Davis, 1970), do not leave them in crèches.

Felten (*in* Pine, 1972) apparently netted a *Carollia perspicillata* with a half grown young, and Tamsitt and Valdivieso (1963*a*) caught lactating *Artibeus lituratus* and *Glossophaga sorcina* carrying young in the vicinity of fruit trees where presumably they were foraging. One *A. lituratus* female carried a young 53.8 per cent of her weight (Tamsitt and Valdivieso, 1965). Mumford and Zimmerman (1964) reported netting lactating *Choeronycteris mexicana* with attached young at a distance of approximately 200 yards from the main daytime roost. Bradshaw (1961) captured a female *Macrotus californicus* in a roost carrying a young weighing 57 per cent of her weight; Cockrum (in Davis, 1970) observed female *Leptonycteris sanborni* moving young within a cave as well as carrying advanced young to a previously abandoned roost. Schmidt and Manske (1973) indicated that *Desmodus* females can carry young up to eight weeks old. A. M. Greenhall (personal communication) has observed *Desmodus* females with attached young of unknown age feeding on cattle; however, these bats were similar in size to young that he had observed crawling around in roosts without the mothers. These young were not newborn and might have been approaching weaning age.

Observations discussed above suggest that phyllostomatids may carry attached young of an advanced age. Whether females forage with the young or simply move them from roost to roost remains to be determined. Certainly, except for *Macrotus waterhousii* (Goodwin, 1970), *Leptonycteris sanborni* (Hoffmeister, 1959), and *Phyllostomus hastatus* (J. Bradbury, personal communication), one does not find reports of crèches of infants in phyllostomatids, although lactating females may roost colonially and segregate themselves from males. Bradbury (personal communication) suggested that female *Carollia*, for example, may move their babies from the day roost to a night roost prior to foraging, which may partly account for the well-developed tendency to carry young in captivity.

Retrieval of young *Carollia* was observed under several experimental conditions. Mothers and young were released into a small holding cage after being weighed and measured; typically, they reestablished contact within 30 minutes to an hour (that is, before being released into the flight room). On several occasions, young were deliberately separated and hung on the outside of the roost, after which time the other bats were released into the flight room. Several different bats would fly past hanging infants, pausing briefly to hover, as though to inspect the young. Usually, a juvenile was inspected several times (both by its mother and other bats) before the mother would alight above her offspring and crawl down to it.

Juveniles that were too young to fly were never observed attempting to regain contact with their mother by climbing higher on the roost. Normally, they hung motionless until the mother made tactile contact with them. Audible vocalizations (ultrasonic calls were given by the mother and young, Gould, 1975) were not heard nor did the infant reveal much sign of disturbance. Licking of the young by the mother usually accompanied retrieval, especially

before the mother flew again. The latency to retrieve was highly variable in the females, ranging from two to 30 minutes. The age of the young did not seem to affect this latency because infants between one and three days old were retrieved within two to 22 minutes.

Mothers clearly recognized their own offspring; we never caught a female with an alien young attached to her. Moreover, mothers and young retained an association (roosted near each other) long after weaning. One *Carollia* mother and daughter were regularly caught together until the daughter was five months old, about a week prior to the next birth.

Development of Young

Carollia are born in an advanced state, with the eyes open (Fig. 2). Neonates are fully furred on the dorsum, and the more sparsely furred venter and muzzle become covered within two to three days after birth. The dark brown juvenile pelage is complete by day 7 to 10.

Of the neonatal phyllostomatids observed, *Macrotus, Leptonycteris* (Gould, 1975), *Carollia, Glossophaga* (this study and Klíma and Gaisler, 1968), *Choeronycteris* (Mumford and Zimmerman, 1964), and *Artibeus* (Tamsitt and Valdivieso, 1966*a*) are born well furred. *Desmodus* (Schmidt and Manske, 1973; Gould, 1975), *Phyllostomus discolor* (Klíma and Gaisler, 1968), and *P. hastatus* (Gould, 1975) are sparsely furred at birth.

Eyes are open at birth in *Carollia* (this study), *Artibeus* (Tamsitt and Valdivieso, 1966*a*), *Desmodus* (Schmidt and Manske, 1973; Gould, 1975), *Macrotus* (Gould, 1975), and *Phyllostomus hastatus* (Gould, 1975). Only *Leptonycteris* and *Phyllostomus discolor* have been reported (Tamsitt and Valdivieso, 1963*a*) to have the eyes closed at birth.

Carollia neonates were active from birth and when handled would squirm, try to crawl away, and often vocalize. This contrasted with their behavior in the flight room during retrieval tests when they hung motionless on the bat roost. The increased activity might have been caused by the temperature of the room in which weights and measurements were taken, which was cooler than was the flight room. Gould (1975) stated that the young of *Desmodus, Phyllostomus hastatus,* and *Leptonycteris sanborni* are active during reunions with the mother, whereas those of *Macrotus californicus* are passive.

C. perspicillata young are born with a complete set of 22 deciduous teeth, with the formula di 2-2/2-2, dc 1-1/1-1, dpm 3-3/2-2 = 22. A comparison of preserved skulls from the U.S. National Museum with living neonates suggests that only 16 of the 22 deciduous teeth are functional. The four lower incisors, barely penetrating the gingivum, disappear several days after birth, and the first upper deciduous premolars are not even visible in live specimens. Lower deciduous premolars are simple, highly reduced spicules, undifferentiated in width from root to crown. The second and third upper premolars, although more prominent than the lower ones, are tiny pegs that taper to a fine point at the crown. The second milk

FIG. 2.—Neonate of *Carollia perspicillata* on the day of birth. Note that the eyes are open, and the animal's dorsum is fully furred. The venter typically has only sparse fur.

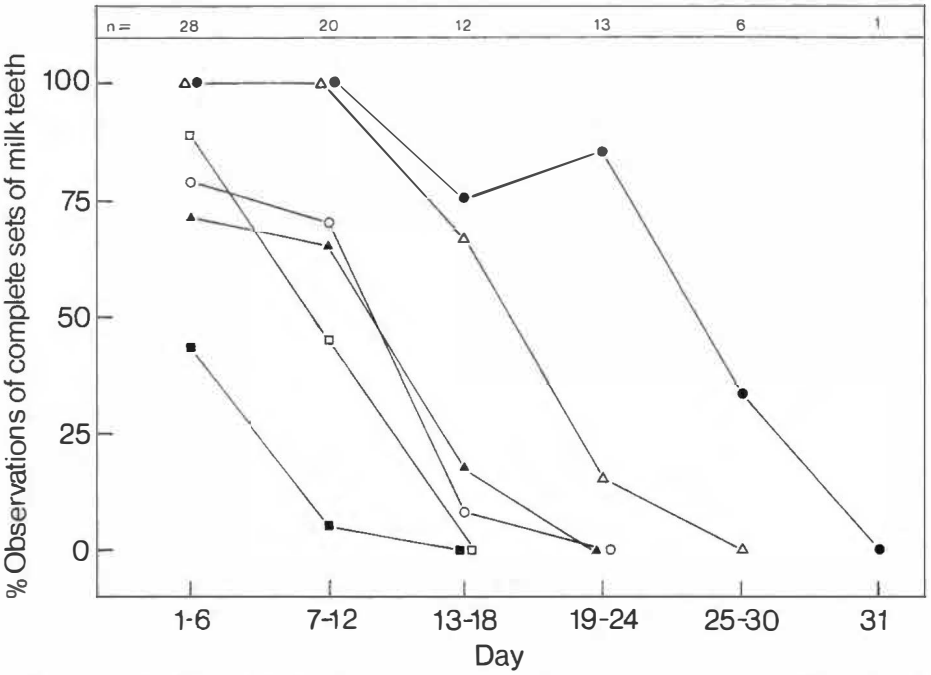

FIG. 3.—The loss of deciduous teeth in juvenile *Carollia perspicillata*. Observations within a given time period may include the same individual. (Symbols are closed circles, upper outer incisors; open circles, upper inner incisors; closed triangles, lower canines; open triangles, upper canines; closed squares, lower premolars; and open squares, upper premolars).

premolar is weakly recurved. Lower canines are slender, mildly recurved spicules that gradually taper to a point. The upper canines and upper outer incisors are the largest, most strongly recurved stylettes; also, they are retained longest. Upper inner incisors are bifid at the distal extremity.

The comparative rate of loss of deciduous teeth is represented in Fig. 3. Lower deciduous premolars are lost during the first two weeks postpartum. Lower canines, upper premolars, and upper inner incisors are shed next. The upper canines and upper outer incisors are retained until one month postpartum, the last milk tooth being lost at 34 days postpartum. The permanent dentition of the upper jaw emerged first. By day 22 postpartum, one-third of the permanent teeth had emerged; by day 26, two-thirds; and by day 31, all were present.

Deciduous upper and lower canines and upper outer incisors are the teeth primarily used to attach to a nipple. Two observed perforations in a female's nipple were a clear result of the upper canines, the distances between the perforations and the canines both measuring 2.6 millimeters. *Carollia* resembles *Tonatia*, *Mimon*, *Chrotopterus*, *Choeronycteris*, and *Phyllostomus* in that the upper outer incisors are more prominent than the upper inner ones.

In *Macrotus, Glossophaga,* and *Leptonycteris,* both outer and upper inner incisors are functional (Phillips, 1971).

In general, the deciduous dentition of most phyllostomatids is reduced and less complex than that of vespertilionids (Phillips, 1971; Miller, 1907). This seems to correlate with the tendency to carry attached young rather than deposit them in crèches, thus suggesting that increased complexity in the deciduous dentition of vespertilionids may function to grasp the returning mother (or any female in species that nurse promiscuously) rather than to maintain a hold on the nipple when already attached.

The development of flight in *C. perspicillata* was investigated by periodically dropping infants and juveniles. Prior to day 14, all young drop straight to the ground, with the wings extended. As infants approached 14 days of age, they occasionally flapped their wings once or twice as they fell. Between days 14 and 16, young bats began flapping the wings when dropped, but could not maintain altitude or turn. They also were unable to land and often collided with obstacles or eventually dropped to the floor. By day 18, they could maintain (and gain) altitude, take off from a roosting position, turn, and avoid obstacles. However, their landing ability was poor, and they often landed with the wings extended. Between days 20 and 23, the ability to land upside-down with the wings folded perfected, and, after day 24, flight development essentially was complete. Juveniles, however, could be distinguished from adults by their flight patterns for several weeks more because they flew more slowly and erratically. Juveniles were first captured independent of the mother on an average of 27.6 days (range 23 to 31, $N=16$) after birth.

There is little information available on flight development in other young phyllostomatids. In *Desmodus,* young achieve flight capability at eight to ten weeks of age (Schmidt and Manske, 1973); Novick (1960) reported that a young *Artibeus* began to fly at approximately 28 days of age. A single juvenile *Glossophaga soricina* was first found separate from its mother and flying at age 25 to 28 days.

Neonates of *Carollia perspicillata* average 5.0 grams at birth (range 4.1 to 5.9; $N=13$), which is 28.4 per cent of the postpartum weight of females. Initial growth in weight is rapid (Fig. 4), but juveniles do not achieve adult weight until 10 to 13 weeks of age. Forearm length at birth is 24.4 millimeters (range 22.4 to 27.5 mm; $N=10$), and forearm growth essentially is complete at six weeks (Fig. 4). At approximately 24 days of age, when the young first begin to fly, forearm length is 93.4 per cent and weight 63.0 per cent of that for adults ($N=10$).

Neonatal and postpartum weights and measurements are not available for most phyllostomatid bats. Table 3 presents some accurate and estimated neonatal to mother weight and measurement ratios for both phyllostomatid and vespertilionid bats, based on known and derived data. Weights and measurements were taken from full-term fetuses and nonlactating females. Young-to-mother weight ratios are poor for comparative purposes because weights tend to fluctuate seasonally, captive and field weights frequently

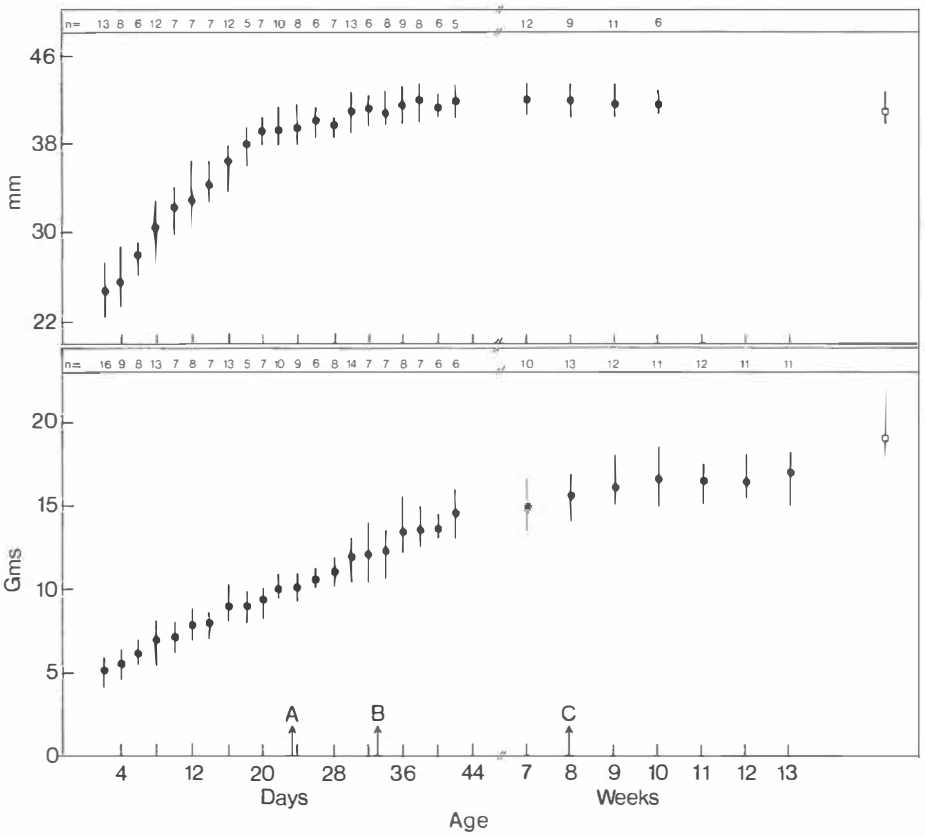

FIG. 4.—Increase in average weight (bottom) and forearm length (top) for *Carollia perspicillata*. A, average day when young were last observed attached to the mother; B, average day when the mother's milk began to thin; C, average day when milk no longer could be expressed from the mother's nipples. These averages are based on measurements from 17 individuals (8 females, 9 males) of known age. The open squares indicate the mean weight and forearm length (and range) for 12 adult males for comparison.

differ, and species may have one to three young per litter. However, most phyllostomatids exhibit ratios greater than 0.25 (for single births). Orr (1970) noted that the ratio in vespertilionids depends on species size, larger species tending to have a smaller ratio. Neonatal-to-mother forearm ratios are a better comparative measure. Table 3 indicates that phyllostomatid bats may be born in a more advanced stage than vespertilionids because seven of eight species of phyllostomatids have a ratio usually exceeding 0.41 whereas this ratio is exceeded in only three of 13 vespertilionids.

DISCUSSION AND CONCLUSIONS

The paucity of information on phyllostomatid development not withstanding, available data suggest that ontogeny and maternal care in phyllostomatids differs in several characteristics from those in vespertilionids.

TABLE 3.—*Average neonate to adult weight and forearm length ratios in selected phyllostomatid and vespertilionid bats. Weights are given in grams, lengths in millimeters, and sample size appears in parentheses.*

Species	Weight			Length of forearm			References
	Neonate	Adult	Percentage of adult size	Neonate	Adult	Percentage of adult size	
				PHYLLOSTOMATIDAE			
Macrotus waterhousii				26		51	Gould, 1975
Phyllostomus discolor	7.6(1)	31.6-36.9(4L)	20.6-24.1	26.2(1)	59.2-63.2 (2M; 2NP)	41.4-44.3	Tamsitt and Valdivieso, 1963*a*; Goodwin and Greenhall, 1961
Phyllostomus hastatus				37		46	Gould, 1975
Leptonycteris sanborni				16		47	Gould, 1975
Anoura geoffroyi	5.1(4)	11.3-16.2(20NP)	31.5-45.1				Goodwin and Greenhall, 1961
Choeronycteris mexicana	4.4(2FF)	16.2(2B)	26.5				Mumford and Zimmerman, 1964
Carollia perspicillata	5.0(13)	17.6(7PP)	28.4	24.4(10)	42.3(10)	57.7	Kleiman and Davis, this study
Artibeus lituratus	7.8-15.5	56.1(6NP)	13.9-27.6	38.7(1)		55.2	Tamsitt and Valdivieso, 1965
	10.7(1)	56.4(1B)	19.0		69.9(4M;10NP)		Tamsitt and Valdivieso, 1966*a*
	8.9(1)	26.1(1B)	34.1				Tamsitt and Valdivieso, 1963*b* (*in* Orr, 1970)
Stenoderma rufum	7.0(1)	19.0(1B)	36.8	29.4(1)	49.6(1)	59.3	Tamsitt and Valdivieso, 1966*b*
Desmodus rotundus	7.0(FF)		21.9				Crespo *et al.*, 1970
				25		43	Gould, 1975
	5.5(3)	24.4-40.4(30L)	13.6-22.5	22.3(3)	56.7-59.6(16)	37.4-39.3	Burns, 1970; Goodwin and Greenhall, 1961

TABLE 3.—*Continued.*

				VESPERTILIONIDAE			
Myotis lucifugus	1.5-1.9	6-7.5	20-31.7				Barbour and Davis, 1969; Orr, 1970
	2.3(1)			16-17		42	Gould, 1971, 1975
			28.3	15.7 (18)	39.5(100)	39.7	O'Farrell and Studier, 1973
Myotis thysanodes			27	16.3(2)	43.8(100)	37.2	O'Farrell and Studier, 1973
Myotis velifer	3.0		25.8	16.0	43.6-48.6	32.9-36.7	Kunz, 1973
Pipistrellus subflavus	1.89*	5.86(5L)	32.2				Lane, 1946
Pipistrellus pipistrellus	1.4(9)	5.9(2PP)	23.7	11.4(7)	32.0(38NP)	35.6	Kleiman, 1969
Eptesicus fuscus	4	16.0(1L)	50.0**	18.0	42-51	35.2-42.8	Davis *et al.*, 1968; Barbour and Davis, 1969
	3.1-3.6			17.0(3)	44-48	35.4-38.6	Gould, 1971
				18		39	Gould, 1975
Eptesicus serotinus	5.8(4)	28.3(3PP)	20.5	22.4(4)	51.9(8)	43.9	Kleiman, 1969
Nyctalus noctula	5.7(10)	28.9(9PP)	19.7	20.7(9)	51.9(17)	39.9	Kleiman, 1969
Lasiurus cinereus				18.6(2)	46-58	32.1-40.4	Bogan, 1972; Barbour and Davis, 1969
Lasiurus intermedius	ca. 3			ca. 16	45-56	28.6-35.6	Jennings, 1958
Nycticeius humeralis	2.0(11)	8(L)	50**	14(11)	32-36	38.9-43.8	Jones, 1967
Plecotus townsendii	2.4(10)	8.5-11.3(32NP)	21.2-28.2	16.6(10)	42-44	37.7-39.5	Pearson *et al.*, 1952; Orr, 1970.
Antrozous pallidus	3.1(2)	25.2(16M)	24.6**	17.5(2)	57.9(13)	31.0	Orr, 1954, 1970
	3.0(9M); 3.2(11F)	22.2(39NP)	27.0; 28.8**	17.4(20)	53.9(103)	32.3	Davis, 1969
Tylonycteris pachypus	1.4*	L	36	8(1)	26-28	28.6-30.8	Medway, 1972
Tylonycteris robustula	2.5*	L	39				Medway, 1972

*Combined weights of twins; **percentage doubled since twin litters common; NP, nonpregnant females; L, lactating females; M, males; B, weight of pregnant female minus neonate weight; PP, postpartum females; FF, full-term fetuses; F, female.

1. Phyllostomatids generally are born in a more precocial condition, (furred, eyes open, mobile, and size large relative to that of the mother) than vespertilionids. As Gould (1975) pointed out, there is no clear dividing line between altriciality and precociality, but within the two families, the degree of overlap in such characteristics as mobility, eye opening, and pelage development is small.

2. In phyllostomatids, deciduous teeth are reduced in size, relatively simple in form, and functional teeth are fewer in number. The deciduous dentition might be related to permanent dentition and different feeding strategies, but it might also correlate with maternal care patterns, as discussed in point 3 below.

3. Phyllostomatid young usually are not deposited in large crèches by foraging mothers. Instead, they remain attached to the mother in the roost during the day and might be carried during foraging. Bradbury (personal communication) suggested that young might be carried to a nocturnal roost before the female begins to forage. The cross-wise position assumed by attached young could be an adaptation of phyllostomatids to frequent carrying by the mother.

The occurrence of these three characteristics in many species of phyllostomatid bats is intriguing, especially when considering how such adaptations evolved. Carrying young during foraging or transferring young to individual nocturnal roosts before foraging could serve as an antipredator strategy for bats living under conditions where other bats have evolved as predators. However, transferral to a nocturnal roost might be an adaptation that could evolve only under stable tropical conditions where temperature fluctuations are not great. By contrast, crèches of vespertilionids might function, in part, to retain heat in the altricial young. Clearly, behavioral studies in the field are needed to determine how ontogency and maternal care in the Phyllostomatidae relate to feeding strategies, social organization, roosting behavior, and possible antipredator mechanisms.

Acknowledgments

We are grateful to E. Gould for providing us with the captive colony of *Carollia perspicillata, Anoura geoffroyi,* and *Glossophaga soricina.* The study specimens examined from the United States National Museum of Natural History, Smithsonian Institution, included five *Carollia perspicillata* and two *C. brevicaudatum* (USNM 104551; 104552; 179612; 284511-284513; 65475). We thank R. H. Pine for his assistance. The literature review for this article was completed in early 1975.

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GENERAL PHYSIOLOGY

JOHN M. BURNS

At first exposure to this volume, as well as its previous companions, one is amazed at the amount of information that has accumulated concerning the biology of New World leaf-nosed bats. Upon closer inspection, however, it is apparent that the vast majority of this information deals with taxonomy, distribution, natural history, and various aspects of morphology. Physiological study of these biologically important mammals has been a neglected area, at least as judged by the published literature.

Two physiological systems that have been examined to a substantial degree and warrant separate consideration are sensory physiology (primarily echolocation) and thermoregulation. Gould (1977) and McManus (1977) have provided excellent reviews of these respective topics and I shall not attempt to duplicate here the information presented in these two papers.

Endocrine studies, in particular, are lacking for phyllostomatids. The reason for this probably can be attributed to the fact that bats are small and therefore have small blood volumes. Until the last decade, measurements of hormone concentrations were dependent mostly on bioassays that required blood to be pooled from several bats. Determination of hormone concentration is no longer a major problem because such techniques as radioimmunoassay (RIA) and fluorescent immunoenzyme assay require only 50 to 100 microliters of plasma. Echolocation and thermoregulation studies, on the other hand, have allowed investigators to work with entire animals without the need for expensive equipment.

Many interesting questions can be raised as to the role of chiropteran endocrine systems in such physiological endeavors as water balance, bone and calcium metabolism, and digestion. For the moment, we can only surmise that such endocrine regulation is similar to that known for other mammals.

Reproductive Physiology

In view of the great deal of emphasis placed on reproductive physiology of animals over the past several decades, one would be inclined to suppose that there is a wealth of such information for phyllostomatid bats. However, the vast majority of literature on reproduction in leaf-nosed bats deals with studies of comparative anatomy, morphology, natural history, and fecundity rather than with the physiological processes of reproduction. As Wilson (this volume) pointed out, reproductive strategies of phyllostomatids are varied. These include such schemes as monestry, polyestry, and a system that Bradshaw (1962) termed delayed development for *Macrotus californicus*; a similar system was reported (Fleming, 1971) for *Artibeus jamaicensis*. A unique gestation pattern was reported in *Macrotus californicus* for thyroid hormone (Burns *et al.*, 1972),

estrogens (Burns and Wallace, 1975), and for progesterone (Burns and Easley, 1977). In each of these reports, biphasic patterns were described in which one peak coincided with the fertilization and implantation period of October and November, followed by a second peak in May and June that corresponded to fetal maturation and parturition. The hormonal data (summarized in Table 1), as well as the histological studies of Bleier (1975*a*, 1975*b*), suggest that the reproductive scheme in *M. californicus* is quite different from delayed implantation.

Krutzsch *et al.* (1976) reported changes in plasma testosterone and testicular ascorbic acid in reproductively active male *M. californicus*; testosterone and testicular ascorbic acid reached a peak concentration of 2.7 ng/ml and 38 ug/ml, respectively, in late summer, and spermatazoa were present in the epididymides from August to early December. The testes began to atrophy by late September, and the levels of testosterone and testicular ascorbic acid declined by December but were detectable the year around (minimum concentrations observed for testosterone were 0.25 ng/ml; ascorbic acid, 1 ug/ml.).

The seminal vesicles and prostate glands were at maximum size in September (15 mm diameter, 19 mg weight) and slowly digressed beginning in late autumn.

In my studies at Texas Tech University, I also found that *M. californicus* is an adaptable animal for laboratory study. After individuals are fed by hand for 2 to 3 days, they are tamed quite rapidly. When bats were housed in large cages, which allow for adequate freedom of flight, attempts to establish breeding colonies proved successful (unpublished).

Thyroid

Reports on thyroid physiology are scarce and usually play a minor role in larger studies related to thermoregulation or reproduction. Sadler and Tyler (1960*a*) examined thyroid function in a nonhibernating bat, *Macrotus californicus*, by means of ^{131}I uptake. Animals were tested over a temperature range of 24° to 37°C, and it was found that chronic exposure to these temperatures did not influence thyroid activity. This is quite different from responses of hibernating species of vespertilionids, which show drastic changes in the rate of thyroid uptake of radioactive iodine when subjected to a similar temperature regime as described above for *M. californicus* (Sadler and Tyler, 1960*b*).

Burns *et al.* (1972) reported a drastic decrease in plasma thyroxine for *M. californicus* during the second trimester of pregnancy (see Table 1). It was found later, however, that triiodothyronine (T3) levels were elevated throughout the gestation period to the extent that total thyroid hormone concentration in the blood during pregnancy remained essentially unchanged (unpublished).

Adrenal Glands

Studies that attempt to describe the role of either adrenocortical or medullary hormones in regulating a host of physiological processes in phyllostomatid bats are unknown. Such a work would represent a "first" for comparative physiology.

TABLE 1.—*Changes in plasma concentrations of various hormones during pregnancy in* Macrotus californicus.

Hormone	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June
Thyroxine[1]		3.5		2.0		1.0	1.0	2.0		5.0	5.0
Progesterone[2]	1		11	16	22	5	8	7	13	31	15
Estrone[3]	0		10	12	15		12	12		25	
Estradiol-17 ß	0		40	55	60		35	40		75	

[1]Thyroxine concentrations were measured by a column chromatography-colorimeter technique and are expressed as microgram per cent. The June sample is from lactating females. From Burns *et al.* (1972).

[2]Progesterone concentrations were determined by radioimmunoassay and are expressed as nanograms per milliliter. The June sample represents preparturition samples. From Burns and Easley (1977).

[3]Estrogens determined by radioimmunoassay and expressed as picograms per milliliter. The values for August mean that estrogen levels were not detectable with this assay. From Burns and Wallace (1975).

There are a few reports that describe the basic morphology of chiropteran adrenal glands (for example, see Christian, 1963) but no attempt has been made to elucidate the role of the adrenal glands in a physiological sense.

Parathyroid Glands

I was unable to find a published report of any investigation that dealt with the function or particular characteristics of the parathyroid glands in any member of the Phyllostomatidae.

Renal Physiology

The great success of Chiroptera in general, and phyllostomatids in particular, suggests that some species have evolved elaborate and highly efficient renal mechanisms for conserving water. Most studies of renal function pertain to evaporative water loss, however, and are orientated more toward thermoregulation than anything else (see McManus, 1977). There is a paucity of information concerning renal physiology and evidently an absolute absence of data dealing with the endocrine regulation of renal function in leaf-nosed bats.

McFarland and Wimsatt (1965, 1969) reported on the unusual ability of the kidneys in the vampire bat *Desmodus rotundus* to concentrate urine. At first, one might question the physiological demand that would result in development of a versatile renal system in an animal with a diet that is approximately 98 per cent water. McFarland and Wimsatt (1969) proposed that the majority of the water content ingested with a blood meal must be eliminated rapidly for purposes of flight. This would result in a meal residue composed almost entirely of protein, which represents a nitrogen load that must be excreted with a minimum of urinary water loss. McFarland and Wimsatt (1969) also reported that the vampire bat concomittantly forms urine at a high rate (4 ml/kg/minute) and a low osmolality (475 mOs) during feeding. Five to six hours after feeding, the rate of urine production falls to approximately 0.2ml/kg/minute, with a surprising high urine concentration (4656 mOs). Wimsatt and Guerriere (1962) also reported on the relationship of volume of blood consumed by *D. rotundus* to amount of urine

excreted. For example, if the blood meal is 35 milliliters, the urine volume excreted shortly after feeding is approximately 26 milliliters. Also of interest is the observation (Wimsatt and Guerriere, 1962) that isolated *D. rotundus* have a somewhat higher average daily consumption of blood than do bats held captive in groups (21.2 as compared to 15.5 milliliters). The physiological significance of these observations is not known.

Whereas *Desmodus rotundus* demonstrates a remarkable ability to concentrate urine, the nectarivorous *Leptonycteris sanborni* has little physiological capability in this regard. Carpenter (1969) showed that even when individuals of *L. sanborni* collected from desert habitats were placed on a high protein diet, the maximum urine concentration was only 342 mOs. This value is even less concentrated than that reported by Schmidt-Nielsen and O'Dell (1961) for semiaquatic mammals such as beaver, *Castor canadensis*. Normally, *L. sanborni* feeds on nectar from a variety of desert plants that are high in water and carbohydrates. Howell (1974) showed that this species obtains proteins and amino acids by consuming pollen of the saguaro cactus as a dietary supplement. The pollen's nitrogenous degradation products are concentrated in the urine and then actively ingested by the bat. This behavior results in a positive nitrogen balance, a condition otherwise impossible on a pollen-free diet.

Respiratory Physiology

Inasmuch as bats lack the more efficient flow-through air sac arrangement characteristic of birds, they must devote a substantially greater portion of their body to respiratory surface tissue. For example, the common crow, *Corvus brachyrhynchos*, has a respiratory surface area in its lungs of approximately 0.6 square centimeter per gram of body weight (McCauley, 1971), whereas small bats, such as those in the vespertilionid genus *Myotis*, must devote 100 square centimeters per gram of body weight so as to meet the metabolic demand of flight. It does not appear, however, that this poses an anatomical disadvantage for bats because flight is an efficient method of travel for chiropterans. For example, Thomas (1975) calculated that *Phyllostomus hastatus* requires only one-sixth the energy needed by a terrestrial mammal of the same size to cover a given distance. He also calculated the metabolic rate, in watts, for flying *P. hastatus* (0.93 kg) as 130.4 w/kg^{-1}. Thomas also stated that such metabolic rates are essentially the same as the predicted values for flying birds of similar body size, but that they are two and a half to three times greater than the highest metabolic rates of which exercising terrestrial mammals of similar size appear capable.

Thomas and Suthers (1972) provided some interesting data concerning the differences in respiration at rest and during flight for *Phyllostomus hastatus*, which are summarized in Table 2.

They also reported that the heart rate of preflight *P. hastatus* was 8.7 beats per second as compared to 13 beats per second (780 beats per minute) in the first few seconds of flight. Lastly, Thomas and Suthers recorded the hematocrit

TABLE 2.—*Comparison of difference in respiration for resting and flying* Phyllostomus hastatus *(from Thomas and Suthers, 1972). Weight is given in grams and metabolic rate in terms of milliliters of oxygen per gram of body weight per hour.*

	Weight	Metabolic rate $ml0_2\ (gh)^{-1}$	Ventillation rate (breaths/second)
Before flight	101	6.78 ± 0.85	2.8
	87	6.12 ± 1.15	
During flight	101	27.53 ± 0.79	10.6
	87	24.68 ± 1.87	

of *P. hastatus* as 60 per cent. This is considerably greater than the percentage of red blood cells found in a given volume of blood from any avian species listed by Sturkie (1965); the higher erythrocyte number probably reflects one of the general physiological adaptations for flight in bats.

Electrophoretic properties of some phyllostomatid hemoglobins have been described. Valdivieso *et al.* (1969) found a single, common hemoglobin band for *Monophyllus redmani, Artibeus jamaicensis, Stenoderma rufum,* and *Erophylla bombifrons.* A similar, more comprehensive electrophoretic survey was reported by Mitchell (1966). Additional hematological data for leaf-nosed bats were reported by Valdivieso and Tamsitt (1971), who concluded that hematocrit values for frugivorous species are lower than those found in insectivorous bats.

Concluding Remarks

This contribution to the biology of New World leaf-nosed bats is an indication of what little is known concerning their physiology rather than a survey and review of a substantial body of knowledge. It also represents perhaps a subtle plea to comparative physiologists to turn their attention to phyllostomatids. Techniques now are available for measuring biological molecules in blood samples of small volume. Hopefully, future investigators will take advantage of this technology.

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POPULATION AND COMMUNITY ECOLOGY

STEPHEN R. HUMPHREY AND FRANK J. BONACCORSO

Bats are the numerically dominant group of mammals in the Neotropics. They comprise 52 per cent of the mammalian species in Costa Rica (Robinson, 1971) and 46 per cent of those in Panamá (Handley, 1966). The family Phyllostomatidae accounts for 55 per cent of all Costa Rican bat species and 59 per cent of the species in Panamá. In terms of number of individuals, the density of some phyllostomatid species far exceeds that of any other kind of mammal in Central America (F. J. Bonaccorso and D. Morrison, unpublished). Additionally, phyllostomatids exhibit great diversity in the types of food used, with specializations for eating fruit, nectar and pollen, insects, small land vertebrates, and blood of birds and mammals. The importance of this family in diversity and relative density suggests an equivalent functional importance in tropical ecosystems.

A recurrent theme in tropical ecology and in this volume is the seasonal variation of tropical climate. The dominant feature of tropical climate is an annual cycle of wet and dry seasons (see Rumney, 1968). It is not uncommon to find tropical dry or wet forests (forest types refer to the classification of Holdridge, 1967) that receive 200 to 400 millimeters of rain per month in the wet season and no measurable rain in some dry season months. Tropical wet and rain forests have less distinct dry seasons but predictably have reduced rainfall in certain months. The influence of wet-dry seasonality on the foraging and reproduction of tropical bats was discussed by Baker and Baker (1936), Mutere (1968, 1970), Liat (1970), Mares and Wilson (1971), Fleming *et al.* (1972), and Heithaus *et al.* (1975).

FORAGING STRATEGY

Optimal foraging strategy requires that animals maximize food intake (benefits) while minimizing expenditure of time and energy (costs) of acquiring food. The distribution of food resources in time and space, the type of food eaten, and competition for food all weigh heavily in shaping foraging strategy (Schoener, 1969). Additionally, transitional stages in the evolution of species or individual life histories may coincide with less than optimal time-energy budgets when animals use excessive energy to exploit new resources. For example, some phyllostomatids that change their diets seasonally may incur such increased foraging costs.

In this section, we discuss factors influencing the foraging strategies of phyllostomatids. We suggest that Neotropical bats feeding on vertebrates and blood can rely on stable and abundant food resources throughout the year. On the other hand, fruits, flowers, and insects are extremely seasonal in abundance.

Some phyllostomatids specializing on these food types may encounter local shortages at predictable times of the year. In order to survive such food shortages, foraging strategies of tropical bats include migration, dietary changes, discontinuation of reproduction, and successfully competing with other species for limited food resources. In addition, phyllostomatids do have seasonal fat cycles (McNab, 1976) and undergo at least diel torpor (McNab, 1969); these strategies also might help in the accommodation of food shortages.

Fruit

Fruit availability in tropical forests varies in complex ways. Some tree species produce fruit synchronously each year at a characteristic season. Some fruit rhythmically but not every year. Others fruit with no discernable pattern from once every few years to several times a year (Richards, 1973; Foster, 1973; Frankie *et al.*, 1975).

Thorough studies of fruiting patterns in tropical dry, moist, and wet forest plant communities have been conducted in Panamá by Foster (1973) and in Costa Rica by Frankie *et al.* (1975). These studies show that edible fruit is available throughout the year, regardless of life zone, but that sharp seasonal fluctuations occur in the number of species fruiting and the total fruit biomass. In dry forest, a single peak in the number of species with mature fruits occurs during the wet season. Both moist and wet forests have two peaks in the number of species fruiting, one each in the dry and wet seasons.

Heithaus *et al.* (1975) studied the foraging patterns and resource use of six fruit-eating phyllostomatids near Cañas, Costa Rica. The tropical lowland dry forest of Cañas has a wet season from May to early November and a dry season from mid-November through April. Virtually no rain falls in the dry season, and the forests are semideciduous, with about half the tree species losing their leaves (Daubenmire, 1972). In each month, between five and 10 species of plants produce fruit eaten by bats. A single strong peak in the number of plant species with "bat fruits" occurs from May through August. During the early dry season, when the fewest kinds of fruits are ripe, a peak in the number of species of blooming "bat flowers" occurs. At that time, all "fruit bats" at Cañas switch in part to a pollen and nectar diet. Three species (*Carollia perspicillata, Sturnira lilium*, and *Artibeus jamaicensis*) that eat fruit, nectar, and pollen reproduce twice each year—once coinciding with the dry season and once with the fruit abundance in the wet season. *S. lilium* undergoes a marked change from nectarivory in the dry season to frugivory in the wet season. Thus, female *S. lilium* on a diet that is either primarily nectar and pollen or primarily fruit are able to nurse young.

Our own unpublished data from a moist forest site, Barro Colorado Island, Panamá, reveal that from six to 19 species of bat fruits are available each month. Again, two peaks in fruit abundance occur, one in the wet season and one in the dry season (Fig. 1), and *Artibeus jamaicensis* correspondingly reproduces twice each year. At this site, few bat flowers are available, and *A. jamaicensis*

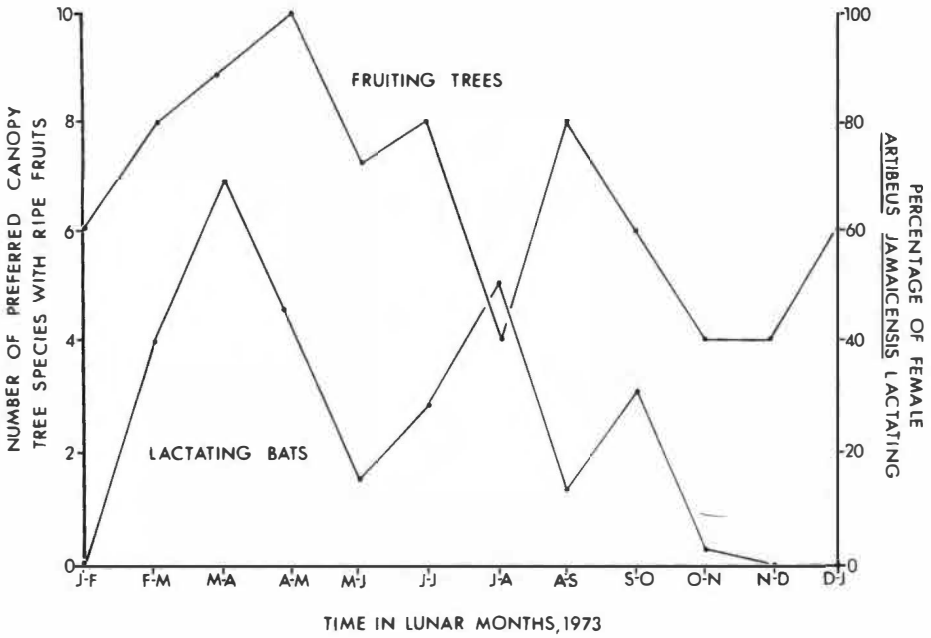

FIG. 1.—Seasonal reproduction of female *Artibeus jamaicensis* and of trees supplying this species with food, on Barro Colorado Island, Panamá.

relies on a diet of fruit from canopy trees throughout the year. The period of an adult female mammal's year that is most expensive energetically — lactation (Miguela, 1969; Studier *et al.*, 1973) — is even more costly in the first reproductive peak of *A. jamaicensis*, which occurs during the late dry season. Then most bats are simultaneously lactating and pregnant with embryos to be born in the wet season. Selective pressure for this postpartum estrus probably arose from the combination of the four-month gestation of *A. jamaicensis* and the occurrence of the second fruiting peak four months into the wet season. This reproductive adaptation places the end of the second lactation period during the year's second fruiting peak. Therefore, coincidence of the first lactation with the year's larger and longer fruiting peak is a doubly vital phase of seasonal timing. The wet season fruiting peak is followed by two months of fruit scarcity; it is accompanied by another postpartum estrus of *A. jamaicensis*, but development of the embryo is delayed until the end of the wet season (Fleming, 1971).

The fruiting patterns of individual plant species often are less important to bats than are the fruiting patterns of inclusive genera. Usually, all members of a genus will have similar fruits, either edible or not. For example, the 18 species of *Miconia* eaten by birds in Trinidad's Arima Valley fruit for periods of one to four months, with fruiting intervals spaced through the year so that from one to seven species always are bearing fruit simultaneously (Snow, 1965). On Barro Colorado Island, Panamá, and at Cañas, Costa Rica, several species

of the shrub genus *Piper* (Fig. 2) are sympatric. Each fruits cyclicly, with species cycles offset so that fruit of the genus is available all year (Heithaus *et al.*, 1975; our data). Pipers are the most important food species for bats of the genus *Carollia* in Central America (Howell and Burch, 1974; Heithaus *et al.*, 1975; our data). The plant genus *Ficus* (figs) has many species that consecutively serve as dietary staples for *Artibeus* and other stenodermines. The same is true for *Cecropia* trees and *Phyllostomus discolor*, in our experience. The year-round availability typical of such dietary staples may result from long coevolution in response to mutualistic seed dispersal (Snow, 1965).

Some important bat fruits are available only for several months and do not have congeners fruiting at other times of the year. For example, *Spondias mombin* is ripe only from September to December on Barro Colorado Island (Smythe, 1970). (Croat, 1974, reported that this species begins to fruit in July, but this is true only along watercourses and drainage ditches.) Its only congener, *S. radlkoferi*, also fruits within this period. Both species of *Spondias* are important food items for bats when few other fruits are available during the heaviest rains of the wet season.

The low densities of tree species in heterogeneous Neotropical forests may force large foraging distances upon herbivorous bats. Large-sized specialists on fruit should have greater foraging distances than smaller generalists. For example, Fleming *et al.* (1972) gave mean recapture distances of 347 meters for *Artibeus jamaicensis* and 167 meters for *Carollia perspicillata*. Heithaus *et al.* (1975) reported that small species feed on resources of high abundance, whereas large species use resources that are more patchy in time and space.

Nectar and Pollen

Community patterns in the timing of flowering for Neotropical plants, like fruiting patterns, are quite complex and vary by life zone. In dry forests, most species flower during the dry season (Allen, 1956, summarized by Janzen, 1967; Fournier and Salas, 1966; Daubenmire, 1972; Frankie *et al.*, 1975). In the dry forest in Costa Rica (Heithaus *et al.*, 1975), the number of species of bat flowers in bloom varied from a low of two in July and August (wet season) to a maximum of seven in January and March (dry season). During the dry season, while bat flowers were abundant, seven species of phyllostomatids were regularly covered with pollen from flower visits. At this time, the flowering periods of plants were displaced — adaptations effectively avoiding competition for the services of bat pollinators. However, as the wet season began and flowers decreased, only *Glossophaga soricina* continued to visit flowers regularly for food. *Phyllostomus discolor* apparently responded to the scarcity of flowers

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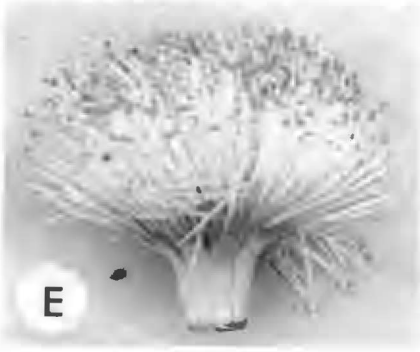
FIG. 2.—Flowers and fruits used as food by phyllostomatids: A, *Cecropia eximia* (Moraceae) fruit; B, *Piper aequale* (Piperaeae) fruit; C, *Astrocaryum standleyanum* (Palmaceae) fruit; D, *Ochroma lagopus* (Bombacaceae) flowers closed during daytime; E, *Pseudobombax septenatum* (Bombacaceae) flower; F, *Markea sp.* (Solanaceae) flower.


A


B


C


D


E


F

by migrating. The other five species switched to fruit diets. This shows how different species react with different strategies to a scarcity in food resources that are shared during times of abundance.

In the moist forest on Barro Colorado Island, only five kinds of flowers appear to be fed on by bats (see Figs. 2*d* and 2*e*; our data). These flowers are available only from late December to late March, during the dry season. Thus, for nine months each year, little nectar or pollen is available to bats. Here, nectar and pollen are important food sources only for *G. soricina* and *P. discolor*. The latter does not migrate as it does in the dry forest studied by Heithaus *et al.* (1975); instead, it switches to a diet of fruit and insects. *G. soricina*, which typically is more dependent on floral resources, is rare on the island but apparently also switches to fruit.

We know of no dry-season flower feeders that switch wholly to insects in the wet season. Instead, they switch to fruit or fruit and insects together (for example, *G. soricina*, Fleming *et al.*, 1972, and *P. discolor* at our Panamanian site). It might be most realistic to view such species as herbivores with omnivorous tendencies, in which case it is proper to wonder if a plant-adapted gastrointestinal tract (Rouk and Glass, 1970) could function effectively on a wholly insectivorous diet.

Taxa, such as *Leptonycteris* and *Choeronycteris*, that are exceptional in not switching from plant food, migrate to stay permanently in "dry season" environments by moving to subtropical and warm temperate thorny vegetation zones where suitable flowers occur in summer. In view of the many potential competitors among insectivorous and frugivorous bats, the selective pressure for migration is true nectar-pollen specialists should not be underrated.

Insects

Wet-dry seasonality strongly affects the distribution and abundance of Neotropical insects. The dry season presents many insects with food shortages and water balance problems. Most tropical insects survive the dry season as adults (Janzen and Schoener, 1968) rather than in diapause (as in winter survival of temperate taxa). However, the precise impact of tropical seasons on the food of insectivorous bats is difficult to assess, because few studies deal with the particular insects of interest. These are nocturnal species either in flight, for bats that catch flying prey, or active on leaves, tree trunks, and the ground, for bats that feed by gleaning.

In a study of mosquito seasonality based on adults flying into a livestock-baited trap, Bates (1945) showed that nocturnal species peak in abundance immediately after the onset of the wet season. Some species exhibited a secondary peak near the end of the wet season, and all species were least common in the dry season. In addition to this annual periodicity, one species underwent population irruptions, with a hundredfold difference in minimum and maximum numbers over a two-year period.

Light-trap samples in moist forest in Panamá (Smythe, 1974) document remarkable seasonal changes, with up to eight times as much insect biomass

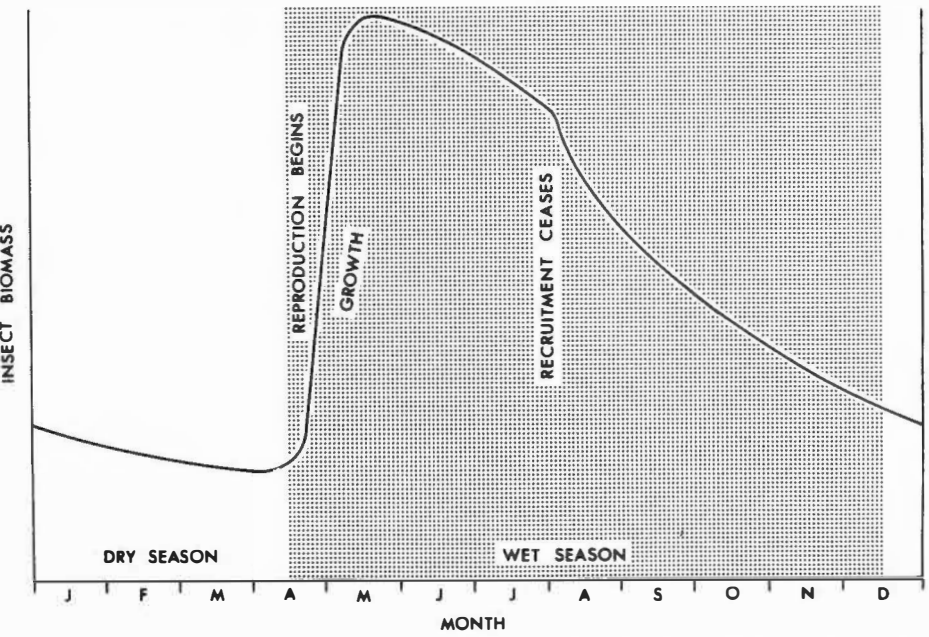


FIG. 3.—Seasonality of tropical insect biomass (after Smythe, 1974). This pattern occurs in Central America where distinct dry seasons occur. The timing varies geographically by one to three months.

in the wet season as in the dry season. Large taxa (>5 millimeters long) were responsible for this change, with Isoptera, Diptera, and Lepidoptera having particularly dramatic population increases early in the wet season. By contrast, small taxa (<5 millimeters long) were of constant abundance throughout the year. Combined data (Fig. 3) show biomass increasing shortly after the wet season begins, peaking about a month later when reproduction, growth, and metamorphosis is complete, and remaining high for the next three or four months. Biomass declines late in the wet season at the time when the heaviest rains occur, and it remains low through the dry season.

Insectivorous phyllostomatids may exhibit at least three responses to the seasonality of their food. One would be to bear young at the beginning of the wet season; the limited data available (see Wilson, this volume) suggest that this often may be the case. Another would be to switch to other types of food. A partial shift occurs in *Micronycteris hirsuta*, which gleans insects as its primary food but supplements this diet with fruit during the dry season (Wilson, 1971). A third response would be to change foraging habitat. In the dry forest near Cañas, Costa Rica, Janzen (1973) noted that night-time numbers of beetle and true bug species decreased much less during the dry season in riparian forest than in nearby pasture land and upland deciduous forest. Thus, riparian forest may serve as a dry season refuge for food of insectivorous bats, assuming that the preferred insect taxa behave similarly.

Few precise data exist on the food habits of insect-eating phyllostomatids. Wilson reported that large roaches, Orthoptera, and scarabaeid beetles are the most important items in the diet of *Micronycteris hirsuta* in Panamá. These insects spend much of their time walking and feeding on vegetation or detritus. Wilson concluded that *M. hirsuta* captures most of its prey by gleaning. This pattern appears to apply to other members of the genus as well (Gardner, 1977). *Macrotus californicus* in the southwestern United States also feeds heavily on large insects, including larval Lepidoptera that probably are gleaned from foliage (Ross, 1967). A gleaning mode of foraging was confirmed for *Macrotus waterhousii* by watching one (S. R. Humphrey, aided by an ultrasonic sensor and a streetlight) for which the feeding flight was confined to the interior of an almost spherical tree crown. F. J. Bonaccarso observed a captive pair of *Tonatia bidens* take large cicadas, katydids, grasshoppers, and beetles by picking them off the walls of their cage.

Phyllostomatids known to be mainly insectivorous have adaptations characteristic of bats that glean prey from vegetation or the ground. Such adaptations include large eyes, large ears, a long robust rostrum, long vibrissae, and a low wing aspect ratio that promotes vertical flight and hovering. Many insectivorous phyllostomatids with these features also have long nose leafs. As suggested by Wilson (1971), many of the same food-gathering skills probably are involved in securing fruit and resting insects. By contrast, none of the Neotropical insectivores of other families (Emballonuridae, Mormoopidae, Furipteridae, Thyropteridae, Vespertilionidae, and Molossidae, possibly excepting Natalidae) appear to have this gleaning morphology, although several Nearctic vespertilionids do (*Antrozous, Euderma, Plecotus, Idionycteris,* and several species of *Myotis*). We suspect an evolutionary character displacement at the family level, in which phyllostomatids were decisively preeminent as insect gleaners. A gleaning morphology well could have provided suitable preadaptations for specializing on vertebrate prey, as in *Chrotopterus auritus* and *Vampyrum spectrum.*

Vertebrates

The literature on foods of vertebrate-eating phyllostomatids is not detailed, but at least lizards, birds, mice, and bats are taken (Goodwin and Greenhall, 1961; Gardner, 1977). We offer information on seasonal abundance of birds by way of example. Peaks of bird breeding should coincide with high population levels. Tropical birds may breed continuously, regularly in concert with wet-dry seasons, or irregularly. In continuous breeders, individuals or pairs breed according to their own activity cycles, with all reproductive stages present in the population at any time. Most regular breeders in regions with a weak dry season breed in the drier months. In regions with a pronounced dry season, most breed in the wet season, but few specialists breed in the dry season. Regions with two annual wet-dry cycles have some species breeding once a year and others breeding twice (Immelmann, 1971). Superimposed on this complex

pattern is the arrival of numerous migrants during austral and boreal winters. Thus, at least in a general sense, it appears that night-roosting birds should be in ample supply at all times of the Neotropical year.

Blood

Aside from man and domestic animals, food for blood-eating phyllostomatids should be a seasonally stable resource, as the birds and mammals parasitized are large and have long life spans. For the same reason, these hosts are likely to occur at low densities and therefore to be difficult for vampires to locate. Conversely, humans and domesticants are high-density hosts that are predictably accessible in time and space. One account (Benzoni, *in* Turner, 1975) suggests that humans were a major host for vampires along the east coast of Costa Rica in the sixteenth century. Now, greater use of houses that limit access makes human bites unusual, but vampires commonly and regularly feed on domestic birds and mammals. In accord with these observations, our impression from mist-netting is that sanguivorous bats are rare except where domestic animals are abundant; see Fig. 6 for some illustrative data.

Roosting Strategy

Like other bats, phyllostomatids spend the daylight hours at rest. A good roost should provide some protection from adverse weather, predators, and nonresident parasites such as diurnal mosquitoes and biting flies. Beyond this, a roost should afford microclimatic conditions that are not stressful and that favor effective use of available energy. At the very least (though hardly a problem), a roost should prevent prolonged exposure to direct sunlight, because phyllostomatids die at body temperatures of 37 to 42°C (McManus, 1977). More importantly, microclimate should be optimal for growth during periods of gestation and lactation.

Roost Type

Phyllostomatids use an amazing variety of natural and man-made structures. These include caves, culverts, buildings, bridges, cisterns, steam banks, cliff crevices, tree foliage, tree hollows (even hollow tree trunks lying on the forest floor), rabbit burrows, and old termite nests. The tent-making bat (*Uroderma bilobatum*) makes shelters by clipping palm fronds so that the frond tips fold down. Most species seem unrestricted to particular sorts of roosts. For example, *Desmodus rotundus* occurs in tree hollows, caves, and culverts. Commonly several species will share a roost, in bodily contact with each other (Goodwin and Greenhall, 1961).

Roost Microclimate

The microclimates of phyllostomatid roosts are known from a single study. McNab (1969) recorded air temperature and relative humidity in roosts of

12 species at the time of capture. Temperature ranged from 13 to 29°C and humidity from 70 to 98 per cent, so microclimate is characteristically mild and moist. Studies of diel, seasonal, and regional variation of these microclimates have not been reported.

A few studies characterize tropical forest microclimate and indicate conditions that might be encountered by a foliage-roosting bat. Dry season data at Barro Colorado Island, Panamá, show a weekly temperature range of 25.8 to 27.4°C at the ground, 24.9 to 33.0° in the subcanopy, and 27.0 to 37.5° in the canopy (Allee, 1926). Relative humidity and light intensity were likewise stratified, and conditions were more extreme in sunflecks than in the shade. Similar daytime temperature profiles occur in other tropical forests (Hales, 1949; Baynton *et al.*, 1965). Allen *et al.* (1972) showed that such stratification is stable all day, breaking down in the evening, and that it is caused by the ameliorating effect of vegetation on air turbulence rather than any constancy of incident conditions. Thus, near-lethal temperatures occur in the canopy, but a bat can easily avoid them by seeking shaded sites in lower foliage.

Studies of phyllostomatid response to cooling, such as would be encountered at high latitudes or altitudes, are inconsistent, apparently because of differing experimental procedures. When bats were exposed to rapidly dropping temperatures for two hours (McNab, 1969), four hours (Carpenter and Graham, 1967), or exposed to cold for several days with food provided *ad libitum* (Arata and Jones, 1967; Arata, 1972), they responded endothermically, surviving by increasing metabolic rate. Exceptions were small stenodermines and the three vampire genera, which died quickly as temperature dropped. Animals with food available fed many times a day when cold. Studier and Wilson (1970) used fed animals but did not provide food during their experiments, lowering temperatures stepwise from 34 to 2.5°C over periods of seven to 10 hours, and allowing body temperatures to stabilize at each step. Most individuals were wholly ectothermic or else partially so, maintaining body temperatures 5 to 15°C above ambient temperatures while both ambient and body temperatures decreased. Below 8°C most bats went into torpor and died after failing to arouse. One lactating female *Carollia perspicillata* remained endothermic at ambient temperatures as low as 5.7°C.

Obviously a bat in a roost with a temperature that is too low can leave for an alternate site, but if it remains it cannot feed and would be exposed to roost temperatures for approximately eight to 12 hours. Realistic thermoregulation studies should employ microtemperatures that are stable or that increase during the day. The limited data on thermal response lead us to hypothesize that at low roost temperatures (1) reproducing female phyllostomatids thermoregulate, incurring the consequent metabolic costs, and (2) nonreproducing females thermoregulate weakly or not at all. In the latter case, presumably the practice would not be fatal at roost microclimates encountered at low altitude in the Neotropics. At higher latitudes or altitudes, ectothermy could be fatal and perhaps phyllostomatids in such circumstances attempt to thermoregulate.

Roosts as a Limiting Factor

Most phyllostomatids roost alone or in small colonies and are not strongly specialized to be highly colonial in order to exploit particular roost types (Dwyer, 1971), as is common in families characteristic of temperate zones (Humphrey, 1975). Known highly gregarious exceptions are *Phyllonycteris, Erophylla, Desmodus, Brachyphylla,* and *Phyllostomus* (Dalquest and Walton, 1970). Satisfactory roosts are available in abundance in the Neotropics. For these reasons, and because of the probable importance of food as a limiting factor (McNab, 1971), it would be expected that roosts seldom limit phyllostomatid abundance and community structure.

Distributional limits of herbivorous and nonmigratory carnivorous phyllostomatids should be determined by food. However, roosts may be limiting factors at the distributional limits of many carnivorous phyllostomatids, including sanguivores and migratory vertebrate-eaters and insectivores. Dwyer (1971) predicted that such bats — that is, tropical species adapted to tropical roost microclimates — will be limited at higher latitudes and altitudes by absence of suitable food and by the increased cost of thermoregulation in caves with cool microclimates. Including bats of all feeding types, Dwyer judged that food would be a more critical factor than roosts. In fact, McNab (1973) calculated that the cost of thermoregulation in cool roosts prevents *Desmodus rotundus* (which, as in any animal, can consume only so much food nightly) from occupying higher latitudes, even though its preferred food is abundant. That no insectivorous phyllostomatids are known to migrate to temperate zones may reflect both their thermoregulatory disadvantage in cool roosts and a probable competitive advantage on the part of vespertilionid insect-gleaners that hibernate in winter. The migratory nectar-pollen feeders, *Leptonycteris* and *Choeronycteris,* move only as far north as the hottest and driest areas of Texas and Arizona, although one preferred food (*Agave*) occurs much farther northward. That these bats appear to be highly colonial at the northern limits of their range (Easterla, 1972) may reflect clustering thermoregulatory behavior.

Demography

Every animal can be said to have a demographic strategy — a combination of performances that adds individuals to the population in concert with factors that subtract individuals, with a pattern of magnitude, balance, and timing that differs for each species. A demographic strategy is a set of responses to an environment; to some degree a species may vary its strategy among environments (for example, in response to different seasonal regimens of climate and food in tropical lowland dry as opposed to wet forest). On the other hand, the evolved nature of some demographic phenomena (for example, biotic potential, the dispersal effect of pioneering, and the ability to avoid predation) results in reasonably fixed numerical expressions. The totality of demographic events produces a growth rate that must be positive or zero over any substantial time

interval if a population is to survive. Demographic lability enables a species to survive in a variety of environments, but demographic limitations make success in other environments unlikely. Values of demographic parameters show specific things an animal does to succeed and simultaneously reveal performances that must be modified to enable use of another location.

Ways that demographic factors interrelate and operate are presented in a flow diagram (Fig. 4). If population size and the natural rate of increase (r) are known, growth trends can be predicted and used to evaluate the progress of the population. Three basic demographic parameters integrate to determine population growth rate and size: natality rate, survival rate, and dispersal rate. Factors affecting the values vary quantitatively as a function of population age structure because the importance of each intrinsic factor (for example, emigration) changes with age. The extrinsic factors and potential regulatory pathways are speculative, as these seldom or never have been demonstrated to operate among phyllostomatids or other bats. However, studies directed toward these factors and pathways should reveal the implications of demographic adaptations of phyllostomatids. Although no demographic strategy is documented thoroughly for these bats, piecemeal data on intrinsic factors (*sensu* Fig. 4) are reported in recent literature.

Number of Births per Year

Most phyllostomatids studied to date are polyestrous (Fleming *et al.*, 1972; Wilson, this volume) with the maximum possible number of estrous cycles being two (possibly three may occur in tropical vespertilionids, as shown by Wilson and Findley, 1971). Two peaks in parturition clearly are indicated by the bimodal pattern of pregnancy of most species, and a maximum number of two is dictated by the long gestation period of *Desmodus rotundus.* Of much more interest than the maximum number of births possible annually however, is the average number actually occurring. To our knowledge such data are unavailable. In cases of bimodal polyestry, individual females could produce offspring at none, one, or both peaks during a year. Frequent observation of females simultaneously lactating and pregnant shows the latter case to be common. *Macrotus californicus* gives birth only once per year (Bradshaw, 1962). Members of the genera *Leptonycteris* and *Choeronycteris* that annually migrate from tropical to warm temperate regions are parturient during the temperate zone summer; available data do not preclude the possibility of a second birth during the tropical dry season. Data on *Leptonycteris sanborni* (Cockrum and Ordway, 1959; Howell, 1972) suggest two peaks in parturition for each female or a single peak that occurs either in the temperate summer or the tropical dry season.

Number of Offspring

All phyllostomatids presently are thought to have a single young at a time. Carter (1970) termed the family "characteristically monotocous," and

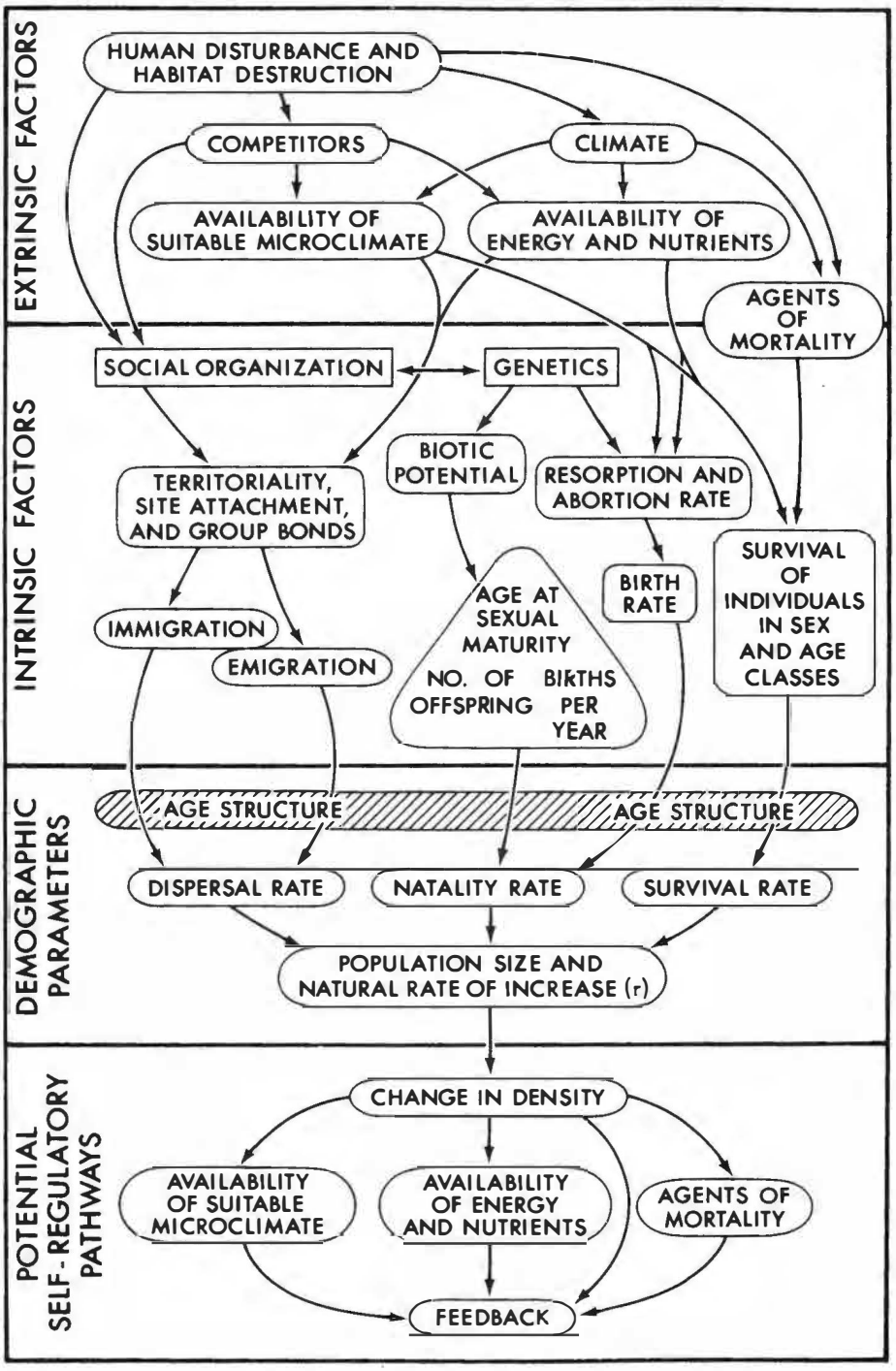


FIG. 4.—Operational pathways of demographic factors.

Fleming *et al.* (1972) stated that in seasonally polyestrous phyllostomatids "one young is produced in each pregnancy." Records of twinning prove to be the exception, not the rule. Barlow and Tamsitt (1968) reported three sets of unborn twins in 195 pregnancies in *A. jamaicensis*, one of 615 in *Glossophaga soricina*, and one of 10 in *Erophylla bombifrons*. Burns (1970) noted one case in *Desmodus rotundus*. In *Artibeus lituratus*, the single young results from reducing the number of ova shed; in a sample of 49 females, the average number of corpora lutea or mature follicles was 1.37, but only one ovum was released at estrus (Tamsitt and Valdivieso, 1965).

Production of a single young in phyllostomatids is consistent with the pattern generally expected (Spencer and Steinhoff, 1968; MacArthur, 1972) in that animals in tropical latitudes have more numerous but smaller litters than those in temperate latitudes. By contrast, Nearctic vespertilionids and molossids are monestrous, with mean number of young ranging from 1 to 3.4 (Humphrey, 1975). The possibility of larger litters in phyllostomatids should not be ignored entirely, however, as some tropical bats of other families regularly produce twins. Examples are the tropical vespertilionids *Rhogeesa parvula* (Cockrum, 1955) and *R. tumida* (Goodwin and Greenhall, 1961).

Birth Rate

One important intrinsic factor can be measured by answering the question, "for each species, what percentage of females gives birth during each birth pulse?" The pregnancy rate may approximate the birth rate in species with synchronous parturition if late abortions and stillbirths are few, as is true of some temperate-zone vespertilionids. Single, fortuitous captures of pregnant phyllostomatids (Mares and Wilson, 1971; Fleming *et al.*, 1972) demonstrate asynchrony or partial synchrony of breeding. Because births are not simultaneous within seasonal birthpulses, these pregnancy data do not indicate which individuals are breeding and which are not. However, in our experience, properly timed samples accounting for pregnancies and early lactations can generate estimates of the proportion reproducing. To our knowledge, no phyllostomatid birth rate data have been published (the values for *Desmodus rotundus* in Turner, 1975, do not permit calculation of annual or seasonal rates).

Age at Sexual Maturity

In *Macrotus californicus*, females breed during their first autumn and give birth at the age of one year (Bradshaw, 1962). Males do not breed until their second autumn, which is not disadvantageous so long as enough males live that long, and it may be an advantage in ensuring that only successful male genotypes are perpetuated.

To our knowledge, this important factor has not been documented for any other phyllostomatid, notwithstanding the unsubstantiated suggestion that females of *Artibeus jamaicensis* become pregnant in the dry season following

their birth (Fleming *et al.*, 1972). Data on age at sexual maturity come only from recapture of marked females of known age taken from one to several breeding seasons after their birth. For example, one *Desmodus rotundus* marked as an infant was pregnant when recaptured 18 months later (Turner, 1975). Careful study may reveal that this parameter varies in response to unusual hardship dictated by climatic or habitat variation (see Christian, 1971).

Survival Rate

The only record of phyllostomatid longevity exceeding two or three years is a recapture of an *A. jamaicensis* seven years after banding (Wilson and Tyson, 1970). Longevity information is useful to indicate the maximum age attainable by a species but is of little importance as a numerical expression of demographic strategy. The parameter of interest is the mean life expectancy (mean life span), the value designated e_0 in a life table. Mean life expectancy reflects the actual performance of a cohort of animals in nature, and it integrates properly with the other rate values. For example, it allows easy calculation of the number of offspring produced during the average lifetime of a female.

The only proven technique for documenting bat survival is frequent recapture of marked individuals of known age and sex. Failure to determine age at the time of marking (for example, banding cohorts of bats during temperate winters) has resulted in voluminous but not especially useful bat survival data in the literature. Such data by definition produce a constant rate of survival throughout life (or nearly so, depending on details of sampling protocol), when actually mammals characteristically have lower survival in immature and elderly stages than during adulthood (Caughley, 1966). The most satisfactory period to mark cohorts of immature bats is just prior to weaning. Obtaining accurate data then depends on recapturing all of the living cohort members at least once annually until the last individual has died. Mortality between birth and weaning should be documented to prevent overestimation of survival. Because marking extremely young bats would cause many deaths, the best available technique is to determine the number of young born in a roost, remove all carcasses from the roost area, and count the number of young dying before they begin to fly. Examples of such data are preweaning survival of a molossid (Herreid, 1967), *Tadarida brasiliensis*, and postweaning survival of a vespertilionid (Humphrey and Cope, 1976), *Myotis lucifugus*. These studies must be done at roosts and require many years for long-lived species.

Aging bats according to tooth cementum annuli is an exciting prospect, as it would provide an "instantaneous" method of constructing survival curves. A disadvantage is that the animals must be killed to acquire the data. This technique has been applied to *Desmodus rotundus*, yielding mean age values of 3.0 years for females and 1.5 years for males in México (Linhart, 1973) and 4.13 years for females and 3.01 years for males in Argentina (Lord *et al.*,

1976). The latter author suggested that apparent differences in sex-specific survival are artifacts of the social structure of the sampled populations. Unfortunately, in neither study were annuli counts checked against known-age control animals to confirm that a line represents one year's growth. Why growth should be periodic when food supply is constant is unclear.

Dispersal Rate

Pioneering is a vital phenomenon for finding available habitats and compensating for local extinctions. For demographic purposes, dispersal rate is the net loss or gain of animals by one-way movement in proportion to the population in a given area. No measurements of phyllostomatid dispersal rates occur in the literature. Studies of dispersal rate of mobile animals must include large geographical areas, and mammalian dispersal is seldom quantified. For examples and discussion of procedural difficulties, see Barkalow *et al.* (1970) and Humphrey and Cope (1976). Site attachment index values and associated movement data on two species of temperate vespertilionids (Humphrey and Cope, 1970, 1976; Humphrey, 1975) indicate little or no dispersal of recruited females in undisturbed populations; whether such a pattern applies to phyllostomatids in the tropics in unknown.

Migration has no effect on the dispersal rate if a migrating individual indeed returns. If the migrator stays away, then it becomes a dispersor, and if it dies while migrating the effect is on the survival rate. These distinctions help prevent confusion about the demographic implications of migration. Migration has not been demonstrated clearly for any phyllostomatid, but many sorts of collateral evidence suggest that *Leptonycteris* and *Choeronycteris* are migratory in the northern part of their range (Hayward and Cockrum, 1971). Further, our unpublished data suggest that some species in Belize and Panamá are migratory or at least nomadic (see beyond).

Community Diversity

Field biologists recognize great differences in the various bat communities that they sample. Although patterns of diversity occur in and among these taxonomic communities, so many characteristics of species and habitat factors are involved that these patterns are difficult to perceive and express.

Species Number

The simplest measure of diversity is the number of species present (in the literature termed variously faunal size, species density, species diversity, and species richness). Often this is the only useful measure of diversity available from specimens taken for taxonomic purposes. Bat communities (and numbers of phyllostomatid species) in the Americas are largest in tropical lowland rain forest. Moving away from that life zone in moisture, altitude, or latitude, the number of species diminishes (Fig. 5). Beyond this common observation, analysis of species number reveals little about the nature of bat communities.

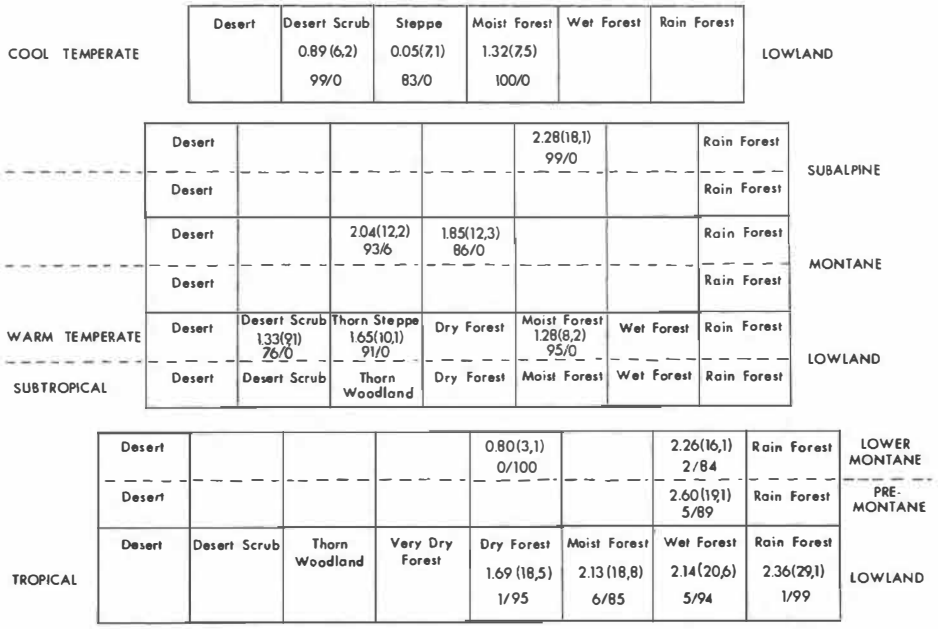


FIG. 5.—Characteristics of bat community structure according to life zone (after Holdridge, 1967). Numbers are : top line, average diversity value, (average number of species, number of samples); bottom line, proportion of the diversity contributed by vespertilionids/phyllostomatids. Because no data are available from boreal or subpolar latitudes or alpine altitudes, corresponding life zones are omitted. All samples were mist-netted in tropical wet seasons, temperate summers, or year-round. Although the best available, these samples are not ideal for diversity analysis. Samples vary in habitat (for example, mature forest, riparian forest, slash-and-burn agriculture) and adequacy of netting vertical strata and full nights. All tropical samples inadequately represent high-flying molossids and taxa more difficult to net than phyllostomatids (for example, emballonurids, mormoopids, and vespertilionids). Summaries and references to sample data are available from the senior author on request.

Species Diversity

More can be learned by finding a concise way to compare communities and the abundance of species within and among communities. Such comparison is afforded by a species diversity index. Details of rationale and application of this analytical tool to bat communities are presented by Humphrey (1975). Briefly, the standard index is that of Shannon and Weaver (1949), $H' = -\Sigma p_i log_e p_i$, where p_i is the number of individuals in the i^{th} species divided by sample size. The contribution of species n to its community's diversity is $H'_n = -p_n log_e p_n$.

Parallel to the pattern of species number, species diversity (Fig. 5) is highest in tropical lowland rain forest and decreases along gradients of moisture, altitude, and latitude. The most diverse single sample ($H' = 2.65$) was taken in garden and forest habitats at San Pablo, Perú (Tuttle, 1970); no doubt this is an overestimate, as data from two habitats are pooled. Average diversity of

warm temperate montane dry forest also is overestimated, because all three sites were chosen for exceptional diversity in topography and vegetation.

Although fairly diverse communities continue into middle latitudes and zones of intermediate moisture, a pronounced shift in the importance of phyllostomatids occurs between subtropical and warm temperate zones. In warm temperate zones, phyllostomatids are replaced by vespertilionids. Presence of two species of nectar-feeding phyllostomatids in warm temperate montane thorn steppe (*Choeronycteris mexicana* and *Leptonycteris sanborni* in Arizona samples) results from migration to take advantage of seasonally available *Agave* and cactus flowers. Bat communities are least diverse in zones of extreme dryness or high altitude or latitude. These correlations with the Holdridgean axes of precipitation, humidity, and temperature suggest that phyllostomatids, as a family, are best adapted to regions where 1) annual precipitation exceeds 1000 mm, or 2) the ratio of potential evapotranspiration to precipitation is less than two, and 3) a mean annual biotemperature about 17°C is available for at least one season of the year (as by migration). The ultimate factors responsible for this pattern will become clear as the functions of the morphological, behavioral, demographic, and physiological adaptations of these bats are better understood. We infer that the pattern represents phyllostomatid response either directly to climate or to biological factors such as vegetation or food.

The general lack of anomalies in diversity trends of phyllostomatid-dominated faunas is striking. One exception is in tropical lower montane dry forest, where small sample size (10) of the single sample may account for low diversity. By contrast, no clear life-zone pattern appears in diversity of warm and cool temperate bat faunas. As shown by Humphrey (1975), the presence of suitable roosts enables strongly roost-adapted vespertilionids and molossids to become exceptionally abundant there. A super-abundant species affects the diversity value because $H'_n1 < H'_n2$, lowering H'. Thus for roost-adapted taxa, perhaps including the tropical mormoopids, we expect such factors as karst topography and forest management practices to be of primary importance.

Some indication of the importance of certain species to their bat communities is given in Figs. 6 and 7. Consistently important species in lowland forest are the feeding generalists *Carollia perspicillata* and small species of *Artibeus*, which eat a wide variety of fruits. When fruit is scarce, *C. perspicillata* also will consume nectar, pollen, and insects. Other generalists such as species of the genus *Sturnira*, however, are consistently minor community members. Specialists on large fruit, *Artibeus jamaicensis* and species of *Vampyrops*, do best in wet climates and decrease in importance in drier forests. High H'_n of *A. jamaicensis* in dry forest is an artifact in that all samples there were in fruit plantations or riparian gallery forest that included many fig trees. High importance of both *A. jamaicensis* and small species of *Artibeus* in forest of intermediate moisture accords with our unpublished data that these bats eat different species of fruit, partitioning food on the basis of particle size. *Glossophaga soricina*, a species that specializes on nectar and pollen but

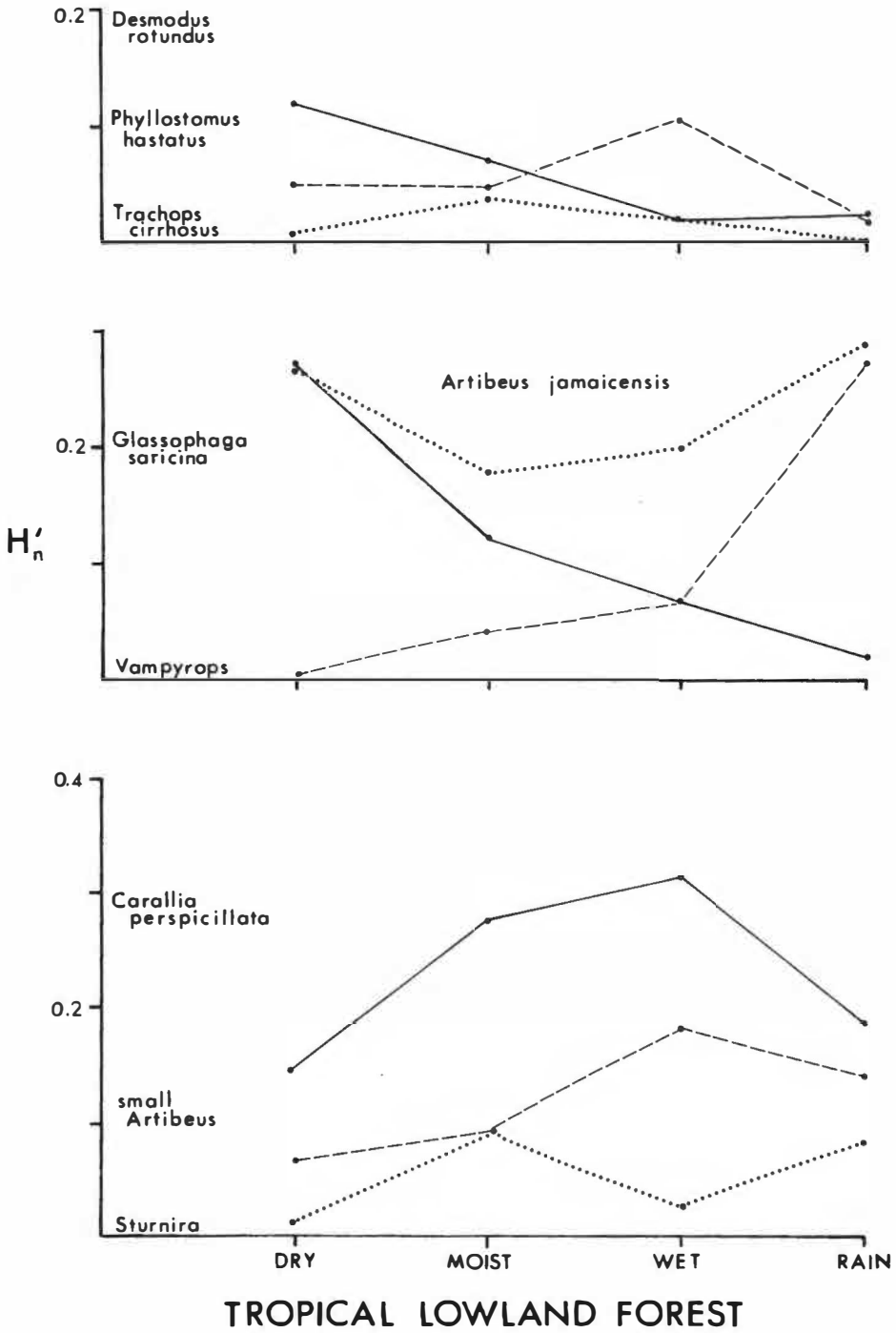


FIG. 6.—Contribution to bat community diversity by species of phyllostomatids along a moisture gradient in tropical lowland life zones. Data are from samples used in Fig. 5.

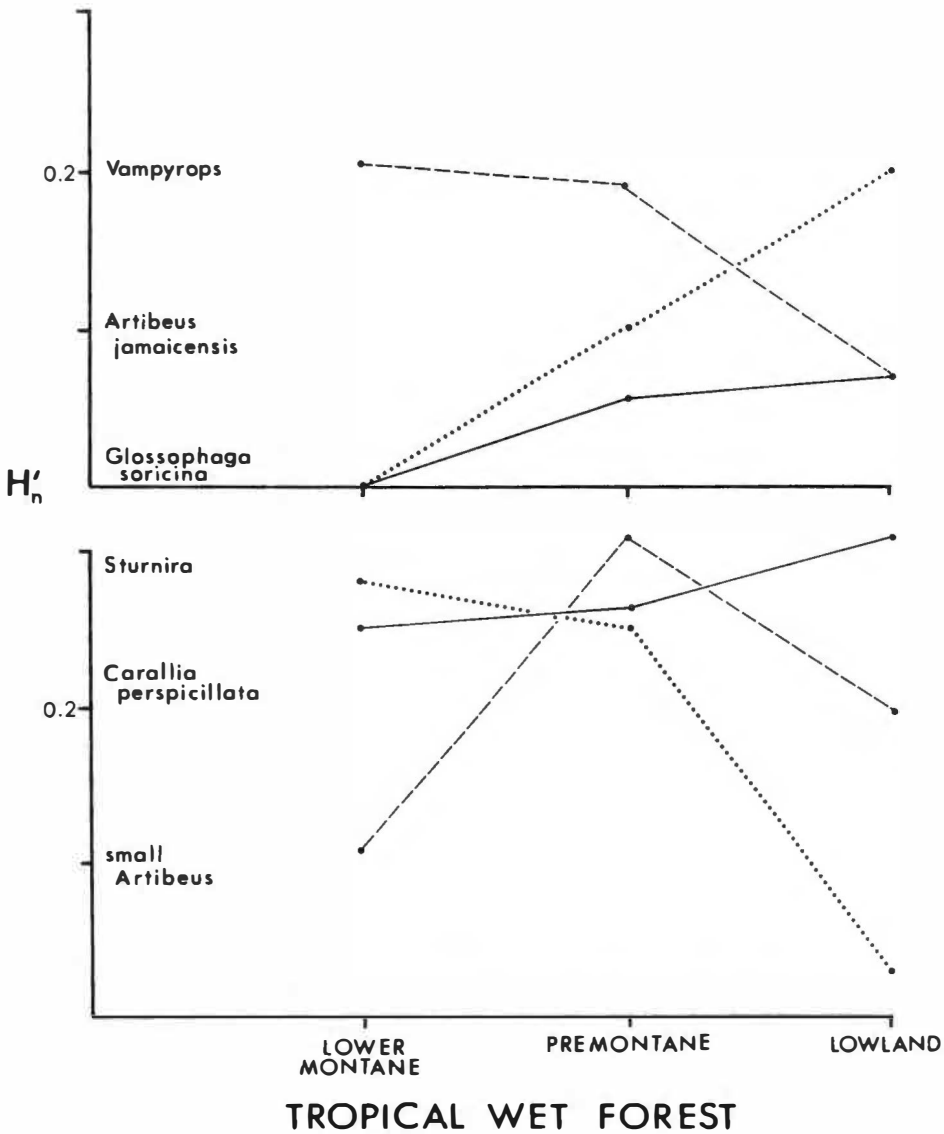


FIG. 7.—Contribution to bat community diversity by species of phyllostomatids along an altitudinal gradient in tropical wet forest life zones. In effect, this graph adds a third dimension, elevation, to Fig. 6, with the origin at the point "tropical lowland wet forest."

switches to fruit in the wet season when flowers are scarce, is of complementary importance to those bats that eat large fruits, increasing its contribution in dry communities. *Trachops cirrhosus*, a specialist on insects and small vertebrates, and *Phyllostomus hastatus*, a large bat that eats fruit, insects, and some vertebrates, are predictably unimportant; we do not understand the higher contribution of the latter in wet forest. *Desmodus rotundus*, a specialist on

mammal blood, is a minor constituent of wet zones but becomes increasingly important in drier forest, probably a function of increasing livestock density.

Altitudinal data (Fig. 7) reinforce the general conclusions derived from lowland data. *Carollia perspicillata* is an important community member at all elevations sampled. *G. soricina*, already seen to be a minor member in wet lowland forest, is equally unimportant in higher forest. The large fruit specialists *A. jamaicensis* and *Vampyrops*, which respond similarly to moisture change in lowland forest, show opposite trends at high altitudes in wet forest — prominence of *Vampyrops* and disappearance of *A. jamaicensis*. The frugivorous generalists of the genus *Sturnira* and small species of *Artibeus* show a pattern similar to that of *Vampyrops*, except that small *Artibeus* decrease in importance at the highest elevation. Perhaps this pattern represents a competition-based displacement or poor response by small kinds of *Artibeus* to the greater daily variation of climate in high altitude forests. The prominence of *Sturnira* may indicate some special adaptations to highlands in view of its unimportance in all lowland forests sampled.

Careful work that samples vertical strata and accounts for differences of habitat and season will reveal much more about tropical bat communities and phyllostomatids. For example, ground-level nets at a site at Belem, Brazil, yielded 18 species with a diversity of 1.93; simultaneous netting with subcanopy and canopy nets placed above the ground nets added seven species of phyllostomatids and increased diversity to 2.40 (Handley, 1967). In all-night netting, LaVal (1970, personal communication) alternately sampled riparian forest and banana groves at Finca La Pacifica, near Cañas, Costa Rica. A decrease in diversity in the plantation (1.63 as opposed to 1.84 in the riparian forest) was accompanied by marked shifts in species composition; most striking was the omnivorous *Phyllostomus discolor*, rare in the forest but by far the most abundant species in banana groves, where presumably it ate banana nectar and pollen. In an area of slash-and-burn agriculture near Frijoles, Canal Zone, D. E. Wilson (personal communication) sampled during the wet season (shortly after the main pulse of births for the year) and in the following dry season. Wet season diversity was 1.93 with 14 species, but dry season values dropped to 1.74 and seven, respectively; all species lost in the dry season were phyllostomatids. Such data suggest exciting patterns of phyllostomatid specialization in foraging strata and habitat and the possibility of seasonal migration or nomadism among habitats.

Ecosystem Functions

The dynamics of energy flow are receiving increased attention by ecologists. Producers and decomposers are recognized as the important organisms in contributing to net productivity. Consumers account for little of the energy flowing through their ecosystems (Fleharty and Choate, 1973; Fittkau and Klinge, 1973). However, they do play key roles in directing ecosystem dynamics. Long-term growth, succession, and stability of plant associations depend partly on ecosystem functions performed by herbivores. Examples are

seed dispersal by birds, primates, rodents, and bats; pollination by bees, moths, and bats; and successional retardation by voles, prairie dogs, and some ungulates.

Phyllostomatid bats fall into several consumer trophic levels. These range from the second level for fruit and nectar-pollen consumers, the third for insectivores and sanguivores (most of the time), and the fourth or fifth for carnivorous taxa such as *Vampyrum spectrum* and *Trachops cirrhosus*, which often eat other carnivores. The interactions of the phyllostomatids with other organisms and the ecosystem functions performed by phyllostomatids will be discussed in the following sections.

Seed Dispersal

Phyllostomatid bats, birds, primates, and rodents are the most important agents of seed dispersal in the Neotropical region (van der Pijl, 1972). Few data exist for shrubs, vines, or epiphytes, but phyllostomatids act as dispersal agents for up to 24 per cent of the forest tree species at some sites. At Finca la Selva near Puerto Viejo in Costa Rica, Gary Hartshorn made the following unpublished observations in a tropical wet forest (4000 millimeters of rain per year; no dry season): in an area containing 20 species of fruit-eating bats, 24 per cent of the 273 tree species counted bore bat-dispersed seeds. F. J. Bonaccorso (unpublished data) recorded similar information for a tropical moist forest (rainfall, 2750 millimeters per year; four to five month dry season) on Barro Colorado Island, Panamá: 7.7 per cent of the approximately 350 tree species identified carried seeds dispersed by bats; 16 species of fruit-eating bats were present. In both of these works, a fruit-eating bat was defined as one with 20 per cent or more of its diet consisting of fruit; trees, as being greater than 10 centimeters dbh or 5 meters tall. These observations suggest that phyllostomatids become increasingly important as dispersal agents in wetter forests, as evidenced by the percentage of trees dispersed by bats and increased number of frugivorous bat species. Where long dry seasons occur, persistent winds disperse the seeds of many trees. At sites without a strong dry season and associated winds, animals (and water) play a major role in dispersing plant species. Some dry forest sites may support higher than expected numbers of frugivorous species because of the abundant quantities of bat flowers during the dry season. At that time, these usually frugivorous bats switch to diets of nectar and pollen (Fleming *et al.*, 1972; Heithaus *et al.*, 1975).

The bat-fruit syndrome.—The relationship between bats and fruiting plants is mutualistic. The plants expend energy on production of edible, nutritious fruits as well as on olfactory and visual stimuli that attract bats. In eating fruits, bats usually transport seeds away from the parental crown and discard them at potential germination sites.

Fruit-eating bats and bat fruits have undergone considerable coevolution, and the resulting set of adaptations are characterized as the "bat-fruit syndrome" (Table 1). Exceptions to this syndrome occur, but when several or all characters of the syndrome occur in a fruit, it is likely to be dispersed by bats.

TABLE 1.—*The bat-fruit syndrome (after Pijl, 1972).*

Fruit characteristics	Bat characteristics
1. Strong, musty odor	Good sense of smell
2. Dull color, often green or brown, fruits visually inconspicuous	Large eyes for orientation, probably color-blind
3. Exposed position outside dense foliage on periphery of branches or on pendulous branches	Approach fruit from air
4. Attachment to tree through maturity	Harvest fruit from tree, not ground
5. Hard skin or pulp to deter other frugivores (many bat fruits are soft externally)	Strong dentition for tearing fruit
6. Requires animal agent to disperse seed	Carry fruits from fruiting trees to night roosts

Fruiting plants are under selective pressure to attract seed dispersal agents and repel or temporally avoid seed predators, such as squirrels and peccaries that frequently eat fruit and seeds. Also, some animals may eat fruits yet neither destroy the seeds nor disperse them, but simply discard seeds below the parental crown. Ceboid monkeys often discard large seeds in this manner. Mature fruits on the tree are available to bats, birds, and arboreal animals, but not to terrestrial rodents, deer, and peccaries. Pendulant fruits of tree species such as *Cecropia* (Fig. 2), exclude arboreal rodents, but not birds or bats that pluck fruits in flight, nor monkeys that hang from prehensile tails and arms, nor procyonids or primates that pull branches with their feet (see Kaufmann, 1962). The strong odor of fruits attracts olfactory-orienting mammals, whereas dull coloration camouflages fruits from visually orienting birds. Fruits having hard edible parts or edible parts covered by a tough husk exclude most birds but do not hinder fruit-eating bats with their strong teeth.

Seed survival and mortality.—Once a plant releases its fruit to a dispersal agent, the chances of seed mortality are high. In response, many plants produce vast numbers of seeds, a few of which survive losses to seed predators, parasites, mechanical damage, and inhospitable germination sites. For seeds to be dispersed successfully by bats, the following conditions are requisites: 1) fruit harvest must occur at maturity; 2) seed displacement must be beyond the crown of the parent plant (in some species); 3) seed deposition must be at a site suitable for germination; and 4) seeds must not be severely damaged.

In our experience, frugivorous phyllostomatids select ripe fruit. Several factors promote this pattern. Unripe fruits have little odor and would not attract bats. Also unripe fruits are hard and difficult to chew, and some are distasteful or toxic when immature. For example, some immature fruits of *Passiflora* contain deadly cyanide compounds but when ripe are eaten by mammals (Saenz and Nassar, 1972). Unripe figs contain latex, which is gummy, and have a bad taste (to humans, at least). The great difference in sugar content of green and ripe fruit (Snow, 1971) suggests that there is little

selective advantage in exploiting unripe fruit. These mechanisms effectively protect seeds until they are mature and viable.

Janzen (1971*a*, 1971*b*) and Wilson and Janzen (1972) demonstrated that seed predators cause heavy mortality of seeds falling under the parental crown because the foraging or egg-laying strategy is to locate areas of high seed density. Seed survival frequently is related to the seed's ability to escape predators in space. Figs that are not taken away by bats or other dispersors, for example, are susceptible to heavy seed predation by lygaeid bugs (Slater, 1972).

As a rule, the Phyllostomatidae and the paleotropical Pteropodidae carry fruits from resource trees to night feeding roosts (Greenhall, 1956, 1965; Nellis, 1971; Osmaston, 1965; Jones, 1972), which may change every few days (D. Morrison, personal communication). Because hundreds, or even thousands, of bats may come to large fruiting trees in a single night, the use of feeding roosts may alleviate crowding and aggression at resource trees. Additionally, this behavior may reduce the attractiveness of bat feeding aggregations to predators such as owls and opossums.

Each plant species has particular requirements with respect to soil, nutrients, drainage, and lighting conditions conducive to subsequent growth and development. Once taken to a feeding roost, seeds are either discarded as the fruit is eaten (somatochory) or ingested with fruit pulp (endochory). Somatochores (Fig. 2C) have seeds too large to swallow, and their dispersal by phyllostomatids is limited by the nature and location of night feeding roosts. Of these, caves and buildings are particularly bad places for seeds to germinate.

Endochores (Fig. 2A, B) have small, numerous seeds scattered through the edible pulp. Endochores are eliminated with the feces and have the potential to land any place a bat moves during a night. Alimentary passage time is usually less than three hours for seeds (Arata, 1972; S. Farkas, personal communication) and typically may be half an hour (Klite, 1965). Quick seed passage time keeps bats at low flight weights and also ensures that many seeds will be eliminated before the bat returns to the day roost, which usually is a poor germination site.

Seed damage may result from mastication or digestion. Bats rarely damage small seeds, and excreted seeds have a high germination rate (S. Gaulin, personal communication). We know of only one species of large-seeded fruit species, *Anacardium excelsum*, regularly damaged by bats. *A. excelsum* seeds commonly are eaten by *Carollia perspicillata*, which acts as a seed predator.

Pollination and the Bat-Flower Syndrome

Based on floral form, Vogal (1969) estimated that bats play some part in pollination of at least 500 Neotropical plant species of 96 genera. It appears that phyllostomatids increase in importance as pollinating agents from mesic to xeric habitats. This pattern is the opposite of that of phyllostomatids acting

TABLE 2.—*The bat-flower syndrome (after Faegri and Pijl, 1971).*

Flower characteristics	Bat characteristics
1. Nocturnal anthesis	Nocturnal foraging
2. Strong, musty odor	Good sense of smell
3. Dull color, often whitish, creamy, or purple	Large eyes for orientation, probably color-blind
4. Exposed position outside dense foliage on periphery of branches or on pendulous branches	Approach flower from air
5. Large flowers	Large body size compared to other pollinators
6. Copious nectar and pollen production	High metabolic rate and large body size
7. Flower tube-like with anthers protruding, or brush-shaped flower	Elongate snout and protrusible tongue for probing deep into flowers

as seed dispersal agents. *Glossophaga soricina* in Panamá uses flower resources for only five months of the year (Fleming *et al.*, 1972), whereas in the dry forest of Costa Rica, *G. soricina* uses flowers all year long (Heithaus *et al.*, 1975).

Flowers pollinated by bats are distinguished by drab colors, musty odors, tube or brush shapes, position free of foliage, large size, nocturnal anthesis, and copious nectar and pollen production. These floral characters (Fig. 2) and corresponding adaptations found in nectarivorous bats are summarized in Table 2. Caution must be taken because bats are highly opportunistic in foraging habits and may sometimes take advantage of flowers not precisely fitting the "bat-flower syndrome." Furthermore, bats may ingest nectar or pollen (or both) of a particular plant species and yet not provide pollination services. Floral parasites are common in nature (for example, flower-piercing hummingbirds and bees). Ratcliffe (1931) reported that flying foxes of Australia eat entire flowers, but we have found no reports of phyllostomatids regularly eating flowers. Baker *et al.* (1971) suggested that *Leptonycteris sanborni* occasionally eats anthers.

The association between these bats and flowering plants is mutualistic. Plants divert energy into production of odors and floral parts that attract bats as well as nectar and pollen that feed bats. In moving from flower to flower for food, bats transport some pollen, which results in fertilization.

It has long been obvious that flower bats obtain carbohydrate in the form of sugars from floral nectaries. Recently it has been demonstrated that pollen is an important source of protein to these bats (Howell, 1974). The cellular contents of pollen grains begin to extrude through the micropores when pollen begins to germinate in the gut. Protein then is extracted by hydrochloric acid produced in the stomach, and protein is leached further by urea from urine ingested by the bat (at least in *Leptonycteris sanborni*). Howell also found that the protein content of pollen eaten by *L. sanborni* was 44 per cent for saguaro and 23 per cent for paniculate agave, much higher than in pollen of closely

related plants for which pollen is not eaten or dispersed by bats. Inasmuch as herbivores must have a rich source of plant protein in order to maintain a high rate of metabolism, the concentration of protein in pollen may be an important avenue of coevolution.

If flower bats eat pollen, then how do they function as pollinators? While probing the flower corolla for nectar, bats become dusted with pollen from noseleaf to uropatagium (Baker, 1970). Phyllostomatids eat pollen only as they groom their flight membranes and fur after a foraging bout (Howell and Hodgkin, 1976; Heithaus *et al.*, 1975). Such behavior would provide for floral pollination during visits to successive flowers while foraging and still permit the bat later to eat the excess pollen covering its body.

Some bats adapted to the exploitation of flowers are known to feed on insects and fruits. Whether insects are taken in the process of nectar-feeding or hunted separately is unknown.

Impact of Predation by Bats

Little is known of the precise diets of insect or vertebrate-eating phyllostomatids, so the impact of their predation on prey populations is undocumented. The prominence of biotic limiting factors in the Neotropics suggests that investigation of this impact is worthwhile.

Competition

Competition for sunlight or food is thought to be the dominant limiting factor for Neotropical organisms (see Janzen, 1967, and MacArthur, 1969). The likelihood of interspecific competition in tropical bats has been discussed (Tamsitt, 1967; McNab, 1971; Dwyer, 1971; Fleming *et al.*, 1972; Howell and Burch, 1974; Heithaus *et al.*, 1975), though documentation of such competition awaits further study. Intraspecific competition for both food and roost space are most likely to occur in the most colonial phyllostomatids, mentioned above.

Enough is known about the three main categories of phyllostomatid food — fruit, nectar and pollen, and insects — to discuss them briefly. Potential competitors in all three categories include insects, birds, arboreal mammals, and other bats, plus insectivorous spiders. Observations cited above of times when food may be in short supply suggest when competition could be acute.

Fruit.—Because fruits are available on a "first come, first served" basis, fruit searching success may be an important component of potential competition. Birds feed heavily on ripe fruits of species eaten by bats. Two of the most important bat fruits in Trinidad—*Cecropia* and *Piper* (Fig. 2)—are eaten in significant quantities by tanagers and honeycreepers (Snow and Snow, 1971). For example, Eisenmann (1961) recorded 24 species of birds feeding on *Cecropia* fruit in Panamá. Potential mammalian competitors include monkeys, marsupials, rodents, and procyonids. Monkeys may be especially important in eating large quantities of unripe fruit (Daubenmire, 1972).

Nectar and pollen.—Diurnal birds and insects seldom compete with bats for nectar and pollen, because many flowers are adapted for pollination at one time of day and might not be open or produce nectar at other times (for example, *Bauhinia pauletia*, Heithaus *et al.*, 1974; Janzen, 1968). Thus, most flowers used by Neotropical hummingbirds (Wolf, 1970; Snow and Snow, 1972) are not visited by bats. However, Baker *et al.* (1971) have shown that *Ceiba acuminata* may be pollinated by both bats and hummingbirds, because these flowers open at night but continue to secrete nectar the next day and are visited by both kinds of animals. Balsa (*Ochroma*) flowers open at dusk (Fig. 2) and are visited by phyllostomatid bats and sphingid moths. Some flowers used by bats are destroyed when monkeys or insects eat them. Alvarez and Gonzalez Q. (1970) concluded that little or no competition for flowers occurs among six genera of glossophagines in México. Heithaus *et al.* (1975) also found nectarivorous bats to feed as generalists with high dietary overlap.

Insects.—Seasonally rapid recruitment rates for insects (as when a hatch is under way) may enable bats to partition temporally a common resource during the night. Additional partitioning is possible because insect taxa differ in periodicity of night-time activity, at least in temperate zones (Williams, 1935, 1939; Lewis and Taylor, 1965). Potential night-time competitors include spiders, tree frogs, caprimulgiform birds, owls, night monkeys, marsupials, rodents, and procyonids.

Roost space.—We know of no published evidence of phyllostomatids competing for roost space. However, such competition frequently may be provided by the more colonial taxa. On Barro Colorado Island, Panamá, a group of *Phyllostomus hastatus* displaced a hollow tree colony of *Carollia perspicillata* (S. Graetz, personal communication). F. J. Bonaccorso observed, on the same island, a displacement of *C. perspicillata* and *Saccopteryx bilineata* from their hollow tree roost by a colony of *Desmodus rotundus*.

Predation on Bats

Little is known about causes of phyllostomatid mortality or the food habits of their potential predators. Reviewers of temperate zone data judge that predation on bats is opportunistic but seldom regular (Allen, 1939; Gillette and Kimbrough, 1970). In the New World tropics, predation on bats may well be more important, in view of the general prominence of biotic interactions and the dominant numbers of bats in mammal faunas. In Haiti, 27 of 147 prey items of a Hispanolean barn owl (*Tyto glaucops*) were phyllostomatid bats (Wetmore and Swales, 1931). In Panamá, three species of owls have killed bats in our nets. Arboreal opossums, procyonids, and snakes may wait for bats visiting resource trees. Opossums (*Didelphis virginiana* and *Philander opossum*) are known to eat bats (Campbell, 1925; Rice, 1957; our observations). The bat falcon, *Falco rufigularis*, may specialize on bat prey. The largest phyllostomatid bats (*Vampyrum spectrum*, *Chrotopterus auritus*, and *Phyllostomus hastatus*) are suspected or known to eat smaller bats (Goodwin and Greenhall, 1961; Valdivieso, 1964; Greenhall, 1968).

An important clue to the role of predation on phyllostomatids may be the inverse relationship between moonlight and flight activity of *Desmodus rotundus* (Crespo *et al.*, 1972; Turner, 1975) and *Artibeus jamaicensis* (Morrison, 1975). Our qualitative observations at several Central American sites are that phyllostomatid foraging is characteristically maximal when no moonlight is incident and minimal under full moonlight. To explain avoidance of moonlight as a response to heightened predator success would be uncomplicated for bats that feed on plants; the behavior of predatory bats must additionally account for the possibility of similar responses by their own prey species.

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